Age determination in polar Crustacea using the autofluorescent pigment lipofuscin

Altersbestimmung polarer Crustaceen anhand des autofluoreszierenden Pigments Lipofuszin

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Contents

List of abbreviations

Abbreviation	Unit in parentheses
a^{-1}	Per year
AF	Area fraction (%)
AFD	Age frequency distribution
AFDM	Ash free dry mass (g)
A_{max}	Maximum age (years)
B	Biomass (g AFDM)
e	Embryo
EASIZ	Ecology of the Antarctic Sea Ice Zone
f	Female(s)
j	Juvenile(s)
k	Growth constant of VBGF (per year)
l	Larva(e)
LCFD	Lipofuscin concentration frequency distribution
LKHV	Lipofuszinkonzentration-Häufigkeitsverteilung
L_{CL}	Carapace length in Decapoda (mm)
L_{cox}	Coxal plate length in *Waldeckia obesa* (mm)
LFD	Length frequency distribution
LHV	Längen-Häufigkeitsverteilung
L_t	Body length at age t (mm)
L_∞	Asymptotic body length (mm)
m	Male(s)
M_{max}	Maximum body mass (kJ)
MSGRM	Mass specific growth rate method
N	Number of individuals
P	Production (g AFDM)
P/B	Production : biomass = productivity (per year)
S.I.	Separation index
T	Temperature (°C or K)
t_0	Theoretical age at which size is zero (years)
TEM	Transmission electron microscopy
WM	Wet body mass (g)
VBGF	von Bertalanffy growth function
Ψ, ϕ	Growth performance parameters
Z	Mortality rate (per year)

Summary

The present knowledge on the functioning of polar benthic communities and ecosystems, in particular their trophic connections and energy flow patterns is still fragmentary. First modelling approaches have revealed benthic crustaceans to be among the most important taxa regarding biodiversity and carbon-flow within the Weddell Sea benthos. Hardly any data on their age structure, growth patterns and productivity are, however, available which is partly due to the lack of appropriate methods for age determination in long-lived Crustacea.

This study investigates the occurrence of the autofluorescent pigment lipofuscin, which accumulates progressively with time in post-mitotic tissue of all eucaryotes, and its potential as an age marker in selected polar Crustacea. Specimens were collected during the expeditions ANT XV/3, ARK XIII/1+2 and ARK XV/1 of RV "Polarstern". Lipofuscin granules were located and identified in resin brain sections of five Antarctic and five Arctic species (decapods, amphipods and an euphausiid) by means of confocal laser scanning and transmission electron microscopy. Lipofuscin quantification was performed by image analysis in which the autofluorescent pigment granules in selected brain areas were discriminated using greyscale thresholding and quantified as area fraction (% AF) related to the surrounding tissue. Based on the lipofuscin concentration frequency distribution of a representative sample of the respective population, maximum age and age distribution were computed for the eastern Weddell Sea populations of the decapod *Notocrangon antarcticus* and the amphipod *Waldeckia obesa*. From those data further population parameters were inferred.

The pigment was found in 375 of 401 analysed individuals and in all ten species, though granules occurred in easily detectable amounts in only five species, esp. in the amphipods *W. obesa* and *Eurythenes gryllus*. The analysed pigment properties widely coincided with those published in literature, except for the location of high density areas in amphipods, which I describe for the first time. This difference required a slightly modified analysis procedure making concentration values incomparable to those of decapods. A modal progression analysis of the lipofuscin concentration frequency distributions of *N. antarcticus* (n = 189) and *W. obesa* (n = 159) showed 8 and 5 regularly-spaced modes, respectively, presumed to reflect consecutive annual age classes. Maximum longevity was estimated as ≥ 10 and 6 years in female and male *N. antarcticus*, respectively, and 8 and 5 years in female and male *W. obesa*, respectively. No regular modes were obvious in the length-frequency distributions (n = 951 and 386, respectively). Pigment accumulation was linear, supported by lipofuscin-analysis of *Chorismus antarcticus* larvae over the first four months after larval release. Accumulation rate did not differ between sexes. Annual accumulation rate in *N. antarctius* (0.2% AF a^{-1}) was considerably lower than rates published for decapod species from lower latitudes (up to 2% AF a^{-1}). Growth rates, annual productivity and mortality rates are also comparatively low in *N. antarcticus* and *W. obesa* (all values $< 1\ a^{-1}$). Values for the growth performance parameter ψ were, however, in the same range as those for lower latitude decapods and amphipods.

My results indicate that morphological lipofuscin regularly occurs in polar crustaceans, though in comparatively low concentrations which are apparently largely explained by the impact of temperature. Successful separation of age groups from lipofuscin concentration frequencies demonstrates the advantage of lipofuscin-based over length frequency-based age determination in slow-growing long-lived crustacean species. The large unresolvable pile-ups in length frequency distributions of *N. antarcticus* and *W. obesa* proved to be multi-age-composed as also previously observed in other species. The inferred population parameters are in accordance with earlier findings in other polar marine invertebrates. Despite low productivity, the Antarctic scavenging amphipod community may be an important energy mediator from carrion to high trophic levels whereas decapods seem rather poorly preyed upon, as indicated by their position in the mortality-growth-continuum (*sensu* Brey and Gage 1997).

The results are encouraging for future use of this method for the assessment of basic population parameters in slow-growing Crustacea, e.g. in commercially exploited species, and possibly non-crustacean taxa. Improvement of the technical procedure is, however, suggested for reasons of timesaving and signal intensity.

Zusammenfassung

Unsere Kenntnis der Funktionsweise polarer benthischer Gemeinschaften und Ökosysteme, insbesondere ihrer trophischen Struktur und des Energieflusses, ist noch lückenhaft. Erste Modellansätze haben gezeigt, daß benthische Crustaceen zu den wichtigsten Taxa hinsichtlich der Biodiversität und des Kohlenstoffflusses gehören. Dennoch liegen kaum Daten über Altersstruktur, Wachstumsmuster und Produktivität von Crustaceen-Populationen vor, was zum Teil daran liegt, daß es keine adäquaten Methoden für die Altersbestimmung langlebiger Krebse gab.

Diese Arbeit untersucht das Vorkommen des autofluoreszierenden Pigmentes Lipofuszin, das in post-mitotischem Gewebe von Eukaryoten mit der Zeit akkumuliert, sowie sein Potential als Altersmarker in ausgewählten polaren Crustaceen. Die Proben hierfür wurden während der Expeditionen ANT XV/3, ARK XIII/1+2 und ARK XV/1 von FS "Polarstern" gesammelt. Die Lokalisation und Identifikation von Lipofuszin-Granula erfolgte in Kunstharz-Schnitten der Gehirne von fünf antarktischen und fünf arktischen Arten (Decapoda, Amphipoda und Euphausiacea) mit Hilfe von konfokaler Laser-Scanning- und Transmissions-Elektronen-Mikroskopie. Die Quantifizierung des Pigments erfolgte durch Bildanalyse, indem die Lipofuszin-Granula in den ausgewählten Gehirnarealen über Graustufen-Grenzwerte markiert und als Flächenanteil (% AF) relativ zum umgebenden Gewebe erfaßt wurden. Basierend auf der Lipofuszinkonzentration-Häufigkeitsverteilung (LKHV) einer repräsentativen Unterprobe der Populationen wurden maximales Alter und Altersstruktur für den Decapoden *Notocrangon antarcticus* und den Amphipoden *Waldeckia obesa* errechnet und daraus weitere Populationsparameter abgeleitet.

Lipofuszin war in 375 von 401 analysierten Individuen und in allen zehn Arten meßbar, wobei die Granula nur in fünf Arten auffällig waren, besonders in den Amphipoden *W. obesa* und *Eurythenes gryllus*. Die analysierten Pigment-Eigenschaften stimmten im Wesentlichen mit den in der Literatur publizierten überein, mit Ausnahme der Verteilung dichter Pigmentanhäufungen in den Amphipoden, die in der vorliegenden Arbeit erstmalig beschrieben werden. Dies erforderte ein leicht modifiziertes Analyse-Prozedere mit der Konsequenz, daß die absoluten Konzentrationswerte zwischen Amphipoden und Dekapoden nicht vergleichbar waren. Eine Modalanalyse der LKHV von *N. antarcticus* (n = 189) und *W. obesa* (n = 159) ergab 8 bzw. 5 Modi in regelmäßigem Abstand, die als aufeinanderfolgende jährliche Altersklassen angesehen wurden. Die maximale Lebensdauer wurde auf ≥ 10 bzw. 6 Jahre in weiblichen und männlichen *N. antarcticus* und 8 bzw. 5 Jahre in weiblichen und männlichen *W. obesa* geschätzt. In der Längenhäufigkeitsverteilungen (LHV) der beiden Arten (n = 951 bzw. 386) waren keine Altersgruppen zu erkennen. Lipofuszin akkumulierte linear mit der Zeit, was durch Lipofuszin-Analyse von Larven des Dekapoden *Chorismus antarcticus* über die ersten vier Lebensmonate unterstützt wurde. Es war kein Effekt des

Geschlechtes auf die jährliche Akkumulationsrate zu finden, die bei *N. antarcticus* (0.2% AF a^{-1}) deutlich niedriger als bei Dekapoden niedrigerer Breiten lag (bis zu 2% AF a^{-1}). Die Schätzwerte für Wachstumsraten, jährliche Produktivität und Mortalität (alle < 1 a^{-1}) lagen ebenfalls vergleichsweise niedrig, während diejenigen für die Wachstumseffizienz ψ denen von Arten aus niedrigeren Breiten ähnlich war.

Meine Ergebnisse zeigen, daß Lipofuszin regelmäßig in polaren Krebsen vorkommt, allerdings in vergleichsweise niedrigen Konzentrationen, was wahrscheinlich wesentlich durch den Faktor Temperatur zu erklären ist. Die erfolgreiche Identifikation von Altersgruppen aus der LKHV demonstriert die Vorteile der Lipofuszin-basierenden gegenüber der Längen-basierenden Altersbestimmung bei langsam wachsenden, langlebigen Crustaceen-Arten. Die Peaks in den LHV von *N. antarcticus* und *W. obesa* waren aus mehreren Jahrgängen zusammengesetzt, wie es bereits von anderen Arten bekannt war. Die abgeleiteten Populationsparameter stimmen in ihrer Tendenz mit früheren Untersuchungen an polaren Wirbellosen überein. Literaturdaten sowie die Position von *N. antarcticus* und *W. obesa* im Mortalität-Wachstum-Kontinuum (*sensu* Brey und Gage 1997) implizieren, daß aasfressende antarktische Amphipoden trotz niedriger Produktivität ein wichtiges trophisches Bindeglied zwischen Aas und höheren trophischen Ebenen sind, während Dekapoden anscheinend weniger gefressen werden.

Die Ergebnisse dieser Arbeit sind vielversprechend hinsichtlich der zukünftigen Nutzung der Methode für die Abschätzung von grundlegenden Populationsparametern bei langsam-wachsenden Krebsen, z.B. kommerziell genutzten Arten, sowie evtl. bei anderen Taxa. Verbesserungen der Methode zum Ziel der Zeitersparnis und Signalverstärkung sind zu empfehlen.

1 Introduction

1.1 Benthic Crustacea in polar systems

Polar marine habitats are generally characterized by low but relatively constant water temperatures, seasonal or permanent ice cover as well as seasonally variable food input from the water column (Hempel 1985, Clarke et al. 1988, Fahrbach et al. 1992, Arntz et al. 1994, Johannessen et al. 1996). Food availability from the water column is, over the year, comparatively low in many areas (Clarke 1988, 1991). All factors combined are thought to be responsible for the relatively low metabolism and productivity as well as high longevity observed in most benthic taxa investigated so far (Brey and Clarke 1993, Arntz et al. 1994, Brey et al. 1995a, Chapelle and Peck 1995, Ahn and Shim 1998, Bluhm et al. 1998). Despite low individual productivity, some areas on the Antarctic and Arctic continental shelves impress by their richness in terms of macrobenthic biomass and diversity (Dell 1972, White 1984, Highsmith and Coyle 1990, Grebmeier 1993, Piepenburg and Schmid 1996, Arntz et al. 1997, Brey and Gerdes 1997). For an understanding of the functioning of polar benthic communities and ecosystems and their sensitivity to potential environmental or anthropogenically caused changes, we need to comprehend their trophic connections and energy flow patterns. In first modelling approaches, Schalk et al. (1993) and Jarre-Teichmann et al. (1997) combined the available suchlike data from the eastern Weddell Sea (e.g. Voß 1988, Priddle et al. 1992, Arntz et al. 1994, 1997, Brey et al. 1994, Brey and Gerdes 1998) to obtain a first idea on trophic flow between the dominant groups of the benthic shelf communities. Polychaeta, Holothuroidea, Ophiuroidea and benthic Crustacea were found to be the most important groups in terms of carbon-flow. The significance of benthic macrofauna for total carbon flow has also been stated for Arctic shelf systems (Grebmeier and McRoy 1989, Grant et al. 1991, Piepenburg 1997, Deubel 2000), though partitioning into taxa has rarely been attempted. Benthic Amphipoda and Ophiuroidea are known to be significant carbon mediators in the Bering and shallow Barents Seas, respectively (Highsmith and Coyle 1990, 1992, Piepenburg et al. 1995). Although crustaceans and especially amphipods are regularly collected in both high abundances and species numbers during expeditions to the Antarctic and Arctic (Heegaard 1941, Yaldwin 1965, Zarenkow 1985, Arntz and Gorny 1991, Jazdzewski et al. 1995, DeBroyer and Jazdzewski 1993, 1996), hardly any data on their population dynamics are available. As these are vital to assess and specify the role of benthic crustaceans in polar systems (Arntz et al. 1994, Jarre-Teichmann et al. 1997), this study aims at filling part of this gap, concentrating on representatives of Antarctic Amphipoda and Decapoda which will be introduced in the following paragraphs.

Only eleven benthic decapod species have been found hitherto on the Antarctic continental shelves and one in the adjacent deep sea (Yaldwin 1965, Maxwell 1977, Kirkwood 1984, Gorny 2000). However, in the southeastern Weddell Sea and the

Lazarev Sea the three most abundant benthic shrimp species occur regularly in considerable numbers and are distributed along an overlapping depth gradient. *Chorismus antarcticus* is most common in shallower waters (200-500 m) where it often preys upon motile organisms associated with large sponges (Gutt and Schickan 1998), while *Notocrangon antarcticus*, often digging itself into the sediment, prefers intermediate depths (300-700 m) with less densely epifauna-covered seafloor. The opportunistic *Nematocarcinus lanceopes* frequently occurs from 600 to >2000 m (Arntz and Gorny 1991, Gorny 2000) on rather flocculent deep-water mud. *N. antarcticus*, the most common shrimp species in these areas, was found in maximum densities of 73 individuals 100 m^{-2} (Gutt et al. 1991). Accordingly, Decapoda may have a remarkable impact on abundance and population structure of their prey taxa, e.g. Polychaeta and other Crustacea (Gorny et al. 1992, Storch et al., in press) as well as on food competitors e.g. echinoderms (Jarre-Teichmann et al. 1997). Larval development of *N. antarcticus* and *C. antarcticus* and population dynamics of the latter have been elucidated (Bruns 1992, Gorny et al. 1993) while information on population dynamics of *N. antarcticus* is lacking.

A faunistic inventory of many Antarctic peracarid taxa has been completed recently (e.g. DeBroyer and Jazdzewski 1993, 1996, Brandt et al. 1998, Mühlenhardt-Siegel 1999), listing > 500 amphipod species, > 70% of them endemic to the Antarctic. Compared to other invertebrate taxa as well as Amphipoda from other latitudes, diversity is especially high in Antarctic Amphipoda (DeBroyer and Jazdzewski 1996, Arntz et al. 1997, Gutt et al. 2000) but few studies have to date been conducted on their life cycles and productivity. This study investigated population dynamics of the circum-Antarctic lysianassid amphipod *Waldeckia obesa* which regularly occurs at littoral sites at the Antarctic Peninsula (Nagata 1986) and down to 1030 m in the eastern Weddell Sea (Klages 1991). Lysianassids, forming the largest amphipod family with > 500 species in 112 genera worldwide (Barnard and Karaman 1991), are one of the most abundant and widespread macro-invertebrate scavenger groups in the world ocean (Slattery and Oliver 1986), degrading and distributing organic matter at the benthic-pelagic interface (Christiansen et al. 1990). They primarily occur at water temperatures < 10 °C, and are common even in the deepest ocean basins (Hessler et al. 1978, Thurston 1979, Smith and Baldwin 1982, Ingram and Hessler 1983, Klages et al., in press), but also in shallow water at high latitudes (Vader 1972, Nagata 1986). The high numbers usually caught using baited traps (Ingram and Hessler 1987, Christiansen 1996) and their remarkable food consumption rates (Hargrave 1985, Klages 1991, Hargrave et al. 1995) suggest an important role in the benthic food web.

1.2 Age determination

Data on population age composition are a key to population dynamics as they allow to calculate growth parameters, mortality, productivity, maturation and, in commercially exploited species, sustainable quota (Pauly 1984, Brey 1999a). Most needed in fisheries and management, ageing techniques were first developed for commercially exploitable species such as fish (Pannella 1971). Only recently, more emphasis has been put on the development of methods for those invertebrates for which accurate ageing methods are still lacking (e.g. within the SCAR program EASIZ). In bryozoans, brachiopods, bivalves, ophiuroids and echinoids, these techniques have already been applied to polar species (Peck and Bullough 1993, Brey et al. 1995a, b, Dahm 1996, Peck and Brey 1996, Bluhm et al. 1998, Brey et al. 1998). Direct methods usually use permanent hard structures retaining age marks such as otoliths in teleost fish (Campana and Neilson 1985), tests or aristotle lanterns in Echinoidea (Gage 1991), vertebral ossicles in Ophiuroidea (Gage 1990a, b) and statoliths in Cephalopoda (Rodhouse 1991). Indirect approaches apply e.g. respiration rates (Schmid 1996, Gatti et al., in prep.) and stable isotopes (Brey et al. 1998). Given the generally low metabolism and growth rates in polar species, highly sensitive techniques are required.

In crustaceans, data on individual age are difficult to obtain due to the lack of permanent hard structures bearing potential age markers. The most common approaches so far attempted in Crustacea, mostly Decapoda, are (i) keeping individuals in captivity including study of growth increment associated with moulting (Plaut and Fishelson 1991, Hill 1992), (ii) recapture of tagged specimens (Campbell 1983, Taylor and Hoenig 1990, Fitz and Wiegert 1991, Somers and Kirkwood 1991), and (iii) 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 error-prone due to the artificial conditions (e.g. Lagardère 1982), and studies are, moreover, time-consuming in long-lived species. Although modern tags are retained through moulting and probably do not inhibit growth (Fitz and Wiegert 1991, Bannister et al. 1994), tagging and recapture is for logistical reasons practically unfeasible in polar deep-water regions. Separating age groups from length frequencies, probably the most common approach, is difficult in slow-growing long-lived species due to merging modes at high age (France et al. 1991, Somers and Kirkwood 1991, Klages 1993, Bannister et al. 1994), as will be discussed below. Moreover, trawls, the most frequently used geartype for this approach, do not cover all size classes representatively. Size can, thus, be an inadequate age predictor in slow growing crustacean species (Belchier et al. 1994, 1998, Sheehy et al. 1998, 1999). Alternatively, I tried to realise the approach proposed by Ettershank (1983, 1984) and Sheehy (1989, 1990a, b), i.e. the use of the physiological correlate lipofuscin as an age marker, and compared the results to those obtained from length frequencies.

1.3 Lipofuscin as an age correlate

Morphological lipofuscin is a yellow-brown, electron dense, autofluorescent, largely solvent-resistant material that progressively accumulates over time in lysosomes of postmitotic eucaryotic cells such as neurones and cardiac myocytes (reviews: Porta 1991, Yin 1996, Terman and Brunk 1998). It was first recorded by Hannover (1842) and has since been found in various invertebrates and vertebrates (e.g. Leibnitz and Wünscher 1967, Reichel et al. 1968, Donato and Sohal 1978, Bassin et al. 1982, Hunter and Vetter 1988, Clarke et al. 1990, Girven et al. 1993). I will briefly outline the present knowledge on the pigment's formation and accumulation and summarize the history of its application as an age marker in crustaceans. Lipofuscin represents a mixture of different chemical substances and is, therefore, not homogeneous with a specifyable chemical composition. Biochemical studies revealed that proteins (30-70%) and lipids (20-50%) form the main constituents (Porta 1991) while carbohydrates (4-7%) and traces of metals are less abundant (Jolly et al. 1995). As lipofuscin is formed from practically all worn-out or damaged cell components, its composition and properties may vary with cell type and taxon. The damaged macromolecules are initially introduced into lysosomal vacuoles by autophagocytosis (Harman 1990, Lee and Marzella 1994). Intralysosomal oxidative modification is ascribed to oxygen-derived free radicals generated in reactions catalysed by e.g. redox-active iron (Thaw et al. 1984). The indigestible portion of the material will remain in the lysosomal vacuole and form the content of lipofuscin granules often called "residual bodies". Various autofluorescent compounds, e.g. conjugated Schiff bases and 1,4-dihydropyridine-3,5-dicarbaldehydes, have been suggested to be formed during the degradative processes as a result of reactions between carbonyls, mainly aldehydes such as malondialdehyde, and amino compounds (Kikugawa et al. 1981, Eldred and Lasky 1993, Yin 1996). Nevertheless, much of the nature of the autofluorescence, the most distinct property of lipofuscin, is not yet completely clear. One of the most favoured theories of the mechanism of lipofuscin accumulation is based on the observation that autophagocytosed material cannot be totally eliminated from postmitotic cells, independent of their age, either by degradation, or by exocytosis (reviewed in Porta 1991). Thus, the formation of lipofuscin will occur at a higher rate than its elimination, if there is any at all, resulting in more or less linear accumulation with time (reviewed in Terman and Brunk 1998). This makes it applicable as an age marker.[1]

In insects, soluble fluorescent age pigments extracted from total specimens have shown to be a successful index of age (Mail et al. 1983, Lehane and Mail 1985). For crustaceans, Ettershank (1983, 1984) first proposed a solvent extraction method which was then used to attempt quantification of age pigments in several species (Hirche and Anger 1987, Sheehy and Ettershank 1988) with supposedly promising results in *Euphausia superba* (Ettershank 1983, 1984, Berman et al. 1989, Nicol et al. 1991).

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[1] There is an important difference between "lipofuscin" and "ceroid", though the nomenclature is not yet generally consistent and has been used exchangeably. Both terms refer to "fluorescent age pigments" or "wear-and-tear pigments". Ceroids may be formed at any period in life, usually pathologically, and their accumulation rates are rapid (Porta 1991). They are formed in any cell type but preferentially accumulate in the mononucleate phagocyte system, though occasionally also extracellularly (Elleder 1990).

These studies, however, have proved to be inconclusive with respect to the relationship between extracted fluorescence and physiological or chronological age. Sheehy (1996) quantitatively demonstrated on the freshwater crayfish *Cherax quadricarinatus* that soluble autofluorescence, previously attributed to lipofuscin, actually bears no quantitative relationship to it. The author concluded that, instead, the histologically based microscopic quantification of *in situ* lipofuscin's fluorescence is a reliable, though laborious, technique. Several recent studies have since aimed at assessing the applicability of morphological lipofuscin as an age marker in laboratory-reared as well as wild-grown - mostly commercially exploited - decapod species (O' Donovan and Tully 1996, Belchier et al. 1998, Sheehy et al. 1998, 1999, Vila et al. 2000). Except for *E. superba* (Sheehy 1990a) no species from polar areas has been studied so far.

For calibrating relative lipofuscin content against age two approaches have been suggested. Preferable, but unfeasible in polar areas, is to provide calibration by wild-grown marked and recaptured individuals of known age as shown for European lobsters by Sheehy et al. (1999). Alternatively, for seasonal spawners, age groups may be derived from concentration frequencies of morphological lipofuscin (Sheehy et al. 1994, 1998), analogous to size frequencies. I applied the latter approach, further explained below, which is unprecedented in (i) populations of unknown-age individuals, (ii) crustaceans from polar areas, and (iii) amphipods in general.

1.4 Aims of this study

The major aims of this study are

(i) to investigate the occurrence of morphological lipofuscin in selected polar crustacean species,

(ii) to assess the applicability of *in situ* lipofuscin as an age marker in slow-growing Crustacea with respect to factors affecting pigment formation, and separation of age classes from lipofuscin concentration frequencies,

(iii) to estimate and discuss lipofuscin-based population parameters in selected polar crustacean species.

Five crustacean species each from the Antarctic and the Arctic covering different taxa were examined for the occurrence of lipofuscin. The eastern Weddell Sea populations of the decapod *Notocrangon antarcticus* and the amphipod *Waldeckia obesa* were selected for modal progression analysis of lipofuscin concentration frequencies and subsequent estimation of population parameters.

2 Material and Methods

The first section of this chapter gives a brief account of how the ten investigated crustacean species were sampled and processed for lipofuscin analysis which was conducted by means of histological and optical methods as well as image analysis. The second part summarizes the used procedure of lipofuscin concentration- and morphometric data-analysis comprising modal progression analysis and standard methods applied in population dynamics, adjusted to lipofuscin-based data.

2.1 Sample processing

2.1.1 Sampling and study area

Specimens from the Antarctic (Fig. 1a) were caught during the expedition ANT XV/3 (EASIZ II, January-March 1998) of R/V "Polarstern" to the eastern Weddell Sea (Arntz and Gutt 1999). Agassiz and bottom trawls and amphipod traps were deployed at depths between 170 m and 2100 m. Average annual temperature close to the sea bottom ranges, depending on water depth, from 0.4 °C (Circumpolar Deep Water) to –1.8 °C (Antarctic Surface Water), with seasonal variability generally < 0.8 °C (Hellmer and Bersch 1985, Fahrbach et al. 1992). Specimens from the Arctic were caught with Agassiz trawl- and epibenthic sledge-hauls during the expeditions ARK XIII/1+2 (May-August 1997) (Stein and Fahl 1997, Spindler et al. 1998) to the northern Barents and the Greenland Seas, and with a remotely operated vehicle during ARK XV/1 (June-July 1999) (Krause 1999, Klages et al., in press) to the Greenland Sea at depths between 140 and 5550 m (Fig. 1b). Average annual temperatures close to the sea floor in these areas are +0.5 °C to -1.5 °C (Coachman and Aagard 1974, Loeng 1989) with little seasonal variation. After sorting the catches, specimens were preserved in 4% buffered formaldehyde-seawater solution. Females of *Chorismus antarcticus* with fertilized eggs attached to the pleopods were kept in aquaria at 0 ± 0.2 °C. In Sept / Oct 1998 eleven females released larvae which were reared under laboratory conditions and were, at intervals, fixed as above for lipofuscin analysis.

2.1.2 Sample treatment

Wet weight, body size and sex of 1883 formalin-preserved specimens were determined according to Walker (1907), Tiews (1957), Smaldon (1979) and Chapelle (1995) (see appendix). Lipofuscin measurement of 401 specimens (see appendix) was prepared as described for various decapod species by Sheehy (1989, 1990a) and Sheehy and Wickins (1994) (Fig. 2): brains, and in case of larvae complete heads, were dissected and dehydrated in ascending ethanol concentrations. Unstained, serial, 6 µm resin sections were made following standard embedding procedures. Individuals for transmission electron microscopy (TEM) were fixed in glutaraldehyde in cacodylate buffer and postfixed in osmium tetroxide. Brain tissue was dehydrated in

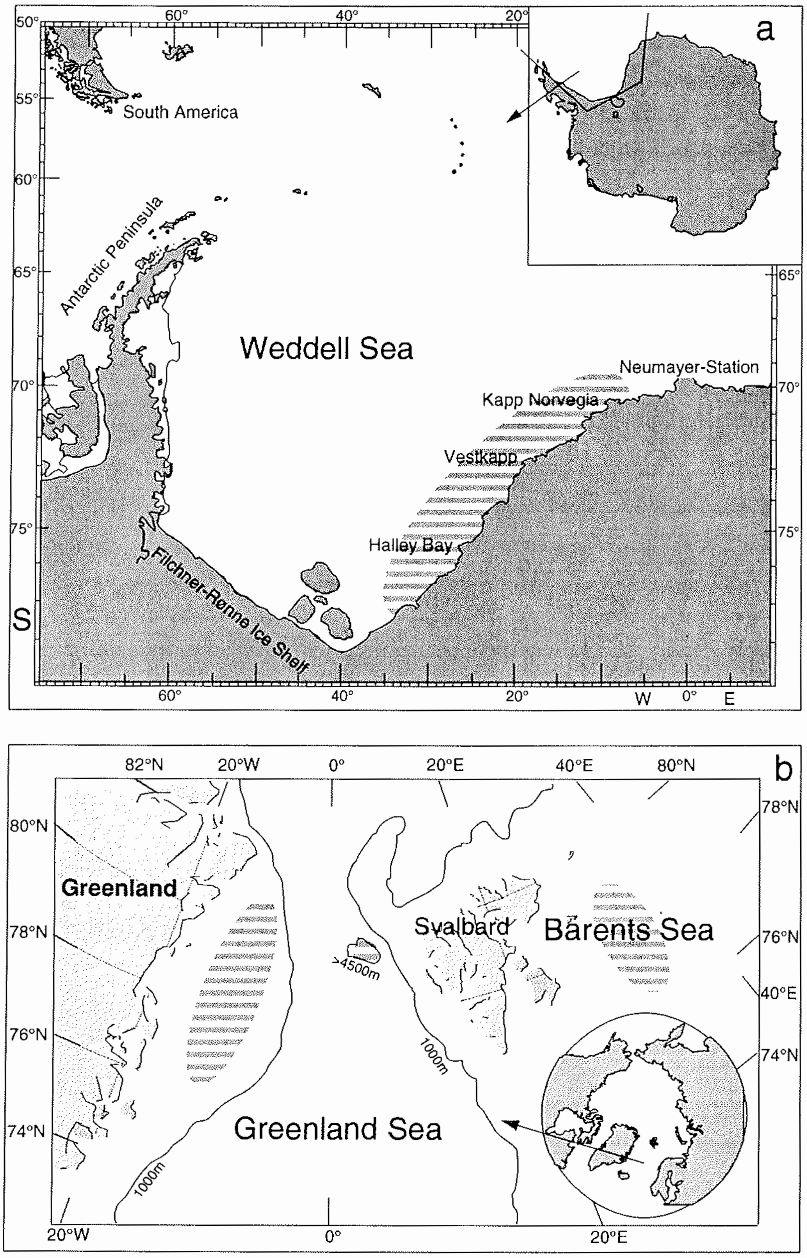


Fig. 1. Study areas (hatched) in the (a) Antarctic (eastern Weddell Sea), and (b) Arctic (Barents and Greenland Seas).

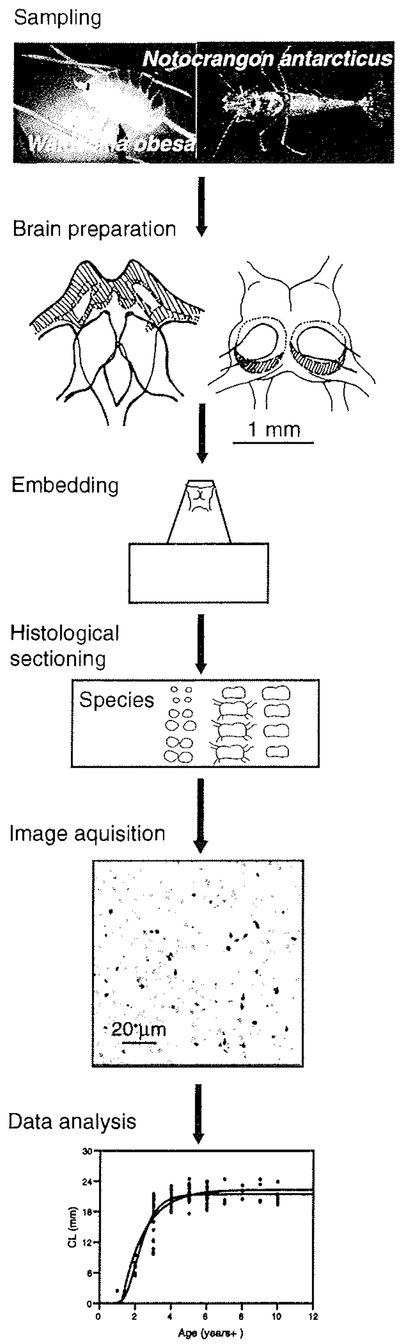


Fig. 2 Diagram of sample processing in lipofuscin analysis. Crustacean brains were dissected, embedded in resin and histologically sectioned. Selected sections were subsequently digitally recorded by confocal microscopy, and images were then analysed for relative lipofuscin concentration. Hatching in the brain sketches mark the areas analysed for lipofuscin. For details see text.

ascending acetone concentrations and embedded in Spurr's resin. Ultra-thin sections (60 nm) were stained in uranyl acetate and Reynold's lead citrate using standard procedures (Reynolds 1963, Nagl 1981), and were studied with a ZEISS 902 TEM.

2.1.3 Confocal microscopy: image acquisition

Brain sections were analysed with a Leica TCS NT confocal microscope at 488 nm excitation (KrAr laser) and ≥ 515 nm emission using a 40 x oil immersion lens (numerical aperture = 1.25). The most important advantage of confocal laser scanning microscopy over conventional fluorescence microscopy is that out-of-focus blur is essentially absent from the image (Sheppard and Shotton 1997). This is reached by (i) exciting a single point illuminated in the plane of the objective by a coherent point light source, i.e. a laser, and (ii) the confocal aperture which ensures that only light from the in-focus plane is fully detected by the photomultiplier tube (Pawley 1995). Fluorescence emission within the conical illumination area above and below the in-focus plane is defocused in the aperture plane and thereby almost prevented from reaching the detector. This allows for direct non-invasive serial optical sectioning of intact and even living organisms, and also improves resolution and signal-to-noise ratio in the xy-plain compared to conventional microscopy. Optical sectioning was not the major focus of this study, but allowed high lateral resolution and strong signal multiplication at remaining high signal-to-noise ratio as autofluorescence (less intense than stains) of rather small structures was investigated.

In decapods, the posterior lateral somacluster of the olfactory lobe (nomenclature after Sandeman et al. 1992) was localized in which lipofuscin is especially dense (Sheehy 1989, 1990b, Sheehy et al. 1995a, 1998). In amphipods, regions of high lipofuscin density were associated with the transition zones of the anterior-inferior lateral and medial somaclusters and the anterior-superior lateral and medial somaclusters (nomenclature after MacPherson and Steele 1980) and the respective neuropils (marked in Fig. 2). In krill, the entire brains were scanned for lipofuscin. High resolution digital images of six to ten approximately equidistant sections each of the respective brain areas were recorded. The sections were additionally viewed using a HBO 50 mercury lamp and 365 nm/450 nm excitation filters to verify the characteristic colour of the pigment's autofluorescence.

2.1.4 Image analysis: lipofuscin quantification

Image analysis was carried out using "Image (National Institute of Health)" software. The outline of the selected brain area was traced manually and the autofluorescent lipofuscin granules therein were discriminated using manual greyscale 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 analysed tissue, multiplied by 100. The geometric average AF over all sections examined for each individual was calculated. The image analysis was performed without prior knowledge of the body length of the specimens to avoid personal bias.

2.1.5 Histochemistry

The characteristic lipophilia of lipofuscin was confirmed in selected sections of each species by staining with Sudan Black. The resin sections were rehydrated in graded ethanols and then stained by immersion in a saturated solution of Sudan Black in ethanol (modified after Romeis 1968 and Sheehy and Wickins 1994). After rinsing excess stain and drying the object slide, the same sections recorded for lipofuscin autofluorescence were analysed for their affinity to Sudan staining.

2.2 Data analysis

2.2.1 Age class identification

In *Notocrangon antarcticus* and *Waldeckia obesa* (Fig. 2 top) length frequency distribution (LFD) histograms from the size-data and lipofuscin concentration frequency distribution (LCFD) histograms from the pigment concentration analysis of subsamples were established. For efficient comparison with the LFD, class intervals in the LCFD histograms were chosen in a way that the main part of the data lay within a similar number of classes as in the LFD histogram. Potential age groups were identified by fitting normal components to modes in the LCFD histogram using modal progression analysis routines according to Hasselblad (1966) and Bhattacharya (1967) of FiSAT (FAO-ICLARM stock assessment tools, Gayanilo et al. 1996) (Fig. 3). 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. Modes were assumed to reflect distinct broods, i.e. subsequent age classes separated by the age difference of one year, referred to as relative age (Pauly 1984). For this parameter, I used the dimension "years+" (i) to imply that exact age depends on what time of the year the sample was taken relative to the hatching period, (ii) to account for natural spread of age in modes, and (iii) to account for the fact that detectable lipofuscin accumulation may start at some point after larval release. 1+ therefore means one year or/and more. 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 were chosen to cover the complete size range present. Hence, the age frequency distribution (AFD) of the lipofuscin subsample is not representative of the population, but most likely reflects the true distribution of age within each size class of the population. From this distribution, the probability of an individual of a certain size to belong to a certain age group was computed and the LFD was transformed into a corrected AFD accordingly. The corrected AFD was used to compute the catch curve (see below).

2.2.2 Growth parameters

Prior to growth analysis, the size-at-estimated age data were, in juvenile age groups, supplemented by information on reproduction and morphology owing to the underlying assumption that mode I does not represent 0+ year old specimens if detectable

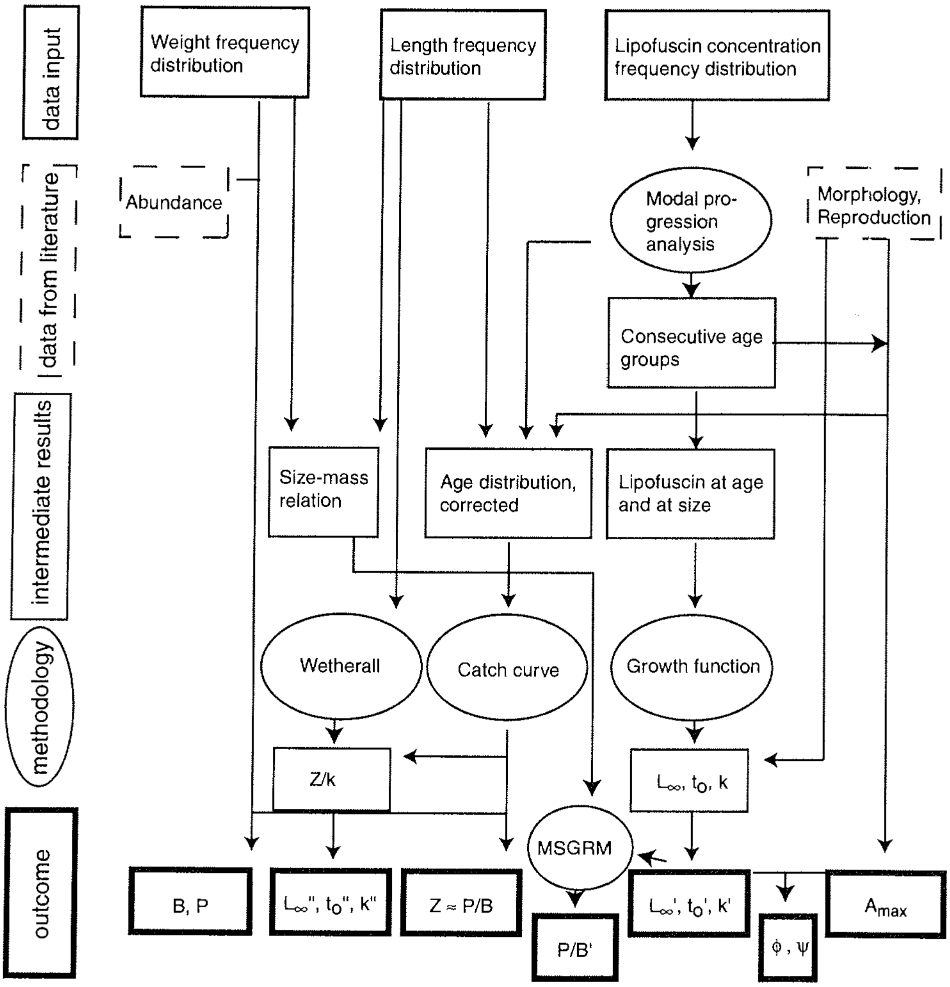


Fig. 3 Summary of data analysis for computing population parameters of *Notocrangon antarcticus* and *Waldeckia obesa*. A_{max} = maximum age, B = biomass, k = growth konstant, L_∞ = asymptotic length, P = production, P/B = productivity, t_0 = theoretical age at zero size, Z = mortality rate, ϕ, ψ= growth performance parameters. Indices with ' and " mark results obtained by different approaches. For details see text.

lipofuscin accumulation does not start right after larval release. The Powell-Wetherall function (FiSAT, Wetherall 1986) was used to derive first estimates of the asymptotic length L_∞ and the growth constant k of the von Bertalanffy growth function (VBGF) in *N. antarcticus*. In both *N. antarcticus* and *W. obesa*, VBGF

$L_t = L_\infty\,(1-e^{-k(t-t_o)})$

and Gompertz growth curves

$L_t = L_\infty\,(e^{-e^{-k(t-t_o)}})$

(L_t = length at age t (years), t_0 = theoretical age in years at which L = 0 mm) were fitted to the size at lipofuscin-estimated age data by an iterative non-linear algorithm.

2.2.3 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 *N. antarcticus*, I additionally applied Brey's (1995, 1999a) empirical function established from data of 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), M_{max} = maximum body mass in (kJ), T = temperature (K)).

2.2.4 Productivity, biomass and production

Mean biomass was calculated for *N. antarcticus* based on abundance data by Gutt et al. (1991) and mean body mass from my data. No abundance data were available for *W. obesa*. Annual production and P/B ratio of each population were estimated from $Z \approx P/B$ (Allen 1971, Brey 1995, 1999a) and by the mass-specific growth rate method (MSGRM, Crisp 1984) which combines the information provided by the LFD, the VBGF and the size–body mass relationship.

3 General Discussion

In the following section I will summarize and discuss the published and some unpublished results of this investigation. A more detailed discussion can be found in the attached publications. The first two chapters will focus on methodological considerations in terms of occurrence of lipofuscin and applicability of the used method in polar crustaceans, while the third part concentrates on population dynamics of two Antarctic crustacean species. Finally, I will draw the attention to some future perspectives.

3.1 Morphological lipofuscin in polar crustaceans

All ten investigated polar crustacean species, encompassing Amphipoda, Euphausiacea and Decapoda, displayed at least some lipofuscin granules in their brain tissues. The observed properties of the pigment (Table 1) widely coincide with the

Table 1 Properties of morphological lipofuscin according to reviews by Porta (1991) and Terman and Brunk (1998) as well as publications I – III and my unpubl. results. 1: *Waldeckia obesa* (Chevreux, 1905), 2: *Euphausia superba* Dana, 1850, 3: *Nematocarcinus lanceopes* Bate, 1888, 4: *Notocrangon antarcticus* (Pfeffer, 1887), 5: *Chorismus antarcticus* (Pfeffer, 1887), 6: *Eurythenes gryllus* (Lichtenstein, 1822), 7: *Uristes* sp. Dana, 1849, 8: *Sabinea septemcarinata* Sabine, 1821, 9: *Sclerocrangon ferox* Sars, 1877, 10: *Pandalus borealis* Krøyer, 1844.

Property	**Literature**	**This study**
MORPHOLOGY		
Granule shape	± Roundish, with irregular outline	Confirmed by confocal optical sectioning[1-10]
Granule size (diameter)	Predominantly 1-3 µm	Likewise in TEM[1,4,5]; up to 5[4,5] and 11[1] µm in fluorescence images, probably merged granules
Granule types	Granular, homogeneous, lamellated and compound (after Terman & Brunk 1998)	All types occur, the latter is most common[1,4,5]
Location within brain	Postmitotic eucaryotic cells; Decapoda: esp. dense in somaclusters of olfactory lobe (Sheehy 1989, 1990b)	Decapoda[3,4,5,8,9,10]: likewise; Amphipoda[1,6]: dense in transition zones of anterior-inferior lateral + medial somaclusters and anterior-superior lateral + medial somaclusters to associated neuropils
Location within cell	Intracellular in cytosol, membrane bound	Likewise[1,4,5], though sometimes integrated into cell membrane[4]
CHEMISTRY		
Chemical composition	30-70% proteins, 20-50% lipids, 4-7% carbohydrates, traces of metalls	*Not studied*
Reaction to histo- and biochemical assays	Positive to Sudan Black, osmium and periodic acid Schiff reaction. Lysosomal enzyme activity. Reactions variable in intensity.	Positive to Sudan[1-10] and osmium[1,4,5] with variable affinity to stain. *Other properties not studied.*
Autofluorescence	Intensely yellow to off-white under UV	Likewise, also intense at 488 nm excitation (KrAr laser) and 515 nm emission[1-10]
Electron density	High	High[1,4,5]
Extractability	Resistant to alcohol and acetone	Likewise[alcohol:1-10, acetone: 1,4,5]
Temperature resistance	*Not mentioned*	At least –30 °C to +100 °C[1-10]
FORMATION	Oxidative modification of damaged cell components in lysosomal vacuoles	*Not studied*
METABOLISM	Little or no degradation, accumulation with time	Accumulation with time[1,4]

morphological and histochemical characteristics described for various invertebrates and vertebrates (Sohal and Wolfe 1986, Sheehy 1989, Jolly et al. 1995, Yin 1996, Medina et al. 2000); chemical properties apart from lipid moieties were not tested. The present study, thus, confirms the occurrence of morphological lipofuscin in polar crustaceans for the first time (publication I). This finding is consistent with previous work which states the universal occurrence of lipofuscin in post-mitotic eucaryotic cells, the ubiquitous nature of lipid peroxidation processes giving rise to lipofuscin (Strehler et al. 1959, Sheldahl and Tappel 1974, Katz et al. 1984, Brunk et al. 1992) and autofluorescence as the most useful feature for histological localization and quantification in crustaceans (Medina et al. 2000). Overall, pigment concentrations were considerably lower in polar than in boreal Crustacea (e.g. Belchier et al. 1998, Sheehy et al. 1998). Granules were only conspicuous in three decapod and two amphipod species with considerable variability in density and fluorescence intensity between and within species. In specimens almost lacking lipofuscin, such as *Euphausia superba* (Sheehy 1990b, publication I), granules may not have been resolvable with the applied methodology. Unprecedented as yet, lipofuscin granules in amphipods were detected to concentrate in the transition zones between somaclusters and neuropils (publications I + III), whereas they are more or less equally distributed throughout the somaclusters in Decapoda (Sheehy 1989, 1990b, Sheehy et al. 1998, Belchier et al. 1998, Vila et al. 2000, publications I + II). While the reason for this difference remains unanswered, the practical consequence is that relative lipofuscin concentrations as area fraction of brain regions cannot be compared between amphipods and decapods. Irrespective of this, the concentrations increased with age in species belonging to either taxon.

Conclusions

- Lipofuscin occurs in polar crustaceans, though in comparatively low concentrations.
- Pigment properties widely coincide with those published in literature, but high-density regions are differently distributed in Amphipoda and Decapoda.

3.2 Lipofuscin as an age marker

Lipofuscin has been called a physiological age marker, associated with „subjective“ (life)time passing at an individual‘s or species‘ pace as opposed to objective time passing at the same pace anywhere. „Subjective“ time is, generally speaking, a function of the metabolic „clock“ which in turn depends on environmental as well as on genetic parameters. Accordingly, formation and accumulation of lipofuscin may be affected by spatial and temporal environmental variability (Sheehy 1990c, O'Donovan and Tully 1996, Sheehy et al. 1996). Thus, the applicability of lipofuscin as an age marker needs to be discussed in general, and regarding polar Crustacea in particular.

3.2.1 Factors affecting lipofuscin formation

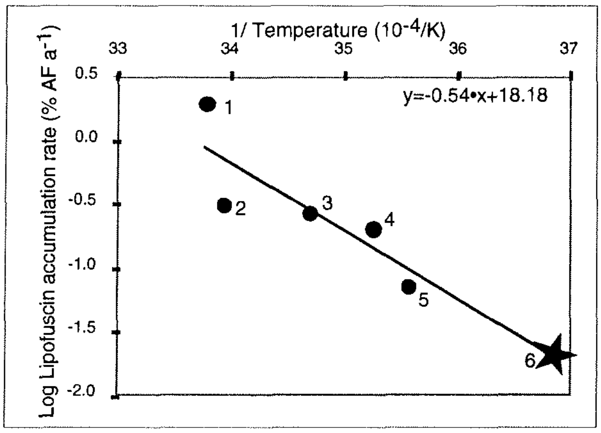


Fig. 4 Arrhenius plot of lipofuscin accumulation rates in various decapod species (r^2 = 0.87); 1: *Cherax quadricarinatus* (23 °C), Sheehy et al. (1994), 2: *Panulirus cygnus* (21.5 °C), Sheehy et al. (1998), 3: *Homarus gammarus* (15 °C), Sheehy et al. (1996), 4: *Pacifastacus leniusculus* (10.5 °C), Belchier et al. (1998), 5: *Homarus gammarus* (8 °C), Sheehy et al. (1996), 6: *Notocrangon antarcticus* (±0 °C), publication II.

Temperature has been identified as one of the primary factors with respect to lipofuscin formation as metabolic rate increases with temperature (Parry 1983, Alongi 1990) and affects the processes producing lipofuscin (Mail et al. 1983, Sheehy 1990b, Sheehy et al. 1994, 1996, Wahle et al. 1996, Medina et al. 2000). This study extended the temperature range of measured lipofuscin accumulation rates in Decapoda by almost 10 °C: In *Notocrangon antarcticus*, the average accumulation rate was 0.02 % area fraction per year (AF a^{-1}) at ± 0 °C (publication II). This is well below rates measured in other Decapoda, which range from 0.07% AF a^{-1} in the long-lived European lobster (8 °C; Sheehy et al. 1996) to 2.0% AF a^{-1} in the relatively short-lived freshwater crayfish *Cherax quadricarinatus* (23 °C; Sheehy et al. 1994). The seemingly close relation between ambient temperature and relative lipofuscin accumulation rates may allow the attempt of a potential universal decapod calibration function (Fig. 4). This could possibly facilitate (i) approximate interpolation of accumulation rates in species distributed over a range of thermal regimes, e.g. *Notocrangon antarcticus* from the Antarctic Peninsula and the Weddell Sea, and (ii) rough age estimates in species in which lipofuscin concentrations of only single specimens are available. Although so far speculative, this approach should be kept in mind with regard to comparable methodology in future investigations. In habitats with considerable seasonal temperature fluctuations, pigment accumulation seasonally changes due to temperature-related variations in metabolism (Vila et al. 2000). In lipofuscin-derived growth models, temperature effects therefore need to be incorporated. In pond-reared *Penaeus japonicus*, Vila et al. (2000) observed a decrease in lipofuscin accumulation rate by 90 % from summer to winter (at ΔT = 11 °C) while body growth continued due to constant food supply. This experiment impressively demonstrates the effect of temperature alone, which in wild-grown specimens usually cannot be distinguished from effects of reduced food input.

Lipofuscin formation, by its linkage to metabolism, may also depend on food availability and, consequently, caloric intake. In most of the study areas, food availability is thought to be comparatively low for much of the year (Clarke 1991, Arntz et al. 1994), although ecologists are still debating whether organisms are resource-limited for at least part of their life spans (Clarke 1998). Particle flux is highly seasonal for all species directly or indirectly trophically linked to primary production, and presumably rather sporadic and erratic for scavengers, though food fall rates are unknown (reviewed in Britton and Morton 1994). Oxygen consumption in the scavenger *Waldeckia obesa* decreased down to 60% after 64 days of starvation and increased again right after feeding due to costs for handling and processing of the food (Chapelle et al. 1994). These results could point towards (i) comparatively low lipofuscin content in polar crustaceans due to overall low food intake, and (ii) potentially discontinuous pigment accumulation on a short time scale (hours or days) due to variable metabolic rate. While this study is not inconsistent with the first assumption, there is so far less conclusive evidence for the second. There are indications that brain metabolism does not oscillate with food-caused metabolic condition of the body or certain organs (Sullivan and Somero 1980, Porta 1987). Even if there was an effect, the pigment should act, on a time scale of years, as an integral over the entire life span of an individual, making effects of short-term variability negligible in long-lived species. Moreover, individuals sampled from the same population are subject to similar environmental conditions and will experience comparable average food availability throughout their entire life spans.

Beside environmental variability, genetically determined factors inherent to a taxon or individual could affect lipofuscin accumulation. Most studies found no effect of sex and brood on pigment accumulation rate (Sheehy 1990c, Sheehy et al. 1994, 1995b, 1996, Vila et al. 2000, publication III). Fig. 4 comprises accumulation rates of decapod species and implies that these are largely explained by temperature alone, although different feeding types and bathymetrical ranges are covered. Sheehy (pers. com.) commented, however, on his unpublished data not agreeing with this trend. My own and published data are inconclusive with regard to possible effects of activity level or feeding type on lipofuscin formation between taxa. Yearly pigment accumulation rates in taxa as distantly related as insects, rats and monkeys were obtained by incomparable methods so that potential (dis)similarities have remained unanalysed as yet (Sohal et al. 1983, Nakano et al. 1993, Oenzil et al. 1994).

If lipofuscin accumulation were to follow weight-specific metabolic rate, it would seem more likely that smaller individuals would accumulate higher quantities of lipofuscin than larger specimens of identical or different ages (Hill and Womersley 1993). Among the reasons why accumulation with age is apparently linear (Strehler et al. 1959, Reichel et al. 1968, Belchier et al. 1998, Sheehy et al. 1998, publications II + III) may be that (i) brain mass is not as variable as body mass over time (Lindstedt and Calder 1981) and (ii) brain metabolism is less affected by parameters influencing body mass change (see above, Sullivan and Somero 1980, Porta 1987). Several authors found, for instance, no significant age- and weight-related changes in the turnover rates of rat mitochondria (Sanadi and Fletcher 1962, Comolli et al. 1972).

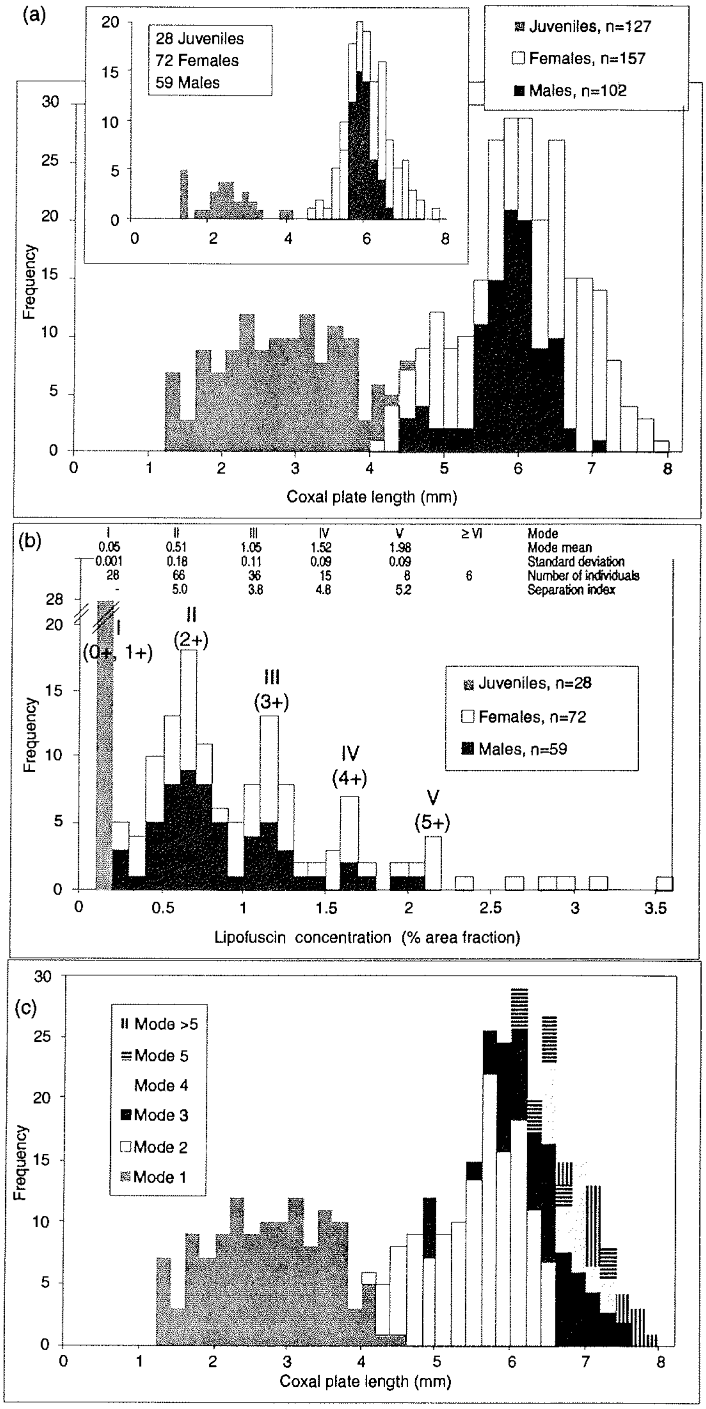
Conclusions

- Environmental factors affect lipofuscin formation.
- Low temperature and metabolism in the study areas coincide with low lipofuscin concentrations and accumulation rates.
- Seasonal differences in temperature and, thus, in lipofuscin accumulation rates within and between habitats need to be incorporated into growth models.
- The accumulation of lipofuscin is linear with time (at constant temperature).

3.2.2 Identification of age groups

Modal separation of the lipofuscin concentration frequency data (LCFD) revealed distinct and well resolvable modes in both *Notocrangon antarcticus* (eight modes) and *Waldeckia obesa* (five modes, Fig. 5) (publications II + III). Regular bell shape and even spacing of modes suggest (i) non-random distribution, (ii) linear accumulation of the pigment with time (illustrated in brain images in Fig. 6), and (iii) seasonal reproduction (confirmed by Chapelle 1991, Gorny et al. 1992). Although the number of individuals in older cohorts is low in both species, several reasons encouraged me to treat those as modes in further calculations. These are (i) the high separation index from modal progression analysis, (ii) significant chi^2, (iii) decreasing number of individuals with increasing lipofuscin concentration, and (iv) 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 environmental or genetic variability, potentially affecting lipofuscin accumulation as discussed above, evoked any obscuring overlaying rhythm of pigment formation, nor did it eradicate modes. Unfortunately, age calibration to validate modes as age classes is lacking, a shortcoming which is also the flaw in most studies using size frequencies for age determination. Lipofuscin measurement in freshly released *Chorismus antarcticus* larvae (release happens eleven months after hatching from the eggs) showed linear pigment accumulation over a 4-months-period at extremely low concentrations. Although the results cannot be extrapolated to total life span as few specimens were investigated over an only short time-period and larvae were moreover laboratory-reared, they are supporting evidence for time-dependent linear pigment accumulation (publication I). True validation was, however, performed on a number of other Crustacea (Sheehy et al. 1994, 1996, 1998, Wahle et al. 1996, Belchier et al. 1998) verifying peaks in the LCFD as age groups.

Length frequency distributions (LFD) have a long tradition in fisheries and have also successfully been used to separate cohorts in low latitude amphipod and decapod species (e.g. Pauly et al. 1984, Collie 1985, Moore and Wong 1996, Jerí 1999 and references therein, Oh et al. 1999), and even in some Arctic species (Beuchel 2000, Poltermann 2000), although age validation was lacking in the latter. The LFD obtained for *W. obesa* (Fig. 5a), *N. antarcticus* (publications II + III) and *Chorismus antarcticus* (unpublished data), in contrast, showed a pile-up of individuals in two modes comprising juveniles and adults, respectively, in *W. obesa,* and mature males and females, respectively, in the decapods. Long-term aquaria observations by Belgian and German colleagues and myself demonstrated that Antarctic



Amphipoda and Decapoda can be maintained for years without much obvious growth, indicating that the large peak in the LFD is composed of many age classes, as demonstrated by lipofuscin analysis (for *W. obesa*: Fig. 5c). Increased resolution of the size measurements led to peaks based on moulting stages which in most cases lack a (precise) time axis (for *W. obesa:* Chapelle 1991). Gorny et al. (1993) and Klages (1993) used the morphology of the appendix masculina in the proterandrous shrimp *C. antarcticus* and the oostegites in female *Eusirus perdentatus* (Amphipoda), respectively, as additional measure to overcome the problem of unresolvable cohorts. The observed distribution pattern is common in long-lived benthic invertebrates (e.g. Brey et al. 1995a, b, Dahm 1996, Piepenburg and Schmid 1996, Bluhm et al. 1998, Gatti, pers. com.) including crustaceans (Phillips 1990, Brewis and Bowler 1992, Gorny et al. 1992, Bannister et al. 1994, Sheehy et al. 1998) and is ascribed to slow and declining growth with age as well as high size-at-age variability, apparently typical of Crustacea (Chittleborough 1976, Pauly et al. 1984, France et al. 1991, Phillips et al. 1992). Moreover, size variability due to non-moulting females during breeding, interference of moulting stages with cohorts, and potential effects of parasites, injuries and starvation on growth can obscure or merge age groups in LFD (Ikeda and Dixon 1982, Somers and Kirkwood 1991, Klages 1993, Wikelski and Thom 2000). France et al. (1991) in their re-appraisal of LFD histograms for age determination and growth in crayfish point out that longevity should not exceed four years as older cohorts are notoriously difficult to separate. Concludingly, my findings support previous results stating size as an inadequate age predictor in slow-growing crustaceans (Belchier et al. 1994, 1998, Sheehy et al. 1998, 1999). Evidence is strong that morphological lipofuscin, in contrast, is a powerful age marker in crustaceans due to its little variability at age compared to high size-at-age variability (e.g. O'Donovan and Tully 1996, Belchier et al. 1998, Sheehy et al. 1998, publications II + III).

Conclusions

- Age modes are not detectable in LFD histograms of the investigated species.
- Modal progression analyses of LCFD of *W. obesa* and *N. antarcticus* allows separation of modes.
- There is strong evidence that these modes reflect consecutive annual cohorts.

Fig. 5 *Waldeckia obesa* from the eastern Weddell Sea. (a) Coxal plate length frequency distribution of 386 trap-caught individuals (inlay: 159 lipofuscin-analysed specimens), (b) lipofuscin concentration frequency distribution including results from modal progression analysis (the frequency (n) of one bar is $n_{\text{total bar}} = n_{\text{females}} + n_{\text{males}} + n_{\textit{juveniles}}$), (c) distribution of modes derived from the modal progression analysis of the lipofuscin concentration frequency histogram as distributed in the length frequency distribution histogram. The number of individuals per age group was adjusted from lipofuscin-analysed subsample to total sample size (see text). $\text{Frequency}_{\text{total bar}} = n_{\text{mode1}} + n_{\text{mode2}} + \ldots + n_{\text{mode>5}}$. Roman numerals = modes, arabic numerals = cohort designation in years +.

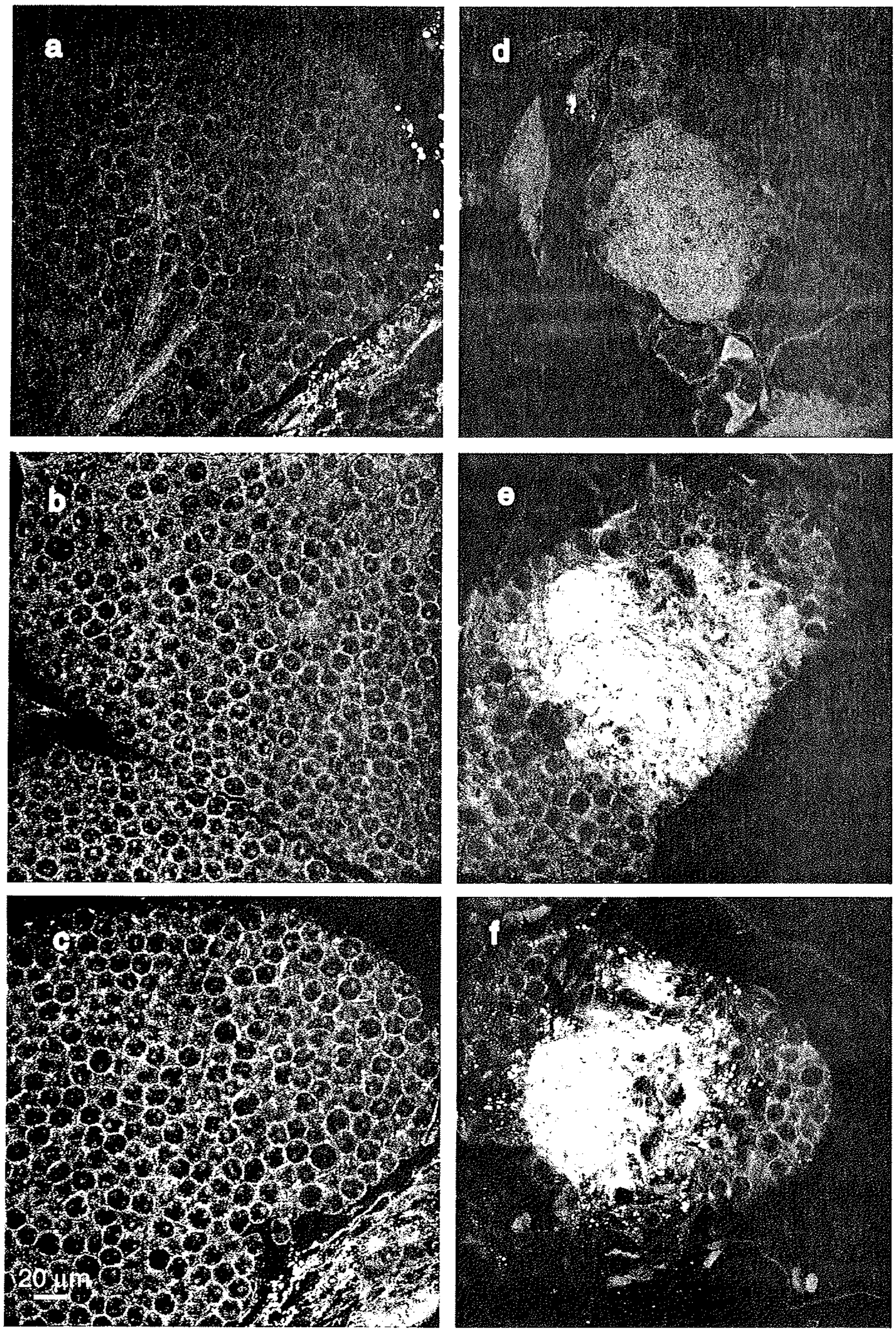


Fig. 6 Age-dependent accumulation of autofluorescent lipofuscin granules in brains of (a-c) *Notocrangon antarcticus* (Decapoda), estimated as (a) 2+ years, (b) 5+ years, and (c) 10+ years old, and (d-f) *Waldeckia obesa* (Amphipoda), estimated as (d) 1+ year, (e) 4+ years, and (f) 7+ years old. Digital confocal images.

Trouble shooting

- Low pigment concentrations require high image quality and number of analysed sections, making image acquisition and analysis extremely time-consuming.
- Background fluorescence due to aldehyde fixation reduces signal-to-noise ratio so that weakly fluorescent granules may remain unidentified.
- Higher number of analysed individuals would help to more clearly identify older cohorts at the expense of time requirement.

3.3 Population dynamics of selected Antarctic Crustacea

3.3.1 Growth and longevity

Body growth in *Notocrangon antarcticus* and *Waldeckia obesa* can be described by von Bertalanffy and Gompertz growth functions (publications II + III). As demonstrated above, size and age are to a considerable extent decoupled (Fig. 5c), so that the parameter values of the growth functions should be interpreted with care. This may, however, also be true for results from other studies. Despite this limitation, estimates for the growth constant k (0.8/0.6 a^{-1} in female/male *N. antarcticus*, 0.5/0.6 a^{-1} in female/male *W. obesa*) lie in the range of the few published values of other cold-water caridean decapods (0.2-0.8 a^{-1}; Dailey and Ralson 1986, Bergström 1992, Baelde 1994, Santana et al. 1997) and amphipods (0.2-0.6 a^{-1}; Bone 1972, Poltermann 2000), respectively. As expected, they are below most values from lower latitude Decapoda, mostly penaeids (0.8-1.6 a^{-1}; Pauly et al. 1984, compilation in Jerí 1999), and Amphipoda (15 a^{-1}, Venables 1981). Male *N. antarcticus* and *W. obesa* reach lower asymptotic sizes and male *N. antarcticus* grow slightly slower than females, as also reported for other carideans and penaeids (Oh et al. 1999, Garcia and Le Reste 1981, Baelde 1994), whereas male *W. obesa* and some penaeid shrimps (compiled in Jerí 1999) grow faster than their female conspecifics.

In contrast to growth rates, overall growth performance of polar Amphipoda and Decapoda, measured by the index ψ (Brey 1999a), was in a similar range (slightly higher in amphipods and slightly lower in decapods) as in lower latitude congeners, as shown in the auximetric grid (according to Pauly 1979, 1984, Fig. 7). This supports Brey's (1995, 1999a) empirically demonstrated conclusion that growth performance is little variable between closely related taxa, obviously intrinsic to those, whereas the growth parameters *per se* are largely subject to varying environmental parameters.

Life span in polar Decapoda and Amphipoda is estimated to range from 5 to 10 and 2 to 8 years, respectively, though such longevity data are scarce (Thurston 1968, 1970, Bone 1972, Hopkins and Nilssen 1990, Highsmith and Coyle 1992, Gorny et al. 1993, Klages 1993, Beuchel 2000, Poltermann 2000, publications II + III). Polar species reach, on average, higher ages than their shallow-water congeners from lower latitudes which rarely attain maximum ages ≥ 3 years (Pauly et al. 1984, Sainte-Marie 1991, Oh et al.

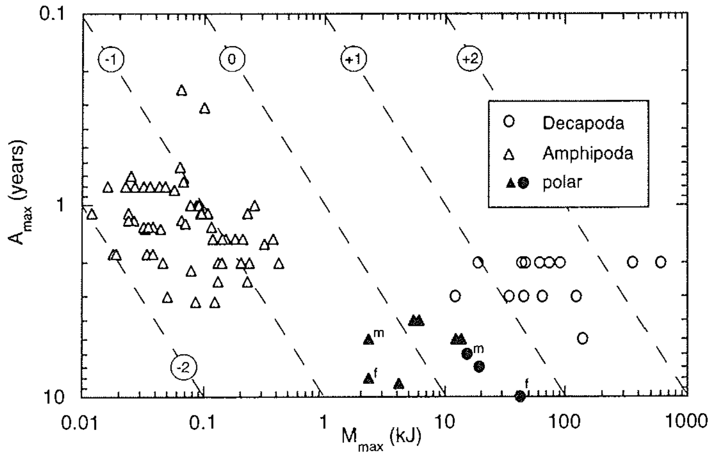


Fig. 7 Auximetric grid comparing overall growth performance ψ = log (maximum body mass M_{max} / maximum age A_{max}) of polar and non-polar Decapoda and Amphipoda. Diagonal lines indicate equal values of ψ (numbers in circles). Data collection: Brey (1999a, b). Polar Amphipoda: *Bovallia gigantea* (Thurston 1968, 1970, Bone 1972), *Gammarus wilkitzkii* (Poltermann 2000), *Waldeckia obesa* (publication III; f and m mark data for females and males, respectively); polar Decapoda: *Chorismus antarcticus* (Gorny et al. 1993), *Notocrangon antarcticus* (unpubl. results; f and m as above).

1999, Jerí 1999, Vila et al. 2000) with most Amphipoda dying before the age of 2 years (Fig. 7, data collection: Brey 1999a, b). Only other cold- and deep-water shrimps and amphipods such as *Heterocarpus reedi* (Roa and Ernst 1996) and *Eurythenes gryllus* (Ingram and Hessler 1987) obtain ages of up to 10 years as well. Higher longevity than in lower latitude relatives is also known from Antarctic Euphausiacea (Siegel 1987), Mysidacea (Ward 1984, Siegel and Mühlenhardt-Siegel 1988) and Isopoda (Luxmoore 1982, Wägele 1987). It should be noted that most longevity estimates might be subject to error due to limitations of size-based and artificial rearing studies. Higher age in female *N. antarcticus* and *W. obesa* than in males is reflected in sex ratios favouring females and higher maximum body sizes (Chapelle 1991, Gorny et al. 1992, publications II + III), although catch effects cannot be totally excluded as explanation. The presented age estimates for *W. obesa* corresponds to Sainte-Marie's (1991) results of his review of 302 populations of gammaridean amphipods, demonstrating that mean life span was significantly longer in (i) cold- than in warm-living populations, (ii) in Lysianassoidea and Eusiroidea compared to other superfamilies, and (iii) supposedly in deep-living compared to shallow-living species.

The "average" specimen should attain reproductive maturity with sufficient time for successful production of offspring. Most berried female *N. antarcticus* were estimated as 4+ years old 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 one year before eggs are attached to the pleopods and hatch the following year (Gorny et al. 1992). Much of size and body mass increment happens prior to first spawning when energy starts being allocated to reproduction, and lipofuscin accumulation is not reflected in body growth any longer. As males lack the long incubation period, they undergo the same number of reproductive events at half the females' life span. Gorny et al. (1993) suggest an age of even $\geq$ 6+ years for breeding female *Chorismus antarcticus* which may be explained by the proterandrous hermaphroditism of the species requiring some time in the males phase to reproduce. If reaching maturity at an age of 2+ years and reproducing annually, female *W. obesa* could produce offspring $\geq$ four times during their lifespan. Based on an estimate of 25 eggs per female and brood (incidential observation by Chapelle 1991), lifetime potential fecundity (125 to 200 embryos (E)) and reproductive potential (25 E per female and year) are within the range given for Lysianassoidea by Sainte-Marie (1991) (1 to 215 E, mean = 82, and 1 to 92 E per female and year, mean = 43, respectively).

Generally, delayed maturity, high longevity and slow ageing in polar invertebrates are explained by limited food availability and low metabolism (Pearl 1928 and Sheehy et al. 1995b: "rate of living theory"; Clarke and North 1991, Brey and Clarke 1993, Thiel et al. 1996). Very low O_2-consumption values were indeed measured in *W. obesa* (Chapelle and Peck 1995) and other Antarctic invertebrates (Peck 1989, Ahn and Shim 1998, Gatti et al., in prep., Heilmayer et al., in prep.). Studies on a variety of terrestrial taxa ranging from nematodes and flies to rats supported the prolonging effect of relatively low caloric intake on life span (e.g. Weindruch and Walford 1982, Sohal and Weindruch 1996). This relationship seems also conclusive for marine invertebrates in seasonally food-limited habitats such as most of the Antarctic, Arctic and deep-sea (Clarke 1988, 1991).

3.3.2 Productivity and mortality

On a worldwide scale, productivity expressed as P/B ratio ranges from 0.5 to 10 a^{-1} and from 0.4 to 61 a^{-1} in decapods and amphipods, respectively. The P/B ratios calculated for *Notocrangon antarcticus* and *Waldeckia obesa* are < 1 a^{-1} (publications II + III) and match with Brey and Clarke's (1993) compilation of P/B ratios of Antarctic invertebrates, therein crustaceans (Thurston 1970, Bone 1972, Highsmith and Coyle 1990, 1992, Poltermann 2000). They lie below those of lower latitude species in which P/B ratios > 30 were calculated for very small, short-lived, (sub)-tropical Gammaridae and Hyalellidae (Fredette and Diaz 1986a, b, Venables 1981). Concluding from P/B ratio and production estimates, a fishery on *N. antarcticus* would be ecologically and economically unsustainable.

Rather low turnover rates and biomass values in polar decapods and amphipods, the latter questioned in Amphipoda by Jarre-Teichmann et al. (1997), do not yet give sufficient indication for the relevance of these taxa in the Weddell Sea system. 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 that they interpret as well protected against predation. Indeed, only small amounts of shrimp were found in stomachs and faeces 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), emperor penguins (Klages 1989, Piatkowski and Pütz 1994, Pütz 1995), fish (Targett 1981, Takahashi and Nemoto 1984) and cephalopods (Kear 1992). In *W. obesa*, in contrast, the relation between Z and k indicates above-average predation pressure. This result supports works revealing Antarctic amphipods to be an important food source for fish (Targett 1981, Daniels 1982, Olaso et al. 2000), ophiuroids (Jarre-Teichmann et al. 1997) and crustaceans (Storch et al., in press). Therefore, amphipods in the Weddell Sea may, despite low P/B ratios, represent an important link in the energy transfer to higher trophic levels and as energy recyclers for carrion. Comparable mediator positions were illustrated for Bering Sea amphipods providing the link from sedimenting primary production to grey whales (Highsmith and Coyle 1992), and for Arctic sympagic amphipods representing a substantial part in cryopelagic coupling (Poltermann 1997, Werner 2000).

Conclusions

- *W. obesa* and *N. antarcticus* are characterized by high longevity, low productivity and mortality as well as delayed maturation.
- The Antarctic scavenging amphipod community may be an important energy mediator from carrion to higher trophic levels whereas decapods seem rather poorly preyed upon.

Trouble shooting

- The fit of a growth function is complicated when knowledge of the age at first pigment deposition is lacking.
- Most gears, e.g. amphipod traps, catch selectively, e.g. potentially neglect ovigerous females and/or smaller specimens. Thus, LFD and maybe AFD may not be fully representative of the respective population.

3.4 Future perspectives

The presented findings are evidence for the applicability of the lipofuscin-based method for age determination and growth models in slow-growing polar Crustacea. Independent of body size and unlimited by artificial rearing conditions or project duration, the lipofuscin age index is likely to provide reasonable longevity estimates for wild populations. With regard to future use of the technique, I want to put forward some considerations and propositions:

(i) Sheehy et al. (1998) emphasized the need to improve the technical procedure of the methodology with regard to its practical application as an economical routine operation in fisheries. Based on some first experiments with improved technology in confocal laser scanning microscopy, e.g. multi-photon microscopy with higher capacity for tissue penetration, I suggest to optically section wholemounts of (possibly fresh) gelatine-embedded brains. Timesavings would be considerable without the need for histological sectioning. Whenever feasible, chemical treatment potentially changing the native fluorescence characteristics of lipofuscin and evoking background fluorescence should be avoided or preserved samples should quickly be processed, thus improving image quality and signal intensity.

(ii) Techniques for age determination are still lacking for a number of invertebrate taxa, especially those without permanent hard structures. As lipofuscin is thought to accumulate in post-mitotic tissue of any eucaryote, it seems reasonable to try the method in taxa such as Ascidia or Turbellaria.

(iii) Sampling techniques which are representatively catching populations, esp. scavenging species, are urgently needed to obtain reliable population data.

(iv) Although substantially difficult, more validation studies are needed to calibrate lipofuscin content against age in wild crustacean populations.

(v) A precise knowledge of the age structure in crustacean populations is essential for the assessment and management of these resources. As such data are difficult to obtain in slow-growing species, results from lipofuscin analysis are especially important. Usually, quotas are linked to minimal allowable catch size in the belief that most specimens of that size are of the same age. Sheehy et al. (1999) showed that, for instance, at least seven age classes enter fishery at minimum catchable size in *H. gammarus.* Size-based age distributions are, thus, prone to lead to mismanaging quota in slow-growing species while lipofuscin has proved to be a powerful and more resource-orientated tool in this respect.

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5 Publications

Below, the publications in progress for this thesis are listed and my share thereof is explained.

Publication I

Bodil A. Bluhm, Thomas Brey, Michael Klages, Wolf E. Arntz
Occurrence of the autofluorescent pigment lipofuscin in polar crustaceans and its potential as an age marker.
Polar Biology, in press

The initial idea for the use of the lipofuscin-method in polar crustaceans was worked out by the second and third author in a DFG proposal (Br1220/4-1). I developed the methodological and conceptual approach, performed the practical work and wrote the first version of the manuscript which was improved in cooperation with the co-authors.

Publication II

Bodil A. Bluhm, Thomas Brey
Age determination in the Antarctic shrimp *Notocrangon antarcticus* (Pfeffer, 1887) (Crustacea: Decapoda) using the autofluorescent pigment lipofuscin.
Marine Biology, in press

I further developed and adjusted the method, designed the experimental concept and performed the laboratory work. The data analysis procedure was developed in close cooperation with the second author. My manuscript draft was discussed and revised with the second author.

Publication III

Bodil A. Bluhm, Thomas Brey, Michael Klages
The autofluorescent age pigment lipofuscin: key to age, growth and productivity of the Antarctic amphipod *Waldeckia obesa* (Chevreux, 1905).
Journal of Experimental Marine Biology and Ecology, accepted

I conducted the practical work and essentially applied the data analysis concept developed for publication II. After writing the manuscript, I revised it in discussion with the co-authors.

Publication I

Occurrence of the autofluorescent pigment lipofuscin in polar crustaceans and its potential as an age marker

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Polar Biology, EASIZ-Symposium Volume, in press

Abstract

The lack of reliable methods for age determination often complicates the determination of individual age which is a fundamental parameter for estimating growth in population dynamics. In crustaceans, the quantification of the autofluorescent age pigment lipofuscin has recently revealed more promising results in boreal and tropical species than traditional methods. The presence of morphological lipofuscin and its possible application as an age marker in polar species was assessed in brain sections of five Arctic and five Antarctic species comprising decapods, amphipods and a euphausiid. Lipofuscin granules were located using confocal fluorescence microscopy and quantified (as % lipofuscin area fraction) from digital images. The pigment was found in 94 of 100 individuals and in all ten species, and granules occurred in easily detectable amounts in five species. Two scavenging amphipod species, the Antarctic *Waldeckia obesa* and the Arctic *Eurythenes gryllus*, revealed the most conspicuous and numerous granules. There was a broad, though weak, correlation with individual body size within a species, but not with absolute body size of one species compared to another. In larvae of the decapod *Chorismus antarcticus*, lipofuscin accumulation was quantified over the first four months after larval release. Factors potentially influencing lipofuscin formation and their relevance for polar species are discussed. Factors explaining the pronounced differences in lipofuscin content between species for the moment remain unknown. The possibility for application of morphological lipofuscin as an index of age is encouraging for those investigated species with a sufficient accumulation rate of the pigment, and further studies will therefore be conducted.

Introduction

Determination of individual age is an important task in population dynamics. Data on population age composition are needed for calculating and interpreting growth parameters, mortality, productivity, maturation etc. (Pauly 1984, Brey 1999). Within the framework of the SCAR programme EASIZ (Ecology of the Antarctic Sea Ice Zone), emphasis has now been put on the development of methods for age determination for those Antarctic taxa for which accurate ageing methods are lacking. For some taxa such as echinoids, ophiuroids, bryozoans and brachiopods, such techniques have already been developed and applied to polar species (Brey et al. 1995a, b, Dahm 1996, Peck and Brey 1996, Bluhm et al. 1998, Brey et al. 1998). Studies on crustacean life span so far tended to concentrate on commercially important species in order to establish economically and ecologically sustainable quota. Those studies and the few attempts to determine age in polar crustaceans (e.g. Bregazzi 1972, Rakusa-Suszczewski 1982, Gorny et al. 1993, Klages 1993) have predominantly used size-based data (except for *Euphausia superba*, see below), as crustaceans are characterized by the lack of permanent hard structures carrying potential age markers. The separation of size-frequency distributions into cohorts, however, is hampered by interference between age classes and moulting stages (Klages 1993) and insufficient resolution in long-lived slow-growing species (France et al. 1991). Moreover, there may be considerable variation in individual growth rates with the consequence that body size may not be a reliable indicator of age (Sheehy 1989, 1990c, Belchier et al. 1998, Sheehy et al. 1998, 1999). Currently, a promising alternative approach is to quantify the autofluorescent age pigment lipofuscin (Belchier et al. 1994, 1998, Sheehy et al. 1994, 1995, 1996, 1998, 1999, O'Donovan and Tully 1996).

Morphological lipofuscin (as opposed to soluble or extractable age pigments) was first recorded by Hannover (1842) and its existence has since been demonstrated in post-mitotic tissue such as nerve tissue, heart and muscles of various invertebrates and vertebrates (e.g. Leibnitz and Wünscher 1967, Reichel et al. 1968, Donato and Sohal 1978, Bassin et al. 1982, Hunter and Vetter 1988, Clarke et al. 1990, Girven et al. 1993). Free radical-induced lipid peroxidation processes are thought to lead to the formation of lipofuscin and seem to occur in all eukaryotic cells (Sheldahl and Tappel 1974, Zg.-Nagy 1988, Sohal 1981). Accumulation of the pigment over the lifespan of an individual appears to be a universal correlate of animal senescence (Katz et al. 1984). In insects, soluble fluorescent age pigments have shown to be a successful index of age (Mail et al. 1983, Lehane and Mail 1985). For crustaceans, Ettershank (1983, 1984) first proposed a solvent extraction method which was then used to attempt to quantify lipofuscin in a number of species (Ettershank 1983,1984, Hirche and Anger 1987, Sheehy and Ettershank 1988) with supposedly promising results in the Antarctic krill *Euphausia superba* (Ettershank 1983, 1984, Berman 1989, Nicol et al. 1991). These studies, however, have proved to be inconclusive with respect to the relationship between extracted fluorescence and physiological or chronological age. Sheehy (1996) first quantitatively demonstrated on the freshwater crayfish *Cherax quadricarinatus* that soluble autofluorescence, previously attributed to lipofuscin, actually bears no quantitative relationship to it. The author concludes that the histologically based quantitative method with concurrent visual microscopic verification of *in situ* morphological lipofuscin's fluorescence and histochemical attributes is a reliable, though laborious, method for quantification. Several recent studies have been attempted to assess the applicability of morphological lipofuscin as an age marker (O' Donovan and Tully 1996, Belchier et al. 1998, Sheehy et al. 1998). With the exception of *E. superba* (Sheehy 1990a) no other species from high latitudes has been studied until now.

The polar environment is unique in some aspects possibly affecting the lipofuscin accumulation of species living there. High latitudes are characterized by low but stable temperatures, varying sea ice cover and a highly seasonal light regime. Consequently, the seasonality in primary production is pronounced and the amount of sedimenting particles varies over the year (summarized in Arntz et al. 1994). Metabolism is generally rather low in polar benthic invertebrates (Chapelle and Peck

1995). There are indications that lipid peroxidation processes also occur at a comparatively low rate at low temperatures (McArthur and Sohal 1982, O'Donovan and Tully 1996).

The two major aims of this study are (i) to investigate the occurrence of lipofuscin in selected polar crustacean species, and (ii) to assess the potential of image analysis of morphological lipofuscin as a quantification procedure for the age marker pigment. Five species each from the Arctic (two amphipod and three decapod species) and the Antarctic (one amphipod, one euphausiid and three decapod species), covering different taxa, feeding types and bathymetric distribution ranges, were examined for the occurrence of lipofuscin and its age dependent accumulation.

Materials and methods

Sampling. Specimens from the Antarctic (Table 1) were caught at depths between 170 m and 2100 m 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). Average annual temperature close to the sea bottom ranges, depending on water depth, from 0.4 °C (Circumpolar Deep Water) to –1.8 °C (Antarctic Surface Water), with seasonal variability generally <0.8 °C (Hellmer and Bersch 1985, Arntz et al. 1992). Specimens from the Arctic (Table 1) were caught during the expeditions ARK XIII/1+2 (May to August 1997) (Stein and Fahl 1997, Spindler et al. 1998) to the northern Barents and the Greenland Seas and ARK XV/1 (June to July 1999) (Krause 1999) to the Greenland Sea at depths between 140 and 5550 m. Average annual temperatures close to the sea bottom in these areas are +0.5 °C to -1.5 °C (Coachman and Aagard 1979, Loeng 1989) with minimal seasonal variation. All investigated specimens were fixed in 4% buffered formaldehyde-seawater solution immediately after sorting the catches and were stored in the solution until analysis in summer 1999.

Life maintenance. Several females of *Chorismus antarcticus* were caught with fertilized eggs attached to the pleopods in the period of January to March 1998. In September to October 1998 eleven females released zoea I-stage larvae which were transferred to 100 ml plastic bottles. The larvae were fed with live *Artemia* spp. nauplii and water was replaced every other day. They were reared at 0° C ± 0.2° C. At intervals, some larvae were fixed in 4% buffered formaldehyde-seawater solution for lipofuscin analysis. After four months all larvae were fixed or had died.

Sample preparation. Sex, wet weight and body size were recorded (carapace length in decapods to the nearest 0.1 mm and body length from rostrum to the end of the telson to the nearest mm in amphipods and euphausiids). Brains of the investigated species were prepared for lipofuscin measurement essentially as described for various 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%. In case of the larvae of *Chorismus antarcticus*, complete heads were embedded due to the small size. Unstained, serial, 6 μm resin (Technovit, Kultzer) sections were prepared following standard embedding procedures, however excluding mounting medium. Fig. 1 shows how brains were orientated and serially sectioned.

Fluorescence microscopy. Sections were analysed with an inverted Leica TCS NT confocal microscope, using 488 nm excitation wavelength of a KrAr laser (Omnichrome) and a 40 x oil immersion lens with a high numerical aperture of 1.25. The sections were additionally viewed using a HBO 50 mercury lamp and 365 nm as well as 450 nm excitation filters fitted to the same microscope to assess the colour of the fluorescence. In decapods, the (posterior) lateral somacluster of the olfactory lobe was localized (nomenclature after Sandeman et al. 1992), which is composed of cell bodies of ascending olfactory projection neurons (Schmidt and Harzsch 1999). Lipofuscin has proven to be especially dense in this area in decapod crustaceans (Sheehy 1989, 1990b, Sheehy et al. 1995, 1998). In amphipods, we identified regions of high lipofuscin density, so far not described in the literature, and afterwards used them for analysis. In *Euphausia superba*, the entire brains were scanned for lipofuscin. Six approx. equidistant sections of the investigated brain areas were selected for lipofuscin analysis. Digital images of 1024x1024 pixels resolution (250x250 μm frame area) were recorded applying Kalman averaging of 4 images each to reduce noise. Photomultiplier intensity, laser power and offset were adjusted whenever necessary.

Lipofuscin quantification. Image analysis was carried out using „Image“ software (National Institute of Health). Autofluorescent lipofuscin granules were discriminated using manual greyscale thresholding. The total area fraction 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 analysed tissue, multiplied by 100. Finally, the geometric average area fraction over all analysed sections per specimen was computed (which - in line with stereological convention – corresponds to volume fraction in % lipofuscin).

Histochemistry. The characteristic lipophilia of lipofuscin was confirmed in selected sections of each species by staining with Sudan Black. The resin sections were rehydrated in graded ethanols (95%, 90%, 80%, 70%) for 2 minutes each. They were then stained by immersion in a saturated solution of filtered Sudan B in 70% ethanol for at least 30 min (modified after Romeis 1968 and Sheehy and Wickins 1994). After rinsing excess stain with ethanol and water, the sections were dried on a heating table for 5 min. The same sections which had been recorded for lipofuscin autofluorescence were recorded digitally for Sudan B staining. Again, no cover glass was applied.

Results

Morphological lipofuscin was found in 94 of 100 individuals and in all species (Table 2). Granules were detected in considerable amounts in 5 of the 10 investigated species and lipofuscin concentrations ranged from < 0.01 to 1 % lipofuscin area fraction (excluding *Waldeckia obesa* which cannot be directly compared, see below). Overall, the two scavenging amphipod species *Eurythenes gryllus* and *W. obesa* revealed the most conspicuous and largest granules with the most intense fluorescence. Among the decapod species, comparatively high individual concentrations were found in *Notocrangon antarcticus, Chorismus antarcticus* and *Sclerocrangon ferox* (max. 0.2 % area fraction). Lipofuscin was not conspicuous, i.e. only single small granules were discriminated, in the amphipod *Uristes* sp., in the decapods *Pandalus borealis, Sabinea septemcarinata* and *Nematocarcinus lanceopes* and in the euphausiid *Euphausia superba*. No general difference was observed between Arctic and Antarctic species.

The characteristics of lipofuscin identified in the investigated species are summarized in Table 3 and examples are shown in Fig. 4. In the investigated decapod species, the autofluorescent, roundish to irregularly shaped granules of predominantly 1-5 µm in size were observed in the posterior lateral somacluster of the olfactory lobe (Fig. 1) as known from other decapod species. In amphipods, lipofuscin granules of comparable shape and average size but of higher maximum size, probably due to aggregating, were associated with the anterior inferior lateral and medial somaclusters (and associated bridge) and the anterior superior lateral and medial somaclusters (nomenclature after MacPherson and Steele 1980, Fig. 1). In *Eurythenes gryllus*, lipofuscin granules concentrated in dense aggregations in which single granules seemed to merge. Those aggregations were more or less evenly distributed over the somaclusters. Granules were also found in neuropils and nervecords though in less dense aggregates. In *Waldeckia obesa*, however, lipofuscin concentrated in the transition zone between the somaclusters and the associated neuropils and was not found in the clusters themselves. For analysis, a different portion of the tissue was therefore selected in this species. This increased absolute values of concentrations and, thereby, made them incomparable to other species but reduced the standard deviation between sections of one individual. In the euphausiid lipofuscin neither occurred in somaclusters nor in nerve cords or neuropils in considerable amounts.

In lab-reared larvae of *Chorismus antarcticus*, age dependent accumulation of lipofuscin was quantified over the first four months after larval release (Fig. 2). Granules were, however, inconspicuous and comparatively small (1-2 µm in diameter, max. 7 µm). No lipofuscin was found in freshly released larvae, whereas a concentration of up to 0.02 % area fraction (s.d.=0.008% area fraction), an order of magnitude lower than maximum concentrations found in adults, was measured in 4 months old individuals. Within the analysed age range, a linear regression fits the data best.

Among the species with considerable amounts of lipofuscin, small and supposedly young individuals within a species tended to contain less lipofuscin than much larger, heavier and supposedly older ones, as shown for *Waldeckia obesa*, *Notocrangon* *antarcticus* and the protandrous hermaphrodite *Chorismus antarcticus* in Fig. 3. Examples taken from two species are imaged in Fig. 4; an individual of *W. obesa* contained 0.5 % lipofuscin area fraction at 23 mm body length (Fig. 4a) while one at 29 mm body length contained 2.8 % lipofuscin area fraction (Fig. 4b). Larvae of *C. antarcticus* contained hardly any granules (Fig. 4c) whereas lipofuscin area fraction measured up to 0.2 % area fraction in adult *C. antarcticus* (Fig. 4d). Within similar sizes, however, different lipofuscin concentrations were observed. Among the species with negligible amounts of lipofuscin, no such trend was measured. In amphipods, the two larger species contained considerably more pigment than the small species, although it must be noted that the maximum size of *Uristes* sp. is not definitely known as yet. *Nematocarcinus lanceopes,* however, with the largest absolute body size of the investigated decapod species contained considerably lower lipofuscin concentrations than the smaller species *N. antarcticus* and *C. antarcticus.* Highest maximum concentrations within a species were found in female specimens compared to males (Fig. 3).

Discussion

This study confirms the occurrence of morphological lipofuscin in polar crustaceans for the first time. All investigated Arctic and Antarctic species displayed at least some lipofuscin granules. These findings are consistent with previous studies which state the universal occurrence of lipofuscin in neural tissue of invertebrates and vertebrates and the ubiquitous nature of lipid peroxidation processes giving rise to lipofuscin (Strehler et al. 1959, Sheldahl and Tappel 1974, Katz et al. 1984). Lipofuscin granules in this study were conspicuous in 5 of the 10 investigated species with considerable variability in density and fluorescence intensity between species. Unlike the lipofuscin distribution in all decapods investigated so far, lipofuscin in the amphipod *Waldeckia obesa* did not occur within the somaclusters but between somaclusters and neuropils. Up to this point we have no explanation for this phenomenon, however, further investigations on this aspect are currently undertaken. Those investigated specimens without obvious pigment granules do not necessarily lack the pigment, but granules may not have been resolvable with the applied methodology. Although we tried to include specimens close to the known maximum size of the species if available, age pigment concentrations ranged an order of magnitude lower than measured in species from lower latitudes (Sheehy et al. 1994, 1998, Belchier et al. 1998). In the following, factors considered to have an effect on lipofuscin formation are discussed with respect to the applicability of the pigment as an age marker in general, and to their impact on polar species in particular. The relation between age and lipofuscin will be evaluated and conclusions drawn as regards future ageing studies on polar crustaceans.

Lipofuscin has been called a physiological age marker, associated with „subjective" (life)time passing at an individual's or species' pace as opposed to objective time passing at the same pace universally. „Subjective" time is, generally speaking, a function of the metabolic „clock" which in turn depends on genetic as well as environmental parameters such as temperature and alimentation. Formation and accumulation of lipofuscin may, therefore, be affected by spatial and temporal environmental variability (Sheehy et al. 1996). Temperature has been identified as one of the primary factors in this respect as metabolic rate increases with temperature, thus affecting physiological ageing processes producing lipofuscin (Mail et al. 1983, Sheehy 1990b, Sheehy et al. 1994, 1996, O'Donovan and Tully 1996). O'Donovan and Tully (1996), for example, found a significant difference in lipofuscin accumulation of European lobsters kept at 8 °C and 13°C. Hence, temperature variability has to be incorporated into growth models based on lipofuscin analysis in geographical regions of varying thermal regime. This seems particularly important if, for example, two broods occur within a year in different seasons. These findings have three major implications for polar species. (i) The rate of formation and accumulation of lipofuscin in polar crustaceans can be expected to be low compared to lower latitudes, as this study confirms. This may also explain the lack of conspicuous lipofuscin in half of the investigated species. (ii) As temperature is relatively constant in the study areas over the year, effects of temperature variability on lipofuscin accumulation may play a less important role than in lower latitudes, and (iii) in species with a large geographical distribution the effect of temperature limits the transferability of a growth model from one geographical region to the other (unless temperature is included in the model), e.g. from the Weddell Sea to the Antarctic Peninsula.

As a second important factor, food availability and, consequently, caloric intake is linked to metabolism and lipofuscin formation processes. After starvation of individuals of *Waldeckia obesa* for 64 days, Chapelle et al. (1994) measured a decrease of oxygen consumption to 60% which after feeding went straight up again, due to costs for handling and processing of the food. These findings indicate that, on a short time scale, lipofuscin may not accumulate with a continuous rate. On a time scale of years, however, the pigment acts as an integral over the entire life span of an individual, making effects of short term variabililty negligible in long-lived species. Individuals sampled from the same population are moreover submitted to similar environmental conditions and will experience comparable food availability during their entire life spans.

Generally, food availability over the year is lower in the study areas of this investigation than in shelf areas of lower latitudes (summarized in Arntz et al. 1994). This, in combination with low temperatures and, consequently, comparatively low standard metabolism (Chapelle and Peck 1995), is assumed to lead to slowed growth observed in many polar invertebrates (e.g. Brey et al. 1995a, b, Dahm 1996, Bluhm et al. 1998). In the light of high longevity corresponding to slowed ageing processes and low lipofuscin accumulation rates (Nakano et al. 1995), the comparatively low observed amounts of lipofuscin found in this study are not surprising.

Beside environmental variability, genetically determined factors inherent to a species and/or individual such as the activity level or feeding type can potentially affect lipofuscin accumulation. Those parameters should be accounted for when comparing lipofuscin concentrations and accumulation rates between taxa or species. Our data, however, are inconclusive in this respect. *Eurythenes gryllus*, for example, known for its strong swimming ability (Ingram and Hessler 1987, Hargrave et al. 1995), displays high lipofuscin concentrations whereas *Euphausia superba*, also permanently active, lacks conspicuous granules. Looking at feeding types, the scavenging amphipods contain considerably more lipofuscin than the predatory decapods as well as the predominantly herbivorous euphausiid. Obviously, an insufficient number of species has been investigated to discern a clear pattern so that this aspect remains speculative as for now. The observed differences could also partly originate from limits in methodology. Moreover, knowledge is lacking as to possible differences between taxa when regarding metabolic processes leading to lipofuscin generation. The crucial factor explaining the pronounced differences between species thus remains unknown. More knowledge in the field of crustacean brain physiology would facilitate insight in this matter.

There are two possibilities for calibrating lipofuscin concentration against age. (i) A group of individuals of known age covering as much of a species' lifespan as possible can provide a calibration. For obvious logistic reasons this is rarely the case in polar studies, especially wild-grown specimens from mark-recapture experiments are lacking. (ii) A lipofuscin-frequency distribution, analogous to the commonly used size-frequency distributions, can reveal distinct groups representing age classes (Sheehy et al. 1998). In the present study, age dependent lipofuscin accumulation was directly measured in lab-reared *Chorismus antarcticus* larvae over the period of 4 months after larval release which happens about 11 months after the eggs have been attached to the pleopods (Gorny et al. 1993). Lipofuscin concentrations were, as expected, very low and granules were inconspicuous, as also observed by Sheehy (1990a) and Sheehy et al. (1994) in *Cherax quadrinatus* during the initial months. As the number of larvae available was rather low and the period of time covered was short, the observed pigment accumulation should be interpreted with caution and the study repeated with a larger sample and over a longer period of time. As in this study, Sheehy (1990b), O'Donovan and Tully (1996) and Sheehy et al. (1998) observed linear accumulation but argue that the limited age range analysed in relation to total life span of the species in focus could introduce bias, and the data should not simply be extrapolated to total life span. Sheehy (1992) and Sheehy et al. (1994), on the other hand, observed apparently decelerating accumulation with advancing age. Indirect evidence for age dependent accumulation is given by analysing lipofuscin concentration in very small compared to very large specimens of unknown age. The results support the general observation that there is a broad correlation between body size and lipofuscin concentration reflecting age. We could also show, however, that there is considerable variation in pigment concentration within specimens of similar size but possibly of different age. In size frequency-distribution histograms of some of the investigated species (Arntz and Gorny 1991 and data unpubl.) a pile-up in frequencies towards the larger size classes is evident. Slow growth in mature individuals is known to lead to the merging of several age class modes within the same size range. These findings seemingly agree with the observation of Sheehy et al. (1994) that morphometric measures can be less reliable predictors of age than lipofuscin. It should also be noted that the absolute size of a species compared to another species does not necessarily seem to be a predictor of higher or lower lipofuscin concentration. First results obtained on *Waldeckia obesa* indicate that the rate of lipofuscin accumulation (i) is continuous compared to stepwise increase in size due to moulting stages, and (ii) is sufficient to distinguish concentration classes presumably representing age classes as described above.

Our findings are encouraging for the future use of lipofuscin for age determination in those of the investigated species displaying a sufficiently high increase in lipofuscin concentration over their life spans. None of the factors potentially influencing lipofuscin formation are presently considered sufficient to reject the applicability of the method. Stable environmental temperatures and long life spans integrating short term variations could possibly be helpful in lipofuscin analysis of some of the presented species. A study is currently underway to assess population age distribution in the amphipod *Waldeckia obesa* and the decapod *Notocrangon antarcticus* by applying a lipofuscin age index.

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Tables

Table 1 Species investigated in the present study. Depth ranges and feeding types are added from literature if available. 0 Personal observations, 1 Arntz and Gorny (1991), 2 Barnard and Karaman (1991), 3 DeBroyer and Klages (1990), 4 Gorny (1999), 5 Gorny et al. (1992), 6 Heegard (1941), 7 Ingram and Hessler (1983), 8 Kirkwood and Burton (1988), 9 Reid et al. (1999), 10 Wenner (1979), 11 Wienberg (1981).

Species	Taxonomy	Sampling area	Depth range (m)		Feeding type
			min.	max.	
		ARCTIC			
Eurythenes gryllus (Lichtenstein, 1822)	Lysianassidae s.l., Amphipoda	Greenland Sea	0[2]	6500[2]	Scavenger[7]
Uristes sp. Dana, 1849	Lysianassidae s.l., Amphipoda	Greenland Sea	?	5550[0]	Scavenger[0]
Sabinea septemcarinata Sabine, 1821	Crangonidae, Decapoda	Barents Sea	30[6]	300[6]	Predator[0]
Sclerocrangon ferox Sars, 1877	Crangonidae, Decapoda	Barents Sea	100[6]	1000[6]	Predator[0]
Pandalus borealis Krøyer, 1844	Pandalidae, Decapoda	Greenland Sea	150[6]	700[6]	Predator, omnivorous[11]
		ANTARCTIC			
Waldeckia obesa (Chevreux, 1905)	Lysianassidae s.l., Amphipoda	Weddell Sea	0[3]	900[0]	Scavenger[0]
Euphausia superba Dana, 1850	Euphausiidae, Euphausiacea	Weddell Sea		pelagic	Herbivorous filterfeeder/ icescraper[9]
Nematocarcinus lanceopes Bate, 1888	Nematocarcinidae, Decapoda	Weddell Sea	600[1]	2505[4]	Predator, omnivorous[10]
Notocrangon antarcticus (Pfeffer, 1887)	Crangonidae, Decapoda	Weddell Sea	5[8]	1320[4]	Predator, omnivorous[5]
Chorismus antarcticus (Pfeffer, 1887)	Hippolytidae, Decapoda	Weddell Sea	5[8]	915[4]	Predator, omnivorous[5]

Table 2 Lipofuscin concentrations in individuals of 10 polar crustacean species: summary of the survey results. Lipofuscin concentration means and standard deviations of the image analysis of 6 brain sections per specimen are given. Maximum sizes and estimates for maximum ages of the species are added from literature if available. BL = body length (Amphipoda, Euphausiacea), CL = carapace length (Decapoda), f = female, m = male, N = sample size; bold print = conspicuous concentrations of lipofuscin. ** Note that most estimates are based on size-data and should for reasons discussed in the text be interpreted with caution. 0 Personal observations, 1 Arntz and Gorny (1991), 2 Berman et al. (1989), 3 Chapelle (1995), 4 Chapelle, pers. comm., 5 Gorny et al. (1993), 6 Ingram and Hessler (1983), 7 Ingram and Hessler, *age at maturity (1987), 8 Marschall (1988), 9 Teigmark (1983), 10 Weslawski (1987).

Species	Depth of sampling (m)	N	Size range analysed (mm CL/BL)		Max. size in study area (mm CL/BL)	Wet weight range analysed (g)		Lipofuscin concentration range (% area fraction) ± standard deviations		Estimated max. age of species (yrs)**
								min.	max.	
ARCTIC										
Eurythenes gryllus	2500	3	33	50	140[6]	0.9	3.2	0.17±0.04	**1.04**±0.21	9(f)/4(m)*[7]
Uristes sp.	5550	2	5	8	14[0]	0.005	0.013	<0.01	0.01±<0.01	?
Sabinea septemcarinata	160	6	8.8	16.4	BL80[10] CL18.0[0]	0.8	4.0	0	0.02±<0.01	4-6[10]
Sclerocrangon ferox	160-300	4	12.8	21.7	29.9[0]	3.3	11.4	<0.01	**0.07**±0.03	4-6[10]
Pandalus borealis	300	6	8.1	22.4	25[9]	0.5	8.2	0	0.01±<0.01	6[8]
ANTARCTIC										
Waldeckia obesa	400-800	32	19	29	33[3]	0.21	0.45	0.44±0.07	**2.79**±0.61	6(-9)[4]
Euphausia superba	400-1400	6	39	41	70[8]	0.7	1.0	0	<0.01	6[2]
Nematocarcinus lanceopes	1680	7	22.1	29.7	35.0[1]	4.5	11.1	<0.01	0.01±<0.01	?
Notocrangon antarcticus	245-440	20	9.5	24.4	27.1[1]	0.8	12.9	<0.01	**0.21**±0.04	?
Chorismus antarcticus	245-440	14	1.8	19.2	21.6[1]	<0.1	5.8	<0.01	**0.21**±0.05	7-10[5]

Table 3 Characteristics of morphological lipofuscin in selected Arctic and Antarctic decapod and amphipod species.

Property	**Lipofuscin characteristics**
Granules shape	± round with irregular outline (confirmed by optical sectioning with confocal microscope)
Granules size range	< 1µm to 15/30 (Decapoda/Amphipoda, probably several granules merged), predominantly 1-5 µm
Colour of fluorescence	Yellow to off-white (under 365 or 470 nm excitation, Leica filter sets I3 and N2.1)
Extractability with alcohol	Resistant
Lipophilia staining (Sudan B)	Positive with variable affinity to stain between species and specimens
Temperature resistance	at least -30 to +100 °C
Location	Decapoda: ± equally distributed in somaclusters (esp. those of olfactory lobe); Amphipoda: associated with anterior inferior lateral and medial somaclusters and anterior superior lateral and medial somaclusters

Figures

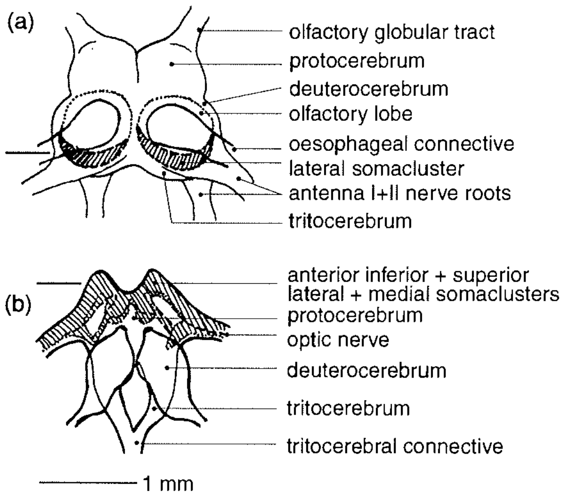

Fig. 1 Schematic views of the brains of a medium sized (a) caridean decapod, and (b) lysianassoid amphipod. Hatchings mark the tissue areas used for lipofuscin quantification. Horizontal lines indicate the plains of sectioning.

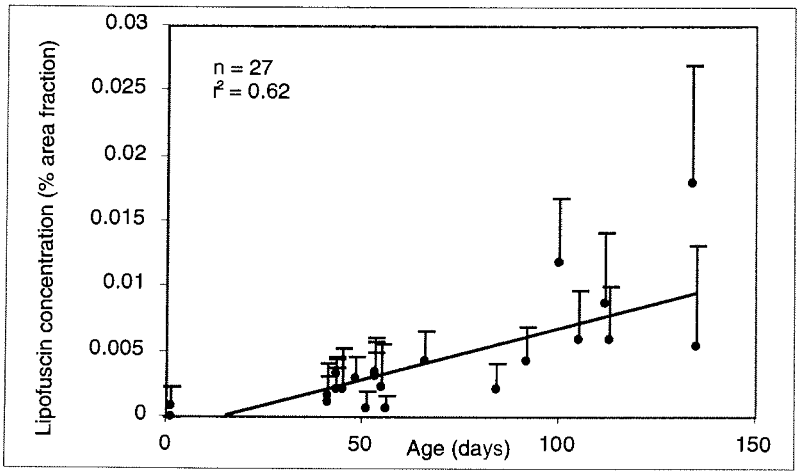

Fig. 2 Relationship between age and lipofuscin in the lateral somacluster of the olfactory lobe of *Chorismus antarcticus* larvae. Means and standard deviations of the image analysis of 6 brain sections per specimen are given.

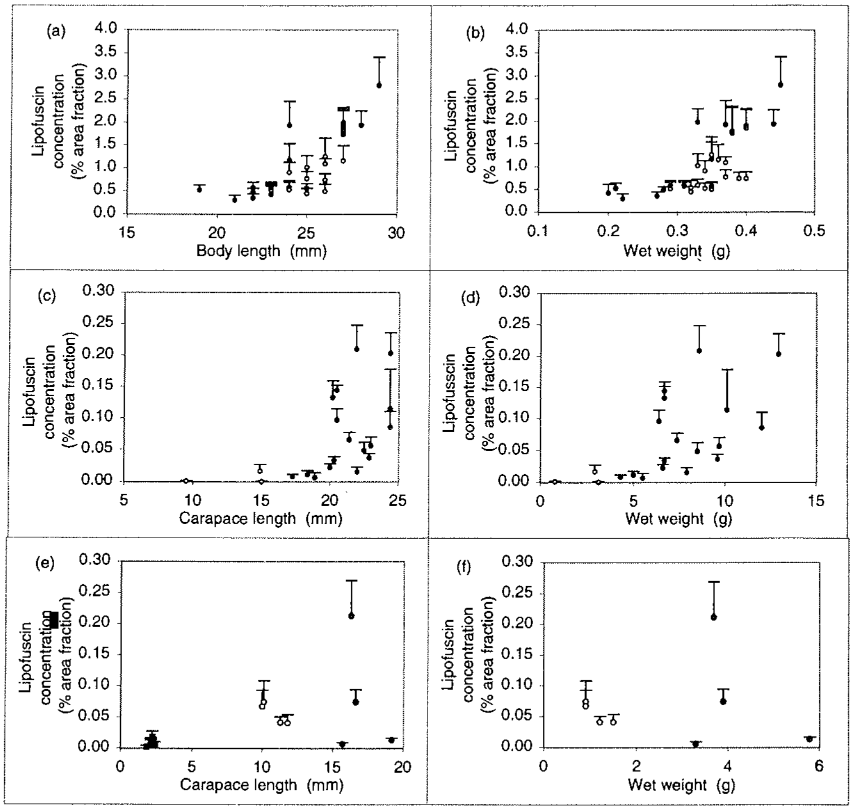

Fig. 3 Relationship between body size respectively body weight and lipofuscin concentration in (a), (b) the amphipod *Waldeckia obesa* (n=32), (c), (d) the decapod *Notocrangon antarcticus* (n=20), and (e), (f) the decapod *Chorismus antarcticus* (n=14). Dots = females, circles = males, squares = larvae. Means and standard deviations of the image analysis of 6 brain sections per specimen are given. Larvae of *C. antarcticus* were not weighed to avoid damage.

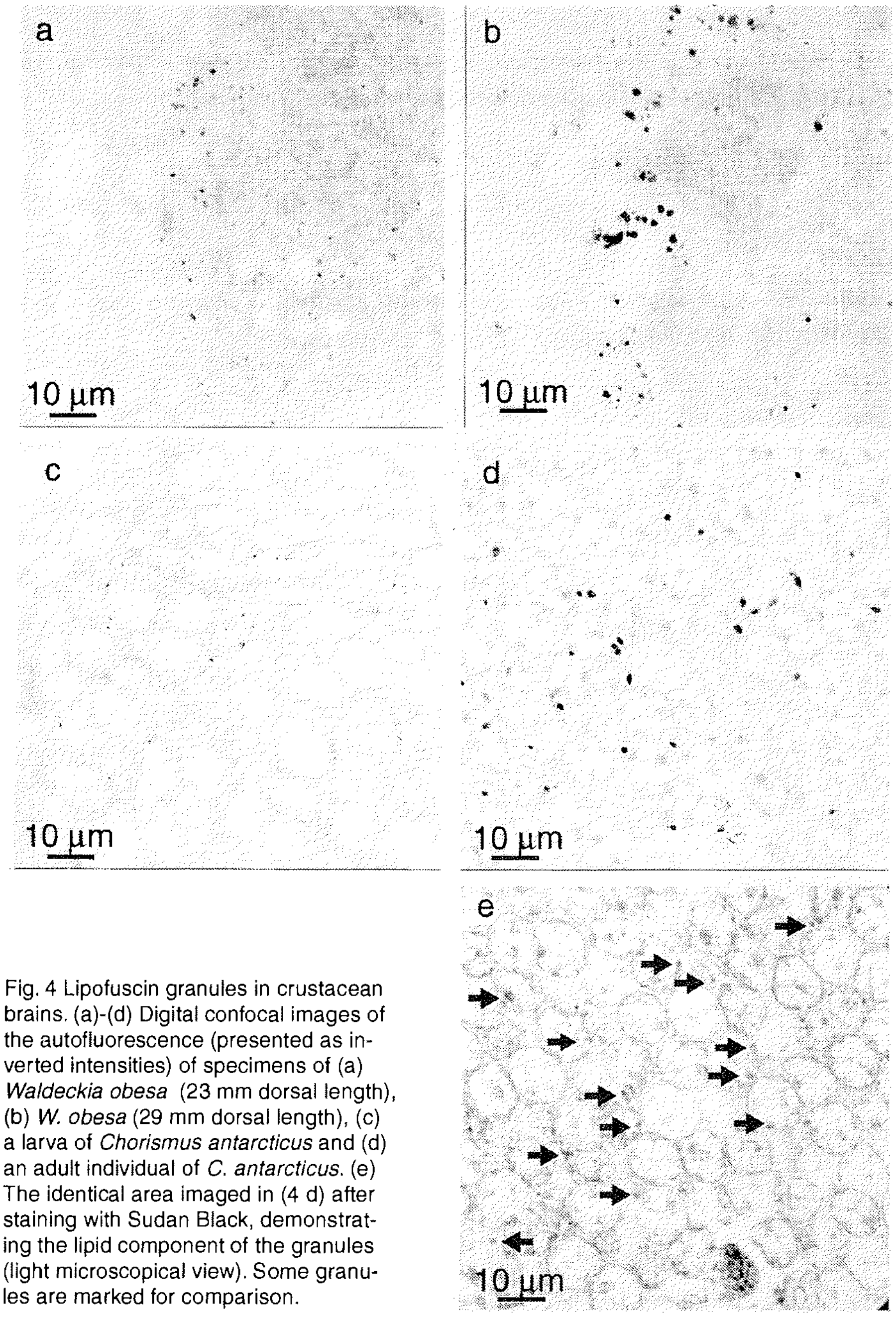

Fig. 4 Lipofuscin granules in crustacean brains. (a)-(d) Digital confocal images of the autofluorescence (presented as inverted intensities) of specimens of (a) *Waldeckia obesa* (23 mm dorsal length), (b) *W. obesa* (29 mm dorsal length), (c) a larva of *Chorismus antarcticus* and (d) an adult individual of *C. antarcticus*. (e) The identical area imaged in (4 d) after staining with Sudan Black, demonstrating the lipid component of the granules (light microscopical view). Some granules are marked for comparison.

Publication II

Age determination in the Antarctic shrimp Notocrangon antarcticus (Pfeffer, 1887) (Crustacea: Decapoda) using the autofluorescent pigment lipofuscin

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Marine Biology, in press

Abstract

Determination of basic population parameters in long-lived crustacea is hindered by the lack of appropriate methods for age determination. This study uses the pigment lipofuscin as an age marker in the common Antarctic decapod Notocrangon antarcticus 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 analysed. 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 per year, 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_∞ and k from the von Bertalanffy growth function were 22.3 mm CL and 0.79 for females, respectively, and 16.9 mm CL and 0.64 for males, respectively. Mortality and P/B ratio, estimated from catch curves, amounted to 0.44 per year in females and 0.92 per year 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 compared to 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 last 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 a minority, 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 number (Yaldwin 1965, Kirkwood 1984), can reach considerable abundances. Notocrangon antarcticus (Pfeffer, 1887), the most common benthic circumantarctic shrimp species, was reported to occur in maximum densities of 73 individuals 100 m^{-2} in water depths of 200 to 600 m (Gutt et al. 1991). Consequently, shrimps can have a remarkable 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 an important tool in studying growth and mortality in a population, are difficult to obtain in 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 (i) keeping individuals in captivity including study of growth increment associated with moultings (Plaut and Fishelson 1991, Hill 1992), (ii) recapture of tagged specimens (Campbell 1983, Taylor and Hoenig 1990, Fitz and Wiegert 1991, Somers and Kirkwood 1991), and (iii) 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 error-prone due to the artificial conditions (e.g. Lagardère 1982), and studies are, moreover, time-consuming in long-lived species. Although modern tags are retained through moulting and probably do not inhibit growth (Fitz and Wiegert 1991, Bannister et al. 1994), tagging and recapture is for logistical reasons unfeasible in polar deep-water regions. 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 realise 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 Notocrangon 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 were caught in water depths of 245 to 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 0.1 mm below 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 whereas they are equally long in females (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), 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 analysed 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 x 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. 1995b, 1998). Eight approximately equidistant sections of the entire cell mass were selected for lipofuscin analysis. Digital images of 1024 by 1024 pixels resolution (250 by 250 µm frame area) were recorded applying Kalman averaging of 4 images each to reduce noise.

Lipofuscin quantification. Image analysis was carried out using "Image" software (National Institute of Health). The outline of the cellmass area analysed was traced manually and the autofluorescent lipofuscin granules therein were discriminated using manual greyscale 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 analysed tissue, multiplied by 100. Each image was analysed threefold 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 volume fraction in % 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 in a way that the main part 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 where 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 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 one year, referred to as relative age (Pauly 1984). For this parameter, we use the dimension "years+" (i) to imply that exact age depends on what time of the year the sample was taken relative to the hatching period, (ii) to account for natural spread of age in modes, and (iii) to account for the fact that detectable lipofuscin accumulation may start at some point after larval release. 1+ therefore means individuals between approximately one and two 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_∞ 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_∞. 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)

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

and Gompertz growth curves

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

(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 of benthic invertebrates:

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

(A_{max} = maximum age (years +), M_{max} = maximum body mass in (kJ), T = temperature (K)). For this estimate, wet body mass in g was converted to body mass in kJ 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 of 935 specimens of Notocrangon 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 CL in juveniles. The size-body mass (WM) relation was $\log(gWM) = 2.89\bullet\log(mmCL)-2.98$ ($r^2=0.97$, $p<0.001$) in females and $\log(gWM) = 2.97\bullet\log(mmCL)-3.07$ ($r^2=0.97$, $p<0.001$) 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.

135 females, 44 males and 10 juveniles of Notocrangon antarcticus were analysed 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 µm diameter (Fig. 3). Lipofuscin concentrations varied between < 0.001 and 0.216 % (± s.d.=0.065) area fraction (AF) (females), 0.056 % AF (± s.d.=0.012; males) and 0.002 % AF (± s.d.=0.002; juveniles). S.D. between the eight analysed sections of one individual was 25% on average in concentrations >0.015 % AF (s.d. 100 % in concentrations ≤ 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 of those while males were present in modes I to 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 $L=0.021 \bullet A+0.022$ ($r^2=0.98$, females) and $L=0.017 \bullet A+0.014$ ($r^2=0.94$, males), corresponding to an annual lipofuscin accumulation rate of 0.021 (females) and 0.017 (males) % AF. 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 (Figs. 4b, c), especially in females ≥ 18 mm CL and males ≥ 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. 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 per year in females and 0.63 per year 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 firstly adding information for zoea II-stage larvae which are about one year of age at an average CL of 2.5 mm (Bruns 1992, Gorny et al 1992). The 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 3+ years. Remaining modes are treated as sequential homogeneous age classes. The underlying assumption is that mode I does not represent one year old specimens if detectable lipofuscin accumulation does not start right after larval release (Sheehy 1990a, c, Nakano et al. 1993 Sheehy et al. 1995b). The fit of the corrected VBGF growth curves resulted in

$CL_t = 22.34\ (1-e^{-0.79(t+0.76)})$, $r^2 = 0.72$ (females, Fig. 5a)
(standard errors: CL_∞=0.38, k=0.07, t_0=0.08)
$CL_t = 16.93\ (1-e^{-0.64(t+1.03)})$, $r^2 = 0.84$ (males, Fig. 5b)
(standard errors: CL_∞=0.74, k=0.09, t_0=0.12).
The Gompertz growth curves estimated
$CL_t = 21.46\ (e^{-e^{-1.62(t-0.04)}})$, $r^2 = 0.78$ (females, Fig. 5a)
(standard errors: CL_∞=0.25, k=0.15, t_0=0.05)
$CL_t = 15.74\ (e^{-e^{-1.22(t+0.23)}})$, $r^2 = 0.87$ (males, Fig. 5b)
(standard errors: CL_∞=0.44, k=0.16, t_0=0.07).

Mortality. Mortality, estimated from the catch curve, amounted to 0.44 per year for female shrimps and 0.92 per year 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 estimated to range between 0.33 and 0.41 per year in females (A_{max} = 8 and 10 a, M_{max} = 42,74 kJ) and between 0.57 and 0.85 per year in males (A_{max} = 4 and 6 a, M_{max} = 15.24 kJ).

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

Discussion and conclusions

The size frequency distribution of Notocrangon 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, pers. com.), including crustaceans (Phillips 1990, Brewis and Bowler 1982, Gorny et al. 1992, Bannister et al.1994, Sheehy et al. 1998). Declining 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), Jerí (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 (i) a non-random distribution, and (ii) 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. (i) the high separation index, (ii) significant chi^2, (iii) decreasing number of individuals with increasing lipofuscin concentration, and (iv) mode means lying 2.5 to 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 (O'Donovan and Tully 1996, Sheehy et al. 1995a), 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 predominantly long life spans integrating short term variations are more likely to favour 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 Notocrangon antarcticus. Variation between sections of the same individual could be reduced by higher sample size and increased number of analysed 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 so far quantifying lipofuscin as age marker in crustaceans, 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 the 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 per year (0.021 % AF per year in females, 0.017 % AF per year in males) lies well below rates measured for other crustaceans, which range from 0.07% AF per year in the long-lived European lobster (Sheehy et al. 1996) to 2.0% AF per year in the relatively short-lived freshwater crayfish Cherax quadricarinatus (Sheehy et al. 1994). These findings reflect that the rate of physiological ageing may be inversely correlated with longevity (Sheehy et al. 1995a). The main governing factor of physiological processes and metabolic rates is temperature (Parry 1983, Alongi 1990). Obviously, lipofuscin accumulation rate also depends on temperature which in our study is below 0 °C, and 8 and 23 °C in the works on 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 and 7), so that the parameter values of the growth functions should be interpreted with caution. Estimates of k of the VBGF (0.79 in females, 0.64 in males) lie in the upper range of what has been published for other deep-water carideans (k ≈ 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 ≈ 0.7 –1.6; cited in Jerí 1999 and Pauly et al. 1984). As reported for Crangon crangon (Oh et al. 1999) and several penaeids (Garcia and Le Rest 1981, Baelde 1994), males reach a lower CL_∞ and grow slightly slower than females, while the opposite trend was observed in other penaeid shrimps (compiled in Jerí 1999). Growth performance of Notocrangon antarcticus as measured by the Phi-prime index Φ log (k) + 2•log (CL_∞) (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, Roá and Ernst 1996, Santana et al. 1996, Oh et al. 1999) and penaeids (2.2-3.5; Pauly et al. 1984, Jerí 1991, Baelde 1994, Jerí 1999).

Maximum life span of Notocrangon antarcticus was estimated as at least eight to ten years for females and four to six 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 ≥ 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 one year before eggs are attached to the pleopods and hatch the following year (Gorny et al. 1992). Most size and body mass increment happens 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 at half the females' life span. Life span differences between sexes may explain the sex ratio observed in Arntz and Gorny (1991) and in this study, although migration and catch effects cannot be excluded. N. antarcticus reach high age 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 to 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 to 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 ageing 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 seems also 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 in 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 Notocrangon 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 faeces 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,

(i) modal progression analysis of lipofuscin concentration frequencies allows estimates of population parameters which in Notocrangon antarcticus are inaccessible with traditional methods;

(ii) 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;

(iii) 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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Figures

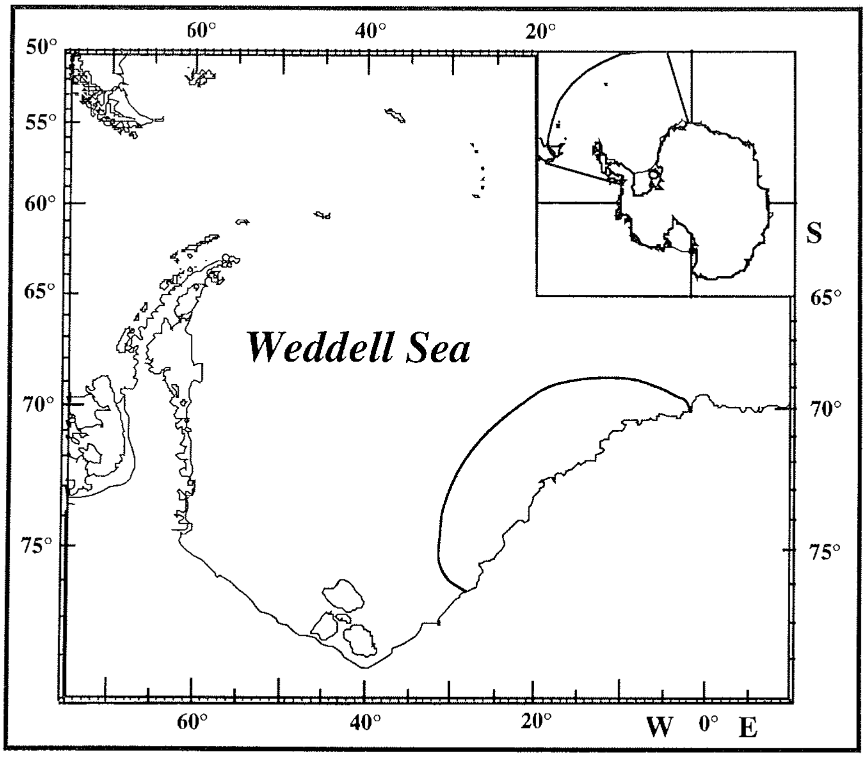
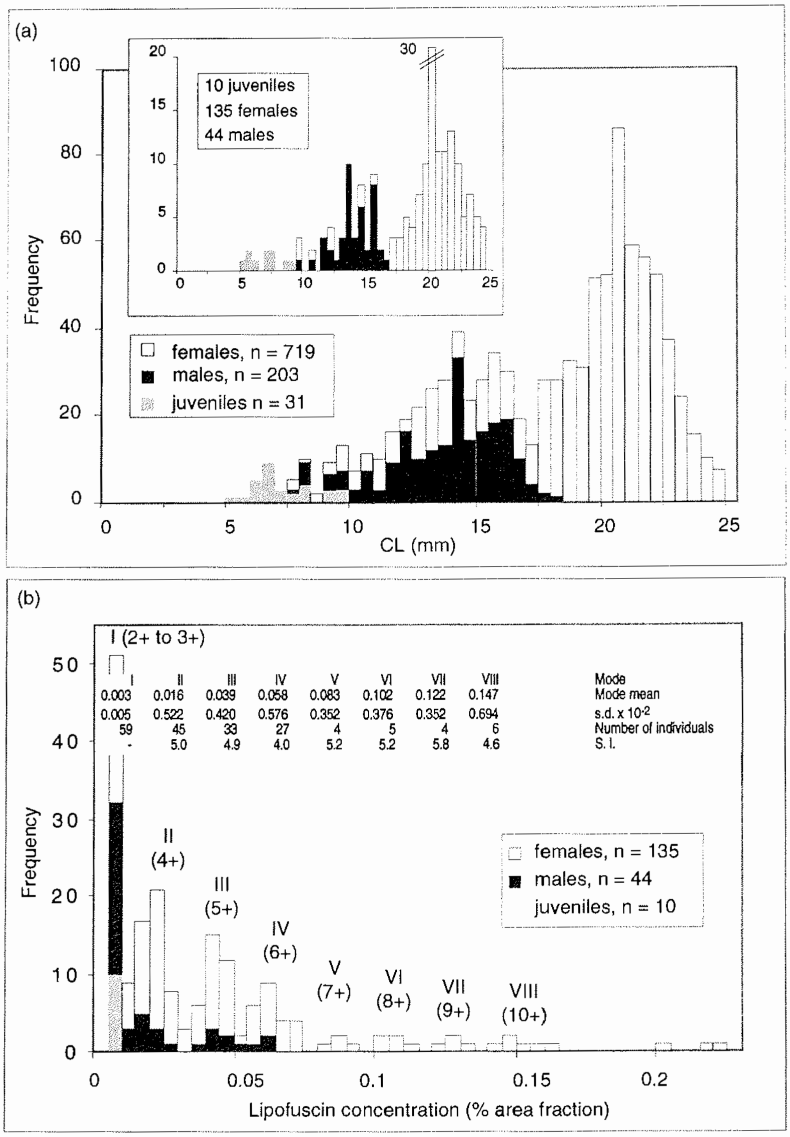


Fig. 1 Study area (shaded) in the eastern Weddell Sea.



I	II	III	IV	V	VI	VII	VIII	Mode
0.003	0.016	0.039	0.058	0.083	0.102	0.122	0.147	Mode mean
0.005	0.522	0.420	0.576	0.352	0.376	0.352	0.694	s.d. x 10^{-2}
59	45	33	27	4	5	4	6	Number of individuals
-	5.0	4.9	4.0	5.2	5.2	5.8	4.6	S. I.

Fig. 2 Notocrangon antarcticus from the eastern Weddell Sea. (a) Length-frequency distributions of total catch and lipofuscin-analysed specimens (inlay), (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 + (see text).

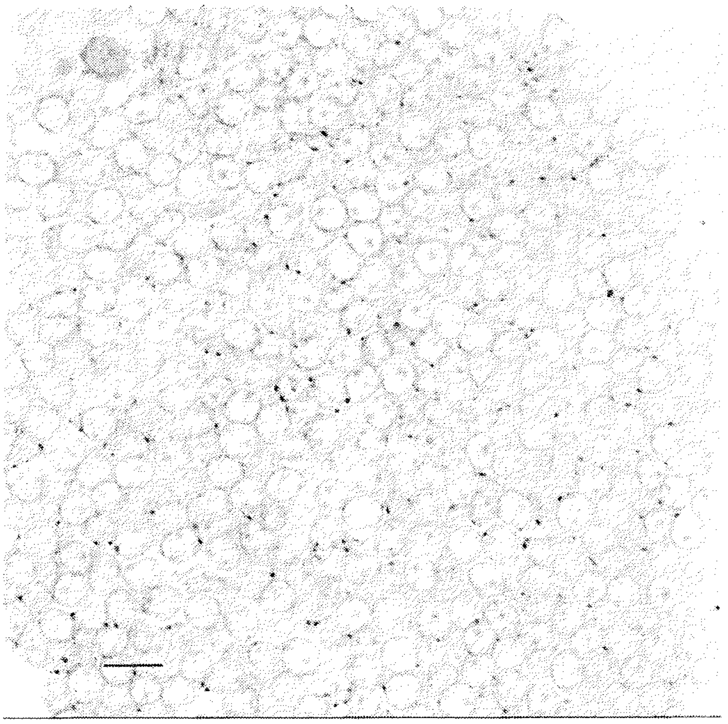


Fig. 3 Notocrangon antarcticus. Fluorescent lipofuscin granules in the olfactory lobe somacluster in a presumably 7+ year old female shrimp. Excitation 488 nm, emmission ≥ 515 nm, digital confocal inverted image. Scalebar = 20 µm.

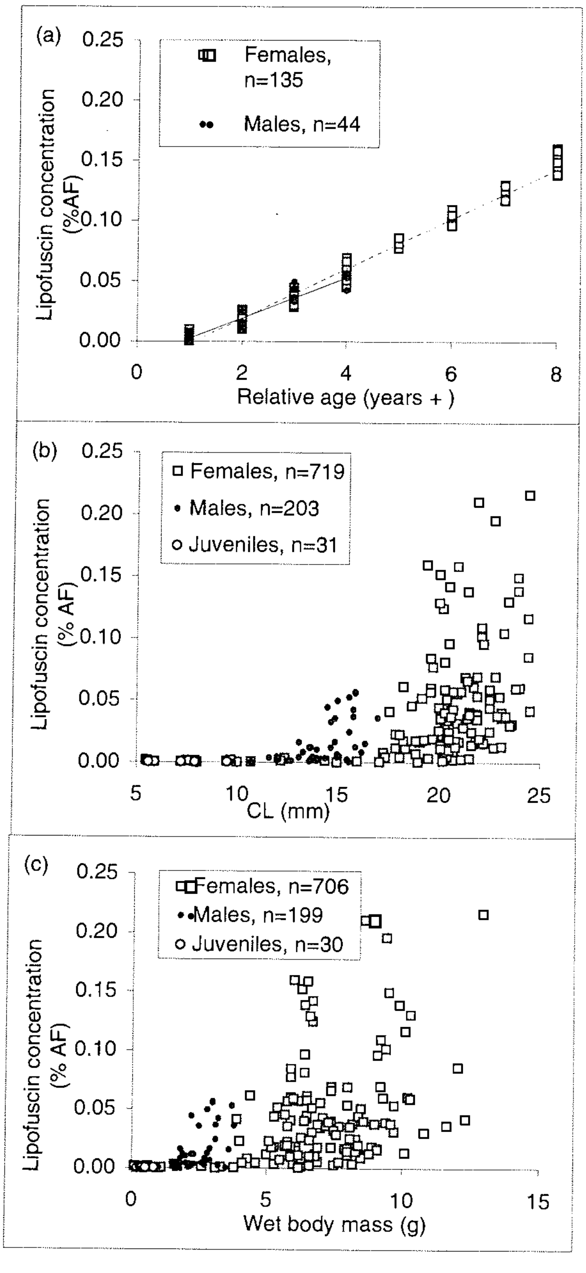


Fig. 4 Notocrangon antarcticus from the eastern Weddell Sea. Lipofuscin concentration in relation to (a) lipofuscin-based estimated age (L=0.021•A+0.022, r^2=0.98, females; L=0.017•A+0.014, r^2=0.94, males; L=lipofuscin concenctration, A=age), (b) body size, and (c) wet body mass.

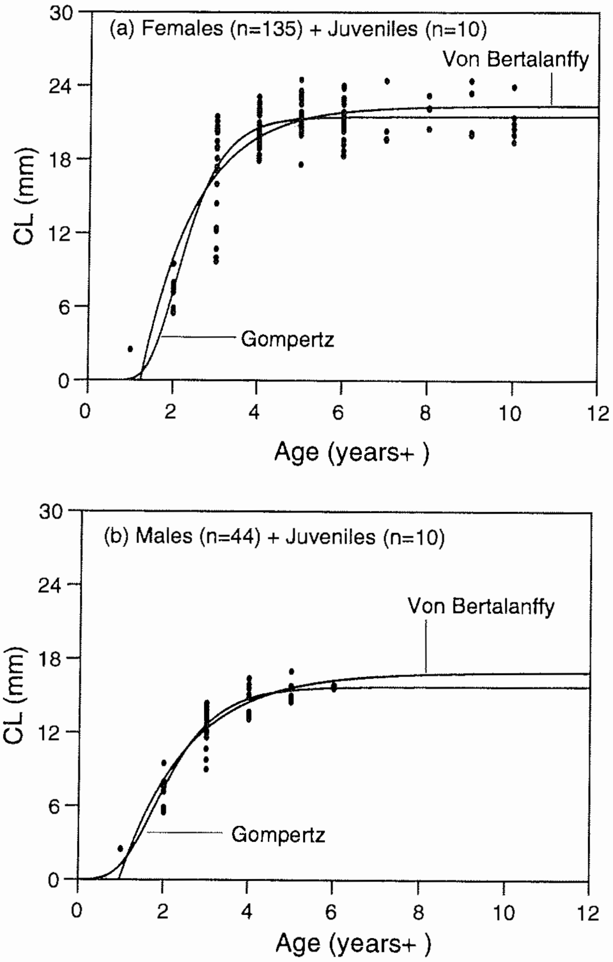


Fig. 5 Notocrangon antarcticus from the eastern Weddell Sea. Growth curves fitted to size at lipofuscin-estimated age data in (a) females and (b) males. Von Bertalanffy: CL_∞ = 22.34 mm, k = 0.79 per year, t_0 = -0.76 years, r^2 = 0.72 (females), CL_∞ = 16.93 mm, k = 0.64 per year, t_0 = -1.03 years,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

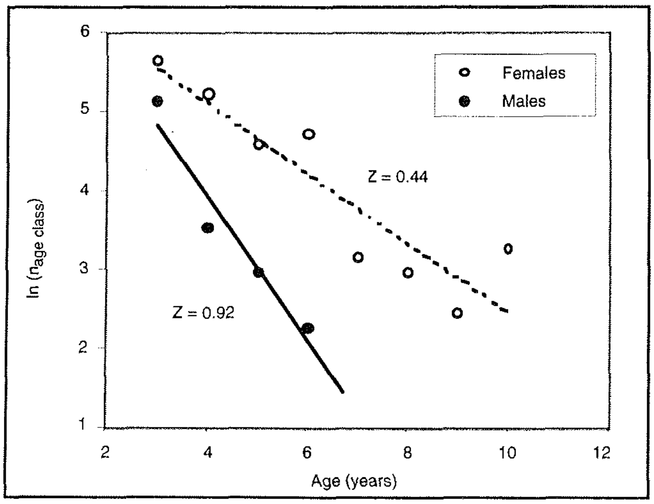


Fig. 6 Catch curve of Notocrangon antarcticus from the eastern Weddell Sea. Females: ln ($n_{age\ class}$) = 5.97-0.442•age, r^2=0.83; males: ln ($n_{age\ class}$) = 5.76-0.918•age, r^2=0.94. The number of individuals per age class ($n_{age\ class}$) was adjusted from lipofuscin-analysed subsample to

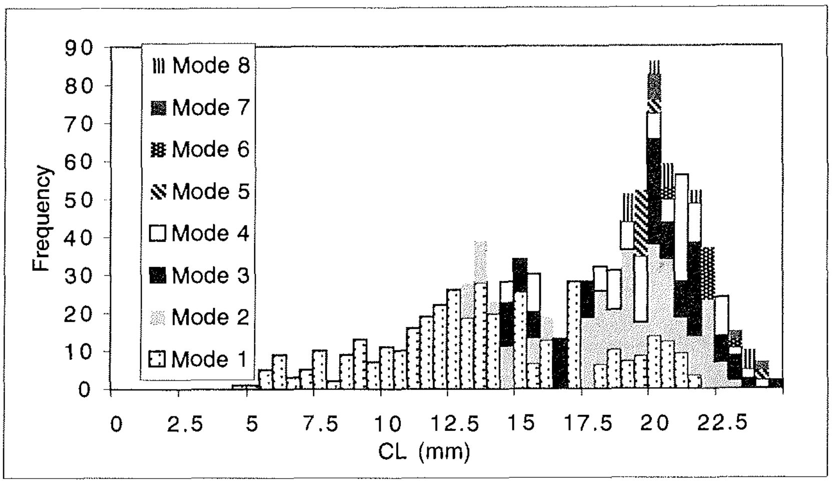


Fig. 7 Notocrangon antarcticus from the eastern Weddell Sea. Distribution of modes derived from the modal progression analysis of the lipofuscin concentration frequency histogram in the length-frequency distribution histogram. The number of individuals per age group was adjusted from lipofuscin-analysed subsample to total sample size (see text). $Frequency_{total\ bar} = n_{mode1} + n_{mode2} + \ldots + n_{mode8}$

Publication III

The autofluorescent age pigment lipofuscin: key to age, growth and productivity of the Antarctic amphipod *Waldeckia obesa* (Chevreux, 1905)

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Abstract

Peracarid crustaceans are among the most important taxa in terms of biodiversity and carbon-flow within the Weddell Sea benthos, but very few data on their age, growth and productivity are available. This study uses the pigment lipofuscin as an age marker in the scavenging amphipod *Waldeckia obesa* (Chevreux, 1905) from the eastern Weddell Sea. Resin brain sections of 159 trap-caught specimens (1.2 to 7.7 mm coxal plate length L_{cox} equal to 5 to 31 mm total length) were recorded digitally by confocal microscopy, and images were analysed. A modal progression analysis of the lipofuscin concentration frequency distribution revealed 5 regularly-spaced modes presumed to reflect consecutive annual age classes. Single females outside the range of mode V occurred, indicating maximum age of up to 8 years in females. No regular modes were obvious from the comparable length-frequency distribution of 386 individuals. Average yearly pigment accumulation was linear, and accumulation rates did not differ between sexes. The estimates of the growth parameters L_∞ and k of the von Bertalanffy growth function were 7.47 mm L_{cox} and 0.50 per year in females, respectively, and 6.92 mm L_{cox} and 0.60 per year in males, respectively. Mortality, estimated from catch curves, amounted to 0.27 per year in females and 0.43 per year in males. P/B ratio, calculated from the mass specific growth rate method, was 0.38 per year for the pooled population (0.25 per year in females, 0.31 per year in males, 2.26 per year in juveniles). The results are discussed with regard to advantages and drawbacks of the methodology, and are compared with results from warmer water habitats.

Keywords: age determination, Amphipoda, Antarctic, lipofuscin, population dynamics

Introduction

Within the Antarctic benthos, crustaceans and especially peracarids are among the most important taxa in terms of biodiversity (Arntz et al. 1997, De Broyer and Jazdzewski 1996), and carbon-flow (Jarre-Teichmann et al. 1997). A faunistic inventory of many peracarid taxa has been completed recently (e.g. Amphipoda: De Broyer and Jazdzewski 1993, 1996; Mysidacea: Brandt et al. 1998; Cumacea: Mühlenhardt-Siegel 1999), listing > 500 Antarctic amphipod species, > 70% of which are endemic. Data on life cycles and population dynamics, however, are still scarce. We contribute to filling this gap by investigating population dynamics of the circum-Antarctic lysianassid amphipod *Waldeckia obesa* (Cheveux, 1905). This species occurs regularly at relatively shallow sites, e.g. on King George Island (15-90 m), Antarctic Peninsula (Arnaud et al. 1986), and down to 1030 m in the eastern Weddell Sea (Klages 1991). Lysianassids, forming the largest amphipod family with more than 500 species belonging to 112 genera worldwide (Barnard and Karaman 1991), play an important role as one of the most abundant and widespread macro-invertebrate scavenger groups in the world ocean (Slattery and Oliver 1986), degrading and distributing organic matter at the benthic-pelagic interface (Christiansen et al. 1990). They occur primarily at water temperatures below 10 °C, and are common not only in the deepest ocean basins (Thurston 1979, Hessler et al. 1978, Smith and Baldwin 1982, Ingram and Hessler 1983), but also in shallow water at high latitudes (Vader 1972, Nagata 1986). The high number usually caught using baited traps (Ingram and Hessler 1987, Christiansen 1996) and their remarkable food consumption rates (Hargrave 1985, Klages 1991, Hargrave et al. 1995) suggest that they play an important role in benthic food webs.

A vast range of shallow-water amphipod species from lower latitudes have been investigated with regard to their life cycles and productivity (reviewed in Sainte-Marie 1991). The conspicuous scarcity of comparable data on high latitude species is due partly to the lack of adequate ageing techniques. The remote location and inaccessibility of high latitudes as well as a tendency for slow growth and high longevity of many polar invertebrates often make conventional methods unfeasible (France et al. 1991, Bannister et al. 1994, Bluhm et al., in press). The lipofuscin method recently applied to decapods by Sheehy (1989, 1990a-c), however, overcomes some of those shortcomings. It makes use of the apparently linear accumulation of the age pigment in post-mitotic eukaryotic cells throughout their life span, caused by free radical induced peroxidation processes (Sheldahl and Tappel 1974, Porta 1991, reviewed in Terman and Brunk 1998). The quantity of lipofuscin in certain brain areas has been shown to be a better predictor of age than size in long-lived decapods (Sheehy 1989, 1990a, b, 1992, Sheehy et al. 1994, Belchier et al. 1998). Separating modes derived from concentration frequencies of morphological lipofuscin, presumably representing age classes, has so far only been attempted in decapod crustaceans (Sheehy et al. 1998, Bluhm and Brey, in press). For the first time, we apply this approach to an amphipod species to estimate maximum longevity, age distribution, growth parameters, mortality and productivity.

Materials and methods

Sampling

Samples were obtained 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) at water depths of 400 to 800 m. Average annual temperature close to the sea floor 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). Amphipods were caught with baited traps, which were deployed for approximately 48 hours and retrieved using acoustic releasers. Mesh size was 500 µm and the entrance openings measured 2 or 5 cm diameter; for details see Mekhanikova et al. (submitted). Amphipods were sorted in the coldroom (0 °C) and preserved in 4% buffered formalin until embedding in spring 1999.

Transmission electron microscopy (TEM)

Specimens for TEM were fixed in 2.5 % glutaraldehyde in 0.1 M cacodylate buffer (pH 7.3) at 4 °C and postfixed in 0.2 M cacodylate buffered 1 % osmium tetroxide for 2 h.

Brains were dehydrated in ascending concentrations of acetone and embedded in Spurr's resin (8 h at 70 °C). Ultra-thin sections (60 nm) were stained in uranyl acetate (methanol) and Reynold's lead citrate using standard procedures and were studied with a ZEISS EM 902 TEM.

Sample preparation for fluorescence confocal microscopy

Body length (L) of straightened formalin-preserved specimens was measured (i) as total L (L_t) from the tip of the rostrum to the end of the telson along the dorsal mid-line to the nearest mm below, and (ii) as diagonal (anterior ventral to posterior ventral) length of the fourth coxal plate (L_{cox}) according to Chapelle (1995), to the nearest 0.1 mm below. For body size, this measure has proven to be more precise than L_t (Chapelle 1995). Sex was determined using the second antennae, which are longer in males (> 18 articles) than in females ($\leq$ 18 articles), as well as the presence of oostegites in females and penial papillae in males (Walker 1907). Specimens without oostegites or penial papillae and fewer than 18 articles were classified as juveniles. Brains were prepared for lipofuscin measurement as described for various decapod species by Sheehy (1989, 1990a), Sheehy and Wickins (1994) and Bluhm et al. (in press). After the brains were dissected, unstained, serial, horizontal 6 µm resin sections were prepared following standard embedding procedures, but excluding mounting medium.

Fluorescence confocal microscopy

Sections were analysed with a Leica TCS NT confocal microscope at 488 nm excitation wavelength and a 40 x oil immersion lens (numerical aperture 1.25, no zoom). In contrast to decapod brains, high density regions of lipofuscin in *W. obesa* were associated with the transition zones of anterior inferior lateral and medial somaclusters (and associated bridge) as well as the anterior superior lateral and medial somaclusters (nomenclature after MacPherson and Steele 1980) and the respective neuropils (Fig. 2). Eight to ten approximately equidistant sections of the described areas were selected for lipofuscin analysis in each individual. Absolute values of concentrations are higher and not comparable with those published for decapod species, but this procedure reduced the standard deviation between sections of the same individual. Digital images of 1024 by 1024 pixels resolution (250 by 250 µm frame area) were recorded applying Kalman averaging of 4 images each to reduce noise.

Lipofuscin quantification

Image analysis was carried out using "Image" software (National Institute of Health). The outline of the selected area was traced manually and the autofluorescent lipofuscin granules therein were discriminated using manual greyscale 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 analysed tissue and multiplying by 100. The geometric average AF over all sections examined for each individual was calculated (which - in line with stereological convention – corresponds to volume fraction in % 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 (L_{cox}) of 386 specimens using class intervals of 0.2 mm. A lipofuscin concentration-frequency distribution (LCFD) histogram was constructed from the pigment concentration analysis of a subsample (159 specimens). For efficient comparison with the LFD, class intervals in the LCFD histogram were chosen in a way so that the main part 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 (Gayanilo et al. 1996, FAO-ICLARM stock assessment tools). Within this program, Bhattacharya's method (after Bhattacharya 1967) was applied to obtain initial values for mode means which where 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-square 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 one year based on observations by Chapelle (1991) on the reproductive mode of *Waldeckia obesa*. These modes are referred to as relative age (Pauly 1984) for which we use the dimension "years+" (i) to imply that exact age depends on what time of the year the sample was taken relative to the hatching period, (ii) to account for natural spread of age in modes (the period of hatching seems to extend over a few weeks and a female releases all hatchlings within 2 or 3 days (Chapelle, pers. com., pers. obs.)), and (iii) to account for the fact that detectable lipofuscin accumulation may start at some point after release of hatchlings. A score of 1+ therefore indicates individuals between approximately one and two 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 von Bertalanffy growth curve (VBGF)

$L_a = L_\infty\,(1\text{-}e^{-k(a-ao)})$

and Gompertz growth curve

$L_a = L_\infty\,(e^{-e^{-k(a-a_0)}})$

were fitted to the size at lipofuscin-estimated age data by the iterative non-linear Levenberg-Marquardt algorithm (Marquardt 1963). (L_a = body length at age a (years), L_∞ = asymptotic body length, k = growth constant, a_0 = theoretical age at which $L_a = 0$ mm).

Mortality Z and Productivity

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. Annual P/B ratio was, first, estimated from $Z \approx P/B$ (Allen 1971, Brey 1995, 1999a). 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

Lipofuscin characteristics

Different types of lipofuscin-like granules were found within cells of various neuropils (e.g. Fig. 3a) and somaclusters (e.g. Fig. 3b). Considerable amounts of the pigment occurred in the transition areas between somaclusters and neuropils while granules were rare in the middle of somaclusters and neuropils, respectively. The structures in question were roundish to irregular in outline and contained variable amounts of membrane remnants of medium to high electron density embedded in granular to homogeneous material. In some cases lipofuscin-like granules were associated with vacuoles. Granules of very high density occurred predominantly in neuropil cells. The described structures ranged in diameter from < 1 to approx. 3 µm and mostly occurred in groups. In the fluorescence image, they measured occasionally up to 10 µm which is probably due to seemingly merged granules at lower magnification. The confocal image (Fig. 3c) shows the pigment's intense autofluorescence used for pigment quantification. As the granules in the TEM micrographs cannot be tested for their fluorescence, we refer to them as "lipofuscin-like".

Age class identification

A subsample of the total catch (n = 386 individuals) was measured and sexed (Fig. 4a). Numbers of females, males and juveniles were 157 (40.7 %), 102 (26.4 %) and 127 (32.9 %), respectively. The size-wet body mass (WM) relation was $\log(gWM) = 2.71 \bullet \log(mmL_{cox}) - 2.537$ ($r^2 = 0.98$, $p<0.001$). Body length ranged from

1.2 to 7.7 mm L_{cox} (5 to 31 mm L_t). The parameters L_t and L_{cox} were linearly related as follows: $L_t = 4.164 \bullet L_{cox} + 0.070$ ($r^2 = 0.98$, $p < 0.001$). The LFD was characterized by two modes (Fig. 4a), the first one comprising juveniles, and the second one predominantly sexually differentiated individuals. No modes reflecting consecutive age classes were distinguishable visually and modal components could not be fitted to the distribution.

Seventy-two females, 59 males and 28 juveniles of *Waldeckia obesa* were analysed for their lipofuscin concentration as described above. Lipofuscin concentrations ranged from 0.13 (s.d. = 0.03) to 3.44 (s.d. = 0.40) % area fraction (AF) in females, from 0.15 (s.d. = 0.05) to 1.90 (s.d. = 0.36) % AF in males and from 0 to 0.07 (s.d. = 0.04) % AF in juveniles. All specimens with concentrations > 2 % AF (n = 10) were females. The standard deviation of the eight to ten analysed sections of one individual was, on average, 20% in adults and 100 % in juveniles. Fitted modes were well resolved with high separation indices ($p < 0.001$, Fig. 4b). Juveniles constituted mode I, and females and males modes II to V. Six females had concentrations outside the range of the fifth mode, suggesting the existence of more than five age groups. The LCFD differed from the LFD in that the former had evenly spaced modes that were clearly distinguishable by eye.

The relationship between lipofuscin content (AF) and lipofuscin-estimated age (A) was highly significant (Fig. 5a, $p < 0.001$). The linear regression equation defining the relationship was $AF = 0.49 \bullet A + 0.49$ ($r^2 = 0.95$, $p < 0.001$), corresponding to an annual lipofuscin accumulation rate of 0.49 % AF. There was no significant effect of sex on lipofuscin accumulation rate (ANCOVA, $p > 0.05$). The relation between lipofuscin concentration and size, in contrast, showed substantial scatter (Fig. 5b), especially in adults ≥ 5 mm L_{cox}. Individuals with high lipofuscin content though, tended to be large, i.e. all specimens (except for one) of and above mode V (n = 14) measured ≥ 6 mm L_{cox}.

Growth parameters

The size-at-age data were modified prior to growth analysis by splitting mode I into juveniles ≤ 2.4 mm L_{cox} (designated age group 0+; n = 14) and those > 2.4 mm L_{cox} (designated age group 1+; n = 14). The underlying assumption is that mode I does not represent one year old individuals if detectable lipofuscin accumulation does not start right after larval release (in decapods: Sheehy 1990a, c, Sheehy et al. 1995). Chapelle (1991) observed 7 juvenile instars in *Waldeckia obesa* with moulting frequencies of ≥ 4 months (Chapelle, pers. com.) and an average increase in size of 0.4 mm L_{cox} per moult. Thus, a newly hatched 1.2 mm L_{cox} sized individual could, after a year, have reached at max. 2.4 mm L_{cox}. The fit of the VBGF growth curves resulted in

$L_a = 7.47\,(1-e^{-0.50(a+0.46)})$, $r^2 = 0.89$, n = 100 (females and juveniles, Fig. 6a)
(standard errors: $L_\infty = 0.35$, $k = 0.07$, $a_0 = 0.08$)

$L_a = 6.92\ (1\text{-}e^{-0.60(a+0.42)})$, $r^2 = 0.87$, n = 87 (males and juveniles, Fig. 6b)
(standard errors: $L_\infty = 0.36$, $k = 0.09$, $a_0 = 0.07$)

The Gompertz growth curves estimated
$L_a = 6.96\ (e^{-e^{-0.89\,(a+0.49)}})$, $r^2 = 0.91$, n = 100 (females and juveniles, Fig. 6a)
(standard errors: $L_\infty = 0.19$, $k = 0.08$, $a_0 = 0.06$)
$L_a = 6.55\ (e^{-e^{-1.02(a+0.39)}})$, $r^2 = 0.89$, n = 87 (males and juveniles, Fig. 6b)
(standard errors: $L_\infty = 0.21$, $k = 0.09$, $a_0 = 0.06$).

Mortality and productivity

Mortality Z, estimated from the catch curve, amounted to 0.27 per year for females and 0.43 per year for males (Fig. 7). Data from juveniles were not included in the regression (according to Ricker 1979, Pauly 1984). The P/B ratio calculated by the MSGRM was 0.25 per year (VBGF) and 0.26 per year (Gompertz) in females, and 0.31 per year (VBGF) and 0.32 per year (Gompertz) in males. The P/B ratio estimates for juveniles was 2.26 per year (VBGF) and 2.20 per year (Gompertz) while the ratio for pooled data was 0.38 per year (VBGF) and 0.39 per year (Gompertz), respectively.

Discussion

Lipofuscin characteristics

According to Sohal and Wolfe (1986) lipofuscin granules are " membrane-bound lysosomal organelles which contain lipoidal moieties, exhibit yellow to brown coloration, emit yellow to greenish fluorescence under UV, and accumulate in the cytoplasm progressively with age under normal physiological conditions". Additionally, they usually react positively to Sudan Black staining (for *Waldeckia obesa* see Bluhm et al., in press) and to Periodic-acid-Schiff and other histochemical reactions, but exhibit variable responses to these (Brunk et al. 1992). Autofluorescence, thus, remains the most useful feature for histological localization and quantification in crustaceans (Medina et al. 2000). Our observations (Bluhm et al., in press, this study) coincide well with the morphological and microscopical characteristics described for Decapoda (Sheehy 1989, Sheehy et al. 1996, Medina et al. 2000, Vila et al. 2000); histochemical tests apart from Sudan staining, however, were not undertaken. Ultrastructurally, granules correspond with the four categories summarized in Terman and Brunk (1998), granular, homogeneous, lamellated and compound, the latter being most common. In contrast to decapods, in which the pigment is especially dense in cells of the posterior lateral somacluster of the olfactory lobe (Sheehy 1989, 1990b, Sheehy et al. 1995, 1998, Bluhm et al. in press), the lipofuscin granules in *W. obesa* concentrated in the transition zones described above. Whether the respective cells are more active than other somacluster cells or neuropil cells, or whatever else may be the reason for this phenomenon, remains unanswered. The practical consequence is that relative lipofuscin concentrations as areal pigment proportion of the studied brain region cannot be compared between *W. obesa* and decapods. Irrespective of this, the concentration increased with age as it did in decapod species (e.g. Belchier et al. 1998, Sheehy et al. 1999, Vila et al. 2000, Bluhm and Brey, in press).

Trap effects

Unbiased size-frequency distributions of scavenging amphipods are notoriously difficult to obtain with baited traps as these are often selective (Thurston 1979, Slattery and Oliver 1986). No ovigerous females of *W. obesa* appeared in our traps; in other studies this phenomenon was interpreted as female avoidance behaviour so as to reduce the probability of being preyed upon (Slattery and Oliver 1986, Moore 1994). Thurston (1979) suggests that a corollary of the highly extendable gut in obligate necrophages is the inability of females to feed and brood at the same time, as they would lose their broods if the gut was greatly extended. On the other hand, our sampling period (January-February) was after females probably had released their young, as hatchling release was reported to begin in early October at the Antarctic Peninsula (Chapelle 1991). If this were true as well for the Weddell Sea population, few ovigerous females would be left to be caught. However, we found relatively few juveniles which might be explained by a different mode of feeding, as suggested by Chapelle (1991) and Klages (1991) for sub-Antarctic as well as high-Antarctic *W. obesa*. The smallest juveniles we caught may, therefore, have been released in the traps rather than having been attracted there by bait. Hence, we assume that our LFD may be reasonably representative above *ca.* 4 mm L_{cox} but is not in juveniles. Parameters derived from the LFD should be interpreted with care.

Size versus lipofuscin

Length frequency distributions have been used successfully to separate cohorts in low latitude amphipod species (e.g. Collie 1985, Moore and Wong 1996) and even in some Arctic species (Beuchel 2000, Poltermann 2000), although age validation was lacking in the latter. The LFD obtained for *Waldeckia obesa*, in contrast, shows a juvenile mode and one large peak in larger size classes in which individual cohorts cannot be distinguished (Fig. 4a), as is often observed in slow-growing invertebrates (Bannister et al. 1994, Brey et al. 1995, Bluhm et al. 1998, Bluhm and Brey, in press). Aquaria observations demonstrated that adult *W. obesa* can be maintained for years without much obvious growth increment (pers. unpubl. obs.), thus indicating that the large peak in the LFD may be caused by a pile up of many age classes (Fig. 8). Applying very high-resolution size measurements Chapelle (1991) separated 13 instars in *W. obesa*, though without a precise time axis. Slow growth combined with non-moulting females during breeding, interference of moulting stages with cohorts and potential effects of parasites, injuries and starvation on growth can lead to remarkable size-at-age variability obscuring age groups in LFD (Fig. 5, Ikeda and Dixon 1982, Somers and Kirkwood 1991). Size can, therefore, be an inadequate age predictor in slow-growing amphipods as was demonstrated for decapods (Belchier et al. 1994, 1998, Sheehy et al. 1998, 1999).

The lipofuscin concentration frequency distribution, although uncorrected for potential trap effects (see above) shows the characteristic feature of synchronously reproducing populations, i.e. distinct age groups. Our findings support Chapelle's conclusion (1991) that *Waldeckia obesa* reproduces seasonally. In scavenging invertebrates, both continuous reproduction (e.g. Ingram and Hessler 1987, Stockton 1982, McKillup and McKillup 1997) and seasonal reproduction (e.g. Rakusa-Suszczewski 1982, Moore and Wong 1996) occur in deep- as well as shallow-water habitats including Antarctic locations. Chapelle's and Klages' presumptions (both 1991) of a non-scavenging feeding mode in juvenile *W. obesa* may explain seasonal coupling of juvenile release to the onset of near-surface primary production and subsequent sedimentation. Hessler et al. (1978) reported indications that deep-sea scavenging amphipods gradually shift from bacterial and sediment-feeding mode to scavenging. Three factors, seasonal reproduction, linear lipofuscin accumulation reflected in regular spacing of peaks, and validation studies on a number of crustacean species (Sheehy et al. 1994, 1996, 1998, Wahle et al. 1996, Belchier et al. 1998) provide strong evidence that peaks in the LCFD reflect age groups.

Growth and longevity

Growth in *Waldeckia obesa* and other polar amphipods is slow (Bone 1972, Poltermann 2000) compared with boreal and tropical species (Venables 1981). In contrast, the overall growth performance, measured by the index Ψ (Brey 1999a), seems to be slightly higher in higher latitudes as shown by an auximetric grid (according to Pauly 1979, 1984, Fig. 9). The index Ψ is calculated by maximum body mass and the time in which it is reached, i.e. maximum age (Brey 1999a). According to lipofuscin analysis, *W. obesa* reaches an age of ≥ 5 years, and presumably up to 8 years in females. Greater age in females is reflected in sex ratio favouring females (1.5:1) and higher maximum body size (Chapelle 1991). Our estimate agrees with Chapelle's rough calculations (1991, pers. com.) from laboratory observations when multiplying an average moulting frequency of 4 to 11 months by 13 instars. Life span in gammaridean amphipods ranges from only a few months (e.g. *Gammarus mucronatus*, La France and Ruber 1985; *Talorchestia margaritae*, Venables 1981) to apparently over 10 years (*Eurythenes gryllus*, Ingram and Hessler 1987) (reviewed in Saint-Marie 1991). Littoral amphipods are typically multivoltine with generation times of 0.5 to 1.5 years (annual) or < 0.5 years (semiannual) in which two or more generations are produced per year (Wildish and Peer 1981). Sublittoral species, in contrast, have either annual or biannual life histories and produce a single or few broods in their lifetimes. Our findings correspond to Sainte-Marie's results (1991) of his review of 302 populations of gammaridean amphipods, demonstrating that mean life span was significantly longer in (i) cold- rather than in warm-living populations, (ii) in Lysianassoidea and Eusiroidea compared with other superfamilies, and (iii) supposedly in deep-living compared to shallow-living species. Investigations on species from high latitudes are still scarce but show a tendency towards life spans exceeding two years (Thurston 1968, 1970, Bone 1972, Highsmith and Coyle 1992, Klages 1993, Beuchel 2000, Poltermann 2000, this study) combined with delayed maturity, comparatively large embryos and semelparity. If reaching maturity at an age of 2+ years and reproducing annually, female *W. obesa* could reproduce at least four times during their lifetimes. Based on an estimate of 25 eggs per female per brood (incidential observation by Chapelle 1991), lifetime potential fecundity (125 to 200 embryos (E)) and reproductive potential (25 E per female per year) are within the range given for Lysianassidae by Sainte-Marie (1991) (1 to 215 E, mean = 82, and 1 to 92 E per female and year, mean = 43, respectively). Generally, delayed maturity, high longevity and slow ageing in polar invertebrates are explained by limited food availability and low metabolism (Clarke and North 1991, Brey and Clarke 1993, Thiel et al. 1996). Very low O_2-consumption values were indeed measured for *W. obesa* (Chapelle and Peck 1995) and match the low activity typically observed in this species (pers. com. Chapelle, pers. obs.). Only after feeding does oxygen consumption rise by a factor of 4 to 7 (Chapelle and Peck 1995). Higher longevity compared to their lower latitude congeners is also known from other Antarctic crustaceans, e.g. Euphausiacea (Siegel 1987), Mysidacea (Ward 1984, Siegel and Mühlenhardt-Siegel 1988), Isopoda (Luxmoore 1982) and Decapoda (Gorny et al. 1993, Bluhm and Brey, in press).

Productivity and mortality

Published P/B ratios in amphipods range from 0.4 to 61 per year. In *Waldeckia obesa* and other Antarctic and Arctic amphipods the ratio is lower (0.38 to 1 per year; Thurston 1970, Bone 1972, Highsmith and Coyle 1990, 1992, Poltermann 2000, this study) than in lower latitude species in which it mostly varies between 2 and 7 per year. Very high P/B ratios of over 30 per year are known from very small, short-lived, (sub)-tropical Gammaridae and Hyalellidae (Fredette and Diaz 1986a, b, Venables 1981). Despite low turnover rates in polar amphipods, production can still be remarkably high if the biomass is high accordingly, as found in *Ampelisca macrocephala*, *A. birulai* and *Byblis* spp. in the Bering Sea (Highsmith and Coyle 1990, 1992). For Antarctic amphipods, however, Gerdes et al. (1992) published comparatively low biomass values, while Jarre-Teichmann et al. (1997) conclude from their Weddell Sea model that values may be markedly underestimated. Data on biomass and abundance of *W. obesa* are, unfortunately, not available. In terms of the growth-mortality-continuum of benthic invertebrates introduced by Brey and Gage (1997), the relation between Z and k is comparatively high in *W. obesa* indicating above-average predation pressure. Antarctic amphipods are indeed known to be an important food source for fish (Olaso et al. 2000), ophiuroids (Jarre-Teichmann et al. 1997) and crustaceans (Storch et al., in press). Amphipods in the Weddell Sea in general and scavengers in particular may, therefore, represent an important link in the energy transfer to higher trophic levels and as energy recyclers of carrion. Comparable control positions were described for Bering Sea amphipods providing the link from sedimenting primary production to grey whales (Highsmith and Coyle 1992), and for Arctic sympagic amphipods representing a substantial element in cryopelagic coupling (Poltermann 1997, Werner 1997).

To conclude,

- modal progression analysis of LCFD of *Waldeckia obesa* allows separation of modes, which presumably reflect age classes,
- *W. obesa* is a "typical high latitude invertebrate" characterized by high longevity and low productivity,
- the Antarctic scavenging amphipod community may be an important energy mediator from carrion to high trophic levels,
- adequate sampling techniques for scavenging species are urgently needed to obtain reliable data on abundance, biomass as well as size and weight frequencies.

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Figures

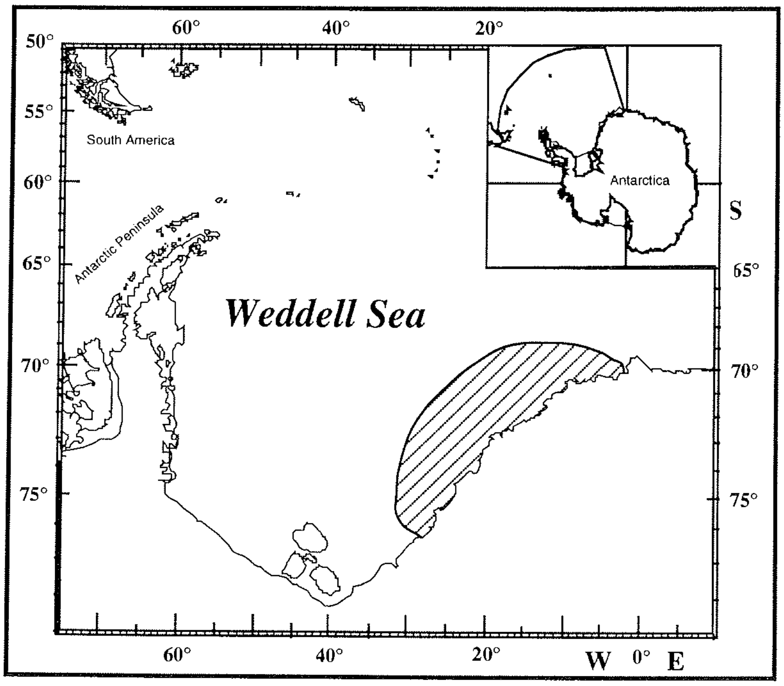


Fig. 1 Study area (hatched) in the Eastern Weddell Sea.

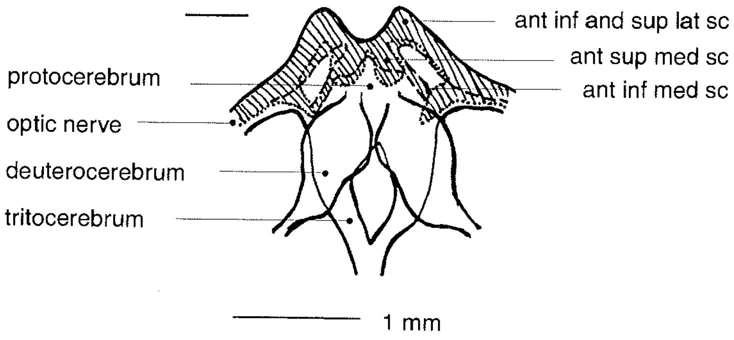


Fig. 2 *Waldeckia obesa.* Schematic view of the brain. Hatchings mark the tissue areas used for lipofuscin quantification. The horizontal line indicates the plane of sectioning. ant: anterior, inf: inferior, lat: lateral, med: medial, sup: superior, sc: somacluster.

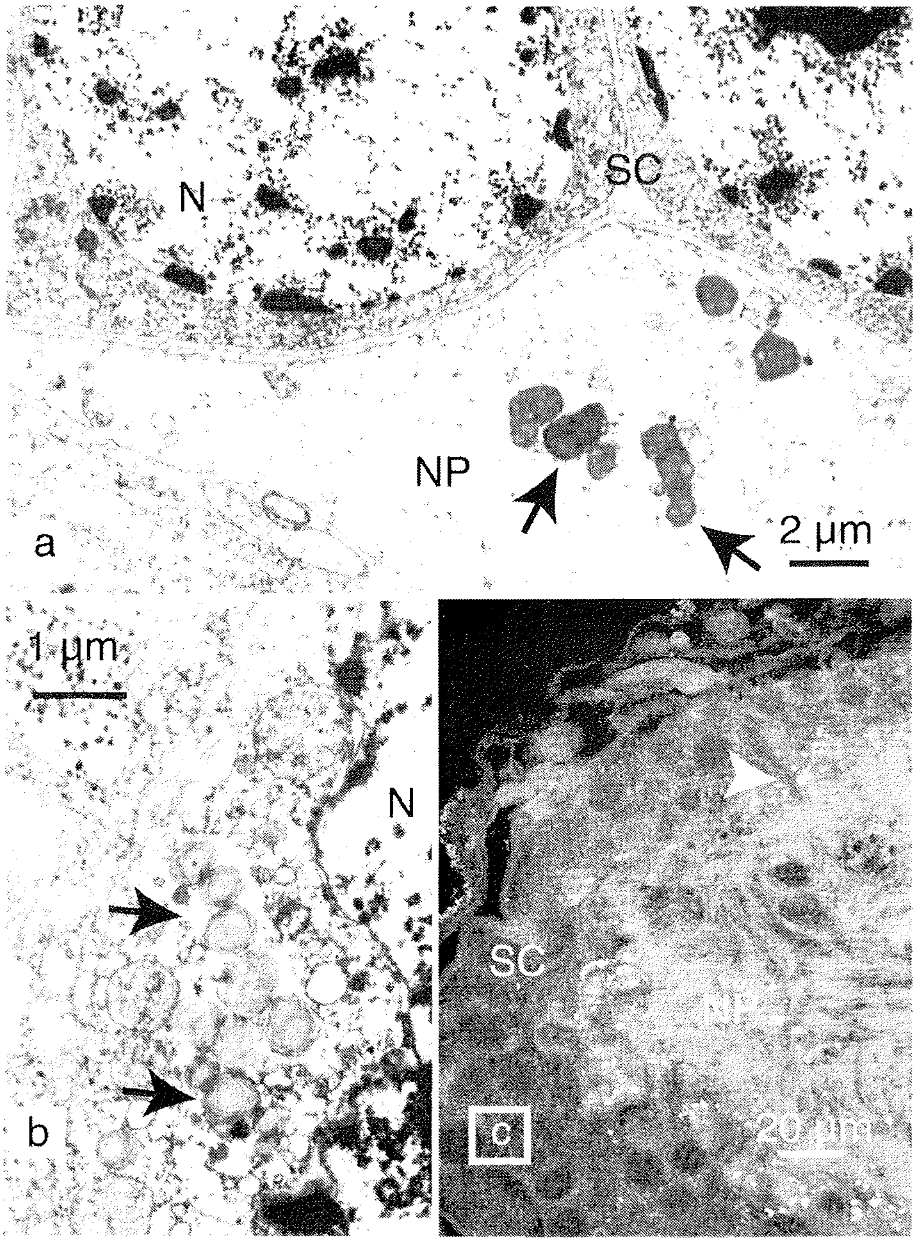
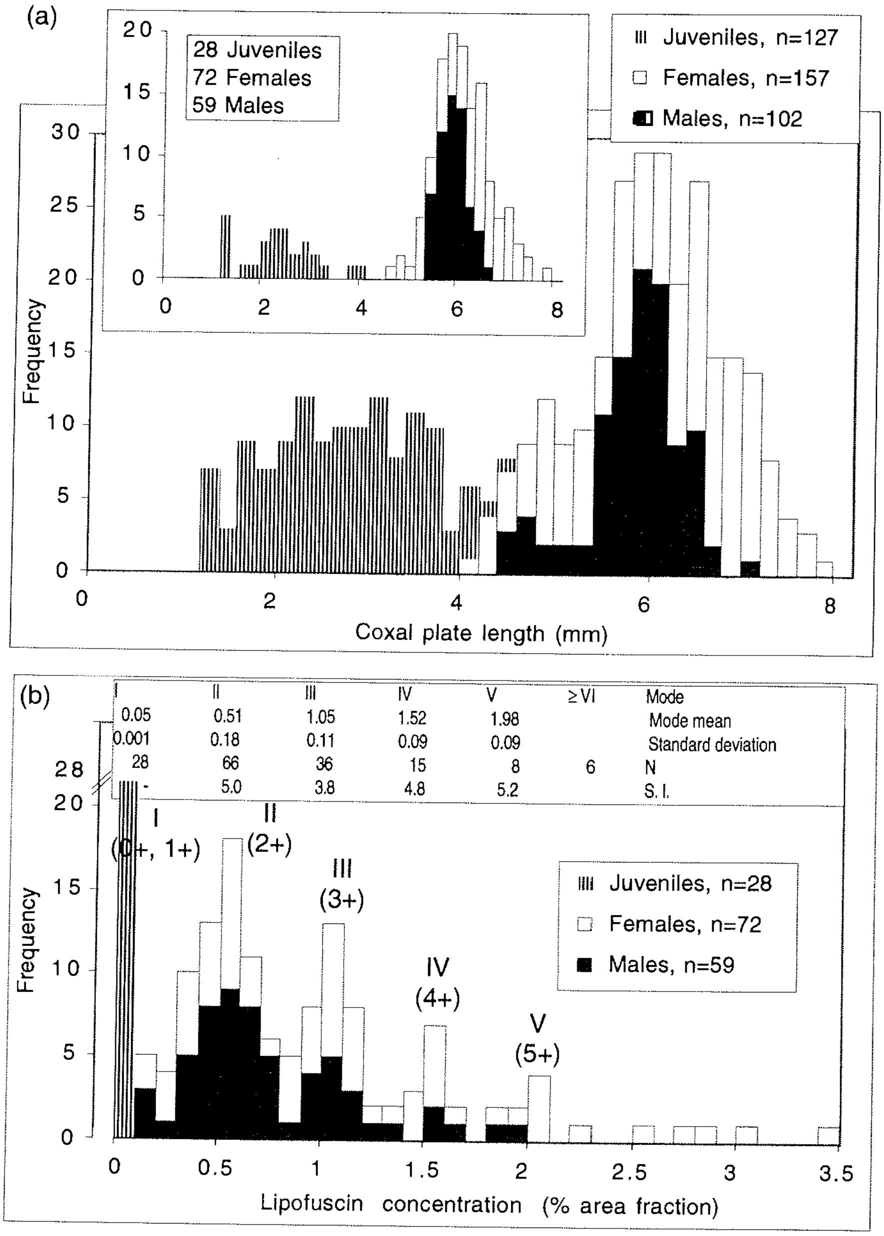


Fig. 3 Brain sections of *Waldeckia obesa*. (a, b) Transmission electron micrographs, (c) confocal fluorescence image. (a) Transition area between somacluster (SC) and neuropil (NP) with lipofuscin-like granules in a neuropil cell, (b) lipofuscin-like granules in a somacluster cell, (c) concentration of lipofuscin fluorescence in a distinct area between somacluster and neuropil. Examples of lipofuscin-like granules are marked with arrows. N = nucleus.



I	II	III	IV	V	≥VI	Mode
0.05	0.51	1.05	1.52	1.98		Mode mean
0.001	0.18	0.11	0.09	0.09		Standard deviation
28	66	36	15	8	6	N
-	5.0	3.8	4.8	5.2		S. I.

Fig. 4 *Waldeckia obesa* from the eastern Weddell Sea. (a) Coxal plate length-frequency distribution of 386 trap-caught individuals (inlay: 159 lipofuscin-analysed specimens), (b) lipofuscin concentration-frequency distribution including results from modal progression analysis. The frequency (n) of one bar is $n_{\text{total bar}} = n_{\text{females}} + n_{\text{males}} + n_{\text{juveniles}}$. N = number of individuals per mode, S.I. = Separation index, roman numerals = modes, arabic numerals = cohort designation in years + (see text).

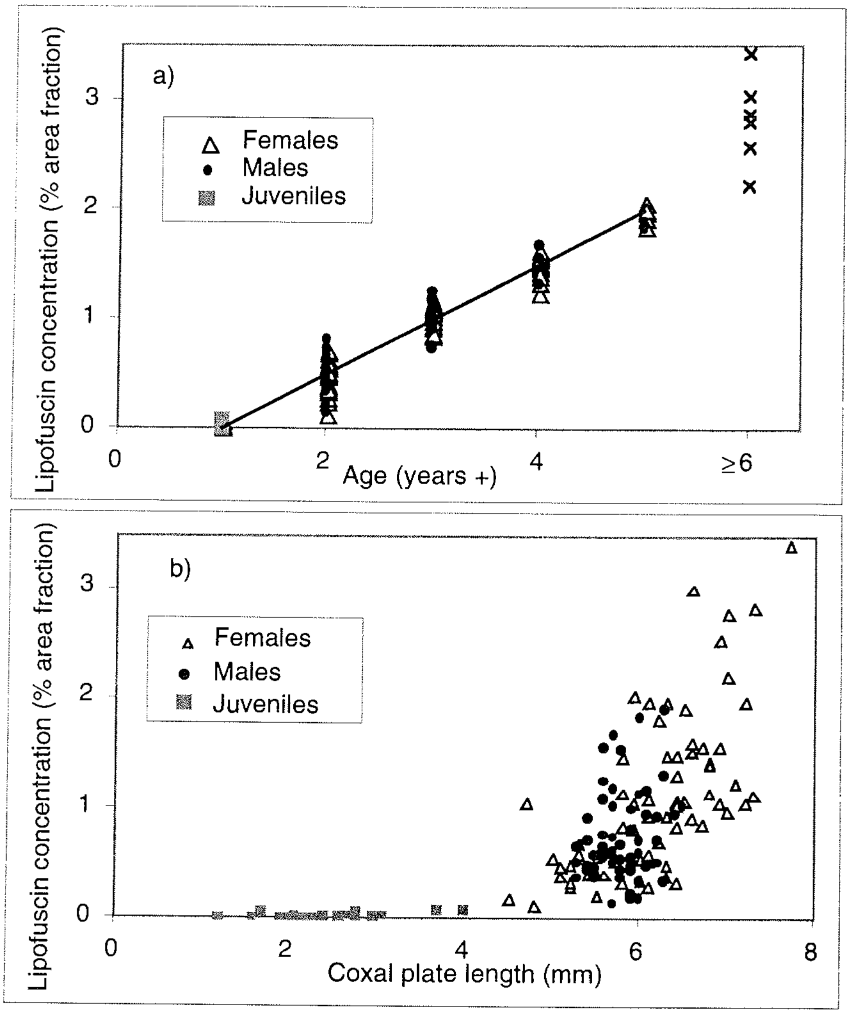
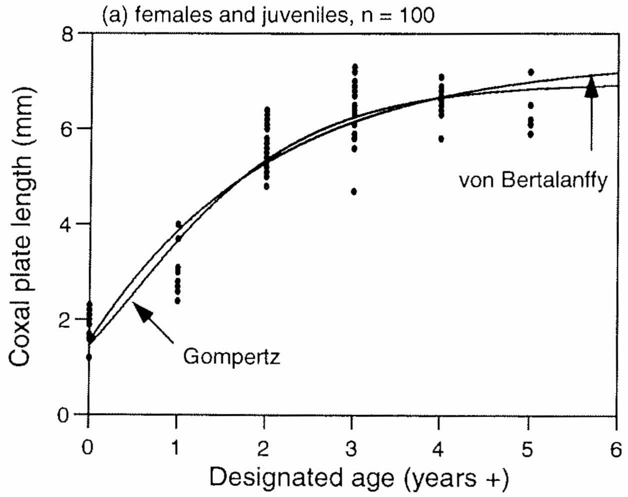


Fig. 5 *Waldeckia obesa* from the eastern Weddell Sea. Lipofuscin concentration in relation to (a) lipofuscin -based estimated age (AF=0.49•age+0.49, r^2=0.95, p<0.001; AF = lipofuscin concentration), and (b) body size.



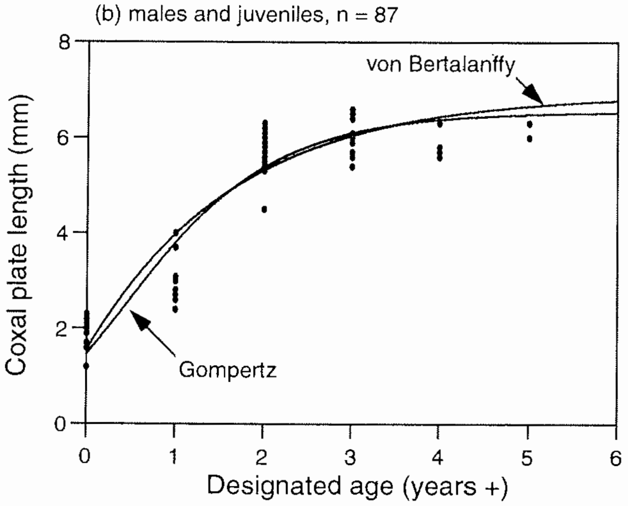


Fig. 6 *Waldeckia obesa* from the eastern Weddell Sea. Growth curves fitted to size at lipofuscin-estimated age data in (a) females and (b) males. Von Bertalanffy: $L_{cox\infty}$ = 7.47 mm, k = 0.50 per year, a_0 = -0.49 years, r^2 = 0.89 (females), $L_{cox\infty}$ = 6.92 mm, k = 0.60 per year, a_0 = -0.42 years, r^2 = 0.87 (males); Gompertz : $L_{cox\infty}$ = 6.96 mm, k = 0.89 per year, a_0 = -0.49 years, r^2 = 0.91 (females), $L_{cox\infty}$ = 6.55 mm, k = 1.02 per year, a_0 = -0.39 years, r^2 = 0.89 (males).

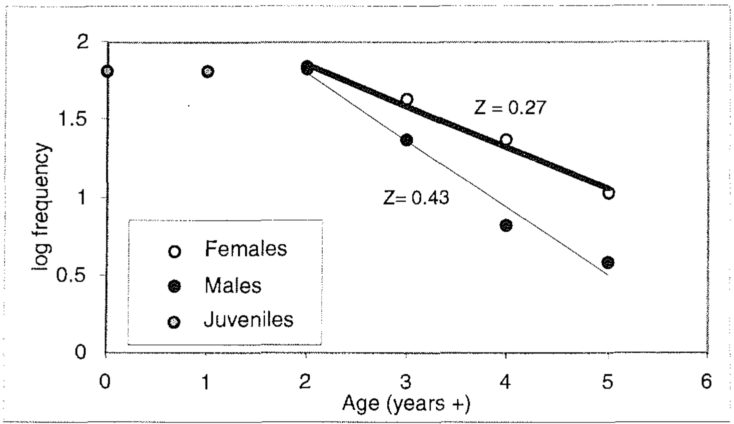


Fig. 7 Catch curve of *Waldeckia obesa* from the eastern Weddell Sea. Females: ln ($n_{age\ class}$) = 2.40-0.27•age, r^2=0.98; males: ln ($n_{age\ class}$) = 2.65-0.43•age, r^2=0.98. The number of individuals per age class ($n_{age\ class}$) was adjusted from lipofuscin-analysed subsample to total sample size (see text).

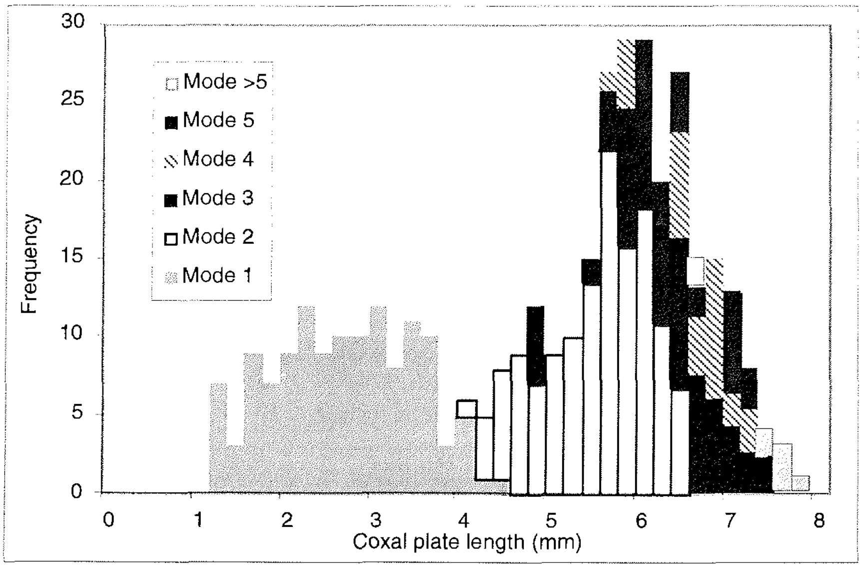


Fig. 8 *Waldeckia obesa* from the eastern Weddell Sea. Distribution of modes derived from the modal progression analysis of the lipofuscin concentration frequency histogram in the length-frequency distribution histogram. The number of individuals per age group was adjusted from lipofuscin-analysed subsample to total sample size (see text). $Frequency_{total\ bar} = n_{mode1} + n_{mode2} + \ldots + n_{mode>5}$

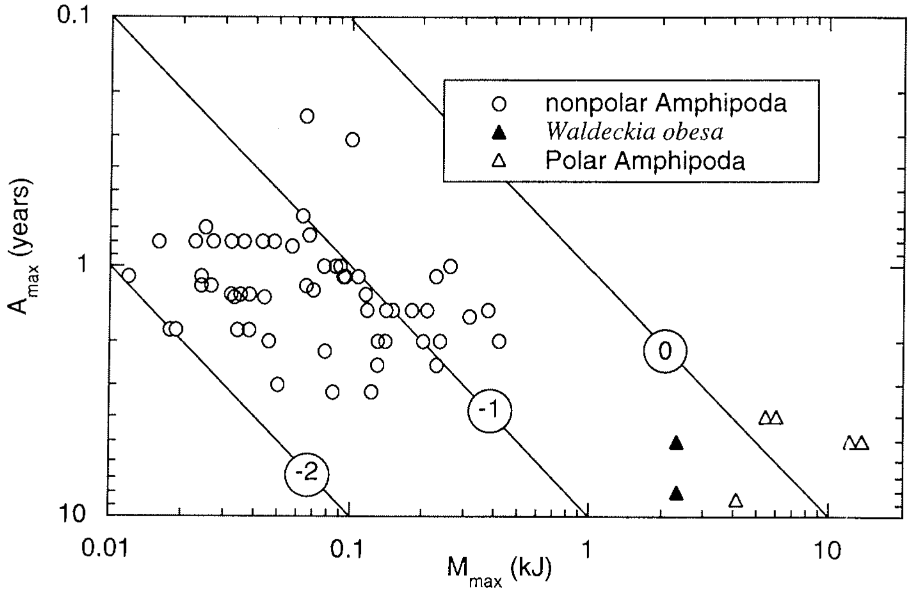


Fig. 9 Auximetric grid comparing overall growth performance Ψ' (=log(maximum body weight/maximum age) of polar and nonpolar Amphipoda. Diagonal lines mark equal values of Ψ' (= numbers in circles). Polar Amphipoda: *Bovallia gigantea* (Thurston 1968, 1970, Bone 1972), *Gammarus wilkitzkii* (Poltermann 2000). Data collection: Brey (1995, 1999b).

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6 Appendix

Table A1 Species and stations sampled for lipofuscin- and morphometric-analysis (publications I – III). AGT = Agassiz trawl, BPN = benthopelagic net, BT = bottom trawl, EBS = epibenthic sledge, N = sample size, ROV = remotely operated vehicle, trap = amphipod trap.

Species	Taxonomy	Expedition	Station	Latitude S	Longitude W	Antarctic Area	Date	Depth (m)	Gear	$N_{size/mass}$	$N_{Lipofuscin}$
Waldeckia obesa (Chevreux, 1905)	Lysianassidae s.l. Amphipoda	ANT XV/3	48-011	72°50.8'	19°15.5'	Drescher Inlet	26.01.1998	377	Trap	47	27
			48-138	74°39.8'	27°13.1'	Halley Bay	09.02.1998	798	Trap	167	74
			48-160	74°40.0'	26°57.9'	Halley Bay	11.02.1998	403	Trap	114	57
			48-280	70°27.4'	07°55.9'	Atka Bay	28.02.1998	550	Trap	59	1
Euphausia superba Dana, 1850	Euphausiidae Euphausiacea	ANT XV/3	48-023	72°51.4'	19°17.2'	Drescher Inlet	27.01.1998	394-2066	BPN		6
Nematocarcinus lanceopes Bate, 1888	Nematocarcinidae Decapoda	ANT XV/3	48-088	73°28.5'	22°30.0'	South of Vestkapp	04.02.1998	1681	AGT		7
Notocrangon antarcticus (Pfeffer, 1887)	Crangonidae Decapoda	ANT XV/3	48/071	70°49.3'	10°28.6'	near Kapp Norvegia	01.02.1998	280	BT	26	2
			48/077	71°09.7'	12°28.7'	near Kapp Norvegia	02.02.1998	350	AGT	179	27
			48/078	72°51.1'	19°15.1'	Drescher Inlet	03.02.1998	390	BT	39	
			48/082	72°50.8'	19°18.8'	Drescher Inlet	03.02.1998	400	BT	14	
			48/084	72°51.0'	19°15.8'	Drescher Inlet	03.02.1998	390	BT	13	
			48/100	73°36.4'	22°07.0'	near Vestkapp	05.02.1998	440	BT	483	139
			48/165	75°00.5'	27°13.2'	Halley Bay	12.02.1998	400	EBS	45	9
			48/194	71°14.1'	12°27.7'	Kapp Norvegia	16.02.1998	245	AGT	126	12
			48/197	71°17.0'	12°36.3'	Kapp Norvegia	16.02.1998	415	AGT	28	
Chorismus antarcticus (Pfeffer, 1887)	Hippolytidae Decapoda	ANT XV/3	48/049	70°52.2'	10°29.0'	near Kapp Norvegia	30.01.1998	260	AGT	65	3
			48/071	70°49.3'	10°28.6'	near Kapp Norvegia	01.02.1998	280	BT	253	11
			48/077	71°09.7'	12°28.7'	near Kapp Norvegia	02.02.1998	350	AGT	82	
			48/078	72°51.1'	19°15.1'	Drescher Inlet	03.02.1998	390	BT	39	
			48/189	71°40.5'	12°45.0'	Kapp Norvegia	15.02.1998	240	AGT	27	
			48/197	71°17.0'	12°36.3'	Kapp Norvegia	16.02.1998	415	AGT	23	
			48/264	72°50.7'	19°26.6'	Drescher Inlet	25.02.1998	444	AGT	20	
						Arctic Area					
				N	E						
Eurythenes gryllus (Lichtenstein, 1822)	Lysianassidae s.l. Amphipoda	ARK XV/1	50/001	79°03.9'	04°11.2'	Greenland Sea	01.07.1999	2517	ROV		3
Uristes sp. Dana, 1849	Lysianassidae s.l. Amphipoda	ARK XV/1	50/002	79°07.9'	02°30.7'	Molloy Deep	02.07.1999	5550	ROV		2
Sabinea septemcarinata Sabine, 1821	Crangonidae Decapoda	ARK XIII/1	44/006	77°00.5'	33°50.6'	Northern Barents Sea	21.05.1997	158	EBS		2
			44/016	76°01.3'	32°49.8'	Northern Barents Sea	24.05.1997	309	AGT		4
Sclerocrangon ferox Sars, 1877	Crangonidae Decapoda	ARK XIII/1	44/016	76°01.3'	32°49.8'	Northern Barents Sea	24.05.1997	309	AGT		4
Pandalus borealis Krøyer, 1844	Pandalidae Decapoda	ARK XIII/2	44/094	80°33.9'	11°21.4'W	Greenland Sea	01.08.2000	300	EBS		6

Table A2 Body size, body mass, sex and lipofuscin concentration in specimens of the ten polar crustacean species investigated in publications I – III. AF = area fraction, f = female, f+ = berried female, j = juvenile, l = larva, Lipof. = lipofuscin concentration, L_t = total body length, L_{cox} = coxal plate length, L_{CL} = carapace length, m = male, WM = wet body mass.

L_t/L_{CL} (mm)	WM (g)	Sex	Lipofuscin (% AF)
Eurythenes gryllus			
33	0.9		0.169
50	3.2		1.038
46	2.8		0.171
Uristes sp.			
8.1	0.013		0.001
5.5	0.005		0.005
Pandalus borealis			
19.7	4.7		0.003
22.4	8.2		0.012
8.1	0.5		0.004
20.5	5.7		0.004
15.5	2.2		0.006
19.4	4.2		0.004
Sclerocrangon ferox			
12.8	3.3		0.004
21.7	11.4	f	0.070
15.4	4.6		0.020
15.3	4.3		0.019
Sabinea septemcarinata			
14.2	2.8	f	0.006
8.8	0.9	m	0.017
16.4	4.0	f	0.002
13.6	2.2	f	0.002
9.2	0.8	m	0.001
12.5	2.2	f	0.000
Euphausia superba			
38.5	0.72		0.000
40.0	0.69		0.001
39.0	0.85		0.001
40.1	0.75		0.000
41.3	1.02		0.000
38.8	0.86		0.000
Chorismus antarcticus			
16.6	3.9	f	0.075
15.7	3.3	f	0.006
19.2	5.8	f	0.014
16.3	3.7	f	0.212
10.1	0.9	m	0.075
10.0	0.9	m	0.067
11.3	1.2	m	0.041
11.8	1.5	m	0.041
1.8		l	0.002
2.1		l	0.010
2.1		l	0.012
2.1		l	0.005
2.2		l	0.018
2.4		l	0.006
Nematocarcinus lanceopes			
26.7	8.3		0.004
28.3	10.2	f	0.010
26.4	7.5	m	0.007
28.3	10.3	f	0.003
22.1	4.5		0.004
23.6	5.5		0.003
29.7	11.1		0.002

Table A2 continued

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
17.3	4.3	f	0.008
21.9	8.6	f	0.210
19.6	5.9	f +	0.060
23.0	9.7	f +	0.053
20.2	6.7	f +	0.124
20.3	6.7	f +	0.030
22.0	7.9	f +	0.017
20.0	6.6	f	0.023
20.5	6.4	f	0.096
18.4	5.0	f	0.011
24.0	10.2	f+	0.060
22.5	8.5	f +	0.050
20.5	6.7	f +	0.142
20.3	6.9	f	0.005
15.6	3.7	m	0.053
19.7	5.9	f	0.077
23.1	8.4	f +	0.040
20.3	5.7	f	0.018
20.4	7.0	f	0.034
19.6	5.9	f	0.084
22.5	10.3	f+	0.059
23.4	10.3	f+	0.130
20.7	6.6	f	0.002
20.2	5.8	f	0.022
17.6	3.9	f	0.041
19.4	6.1	f+	0.018
20.7	6.5	f +	0.043
20.4	6.1	f	0.015
19.1	8.0	f	0.017
15.8	3.1	m	0.037
21.5	5.9	f	0.041
19.2	5.3	f	0.018
19.4	6.0	f+	0.160
22.7	6.8	f	0.012
20.2	6.0	f	0.003
20.5	8.3	f +	0.024
22.1	9.2	f +	0.109
23.8	9.3	f	0.060
20.1	5.8	f	0.035
20.5	8.5	f+	0.011
20.0	6.3	f	0.152
19.7	5.7	f	0.019
20.1	7.7	f	0.036
20.7	8.5	f	0.009
19.6	5.8	f	0.057
19.3	5.9	f	0.018
19.2	5.4	f	0.052
15.6	3.5	m	0.000
20.9	7.5	f	0.032
21.6	8.2	f +	0.037
10.0	1.0	f	0.000
12.2	1.7	f	0.001

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
18.9	6.9	f	0.017
21.0	9.1	f+	0.017
22.1	9.4	f+	0.101
17.4	4.1	f+	0.004
20.9	6.5	f	0.158
23.9	9.5	f +	0.149
18.7	5.7	f	0.045
20.3	6.4	f	0.081
21.1	7.5	f	0.002
22.5	8.4	f	0.044
24.5	12.3	f	0.042
20.5	8.0	f +	0.011
21.7	6.5	f	0.061
20.4	7.7	f+	0.005
21.8	7.4	f	0.040
22.1	8.3	f	0.015
20.8	7.4	f	0.017
22.1	8.9	f	0.018
20.5	5.9	f	0.010
21.9	7.4	f	0.069
20.1	7.1	f	0.043
18.1	4.6	f	0.004
15.6	3.1	m	0.025
20.2	5.3	f	0.044
17.1	3.8	f	0.001
17.9		f	0.011
15.0	2.8	m	0.050
21.5	8.6	f +	0.040
21.9	9.4	f +	0.039
21.8	8.3	f	0.018
23.1	10.1	f +	0.013
23.6	9.7	f +	0.031
20.0	6.5	f	0.044
21.5	8.2	f +	0.003
21.3	8.0	f	0.069
20.4	5.8	f	0.019
21.6	8.3	f	0.025
20.9	7.0	f	0.056
14.7		m	0.033
20.5	6.8	f	0.010
21.4	7.2	f+	0.036
20.3	6.4	f	0.040
17.0	3.8	m	0.036
12.1		m	0.003
23.2		f +	0.104
23.1	11.6	f +	0.036
22.2	9.1	f	0.016
22.2	9.1	f	0.096
20.5	6.6	f	0.010
16.4	3.6	m	0.016
15.8	3.2	m	0.043
15.9	2.8	m	0.012

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
20.1	8.0	f	0.014
18.3	5.2	f	0.017
22.7	9.4	f +	0.195
19.5	5.3	f	0.003
20.0	6.3	f	0.026
21.1	6.2	f	0.057
21.2	7.6	f	0.028
20.2	6.3	f	0.001
21.6	8.3	f	0.014
24.4	10.1	f+	0.117
14.0	2.7	m	0.003
15.5	3.2	m	0.002
12.7	1.7	m	0.001
22.0	8.4	f	0.019
24.4	12.9	f+	0.216
21.9	8.1	f +	0.035
21.9	8.0	f	0.053
20.1	6.2	f	0.011
20.7	6.5	f	0.057
20.3	6.0	f	0.059
21.4	6.4	f	0.138
20.6	6.9	f	0.037
17.9	4.0	f	0.023
14.9	2.5	m	0.036
23.5	10.8	f +	0.030
20.8	8.8	f+	0.012
23.3	9.0	f +	0.037
22.8	9.2	f	0.069
22.5	8.1	f	0.025
21.5	7.3	f +	0.039
20.4	6.7	f	0.051
18.1	5.1	f	0.022
18.3	4.4	f	0.062
15.0	2.9	m	0.007
20.5		f	0.019
13.7	2.2	m	0.003
13.7	1.9	m	0.012
12.5	1.6	m	0.001
14.0	2.0	m	0.010
13.8	2.0	m	0.004
13.1	2.1	m	0.004
12.4	1.6	f	0.003
13.6	2.1	m	0.001
12.0	1.5	m	0.004
23.9	9.9	f	0.138
14.4	2.6	f	0.001
16.2	2.7	m	0.008
19.0	6.2	f+	0.001
8.0	0.4	j	0.000
5.9	0.2	j	0.000
5.5	0.1	j	0.002
5.6	0.2	j	0.001

Table A2 continued

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
10.7	1.1	f	0.000
9.5	0.8	j	0.001
16.0	3.3	f	0.001
15.9	3.0	m	0.056
14.5	2.2	m	0.045
13.8	2.2	m	0.002
11.6	1.5	m	0.004
12.0	1.7	m	0.002
10.7	1.0	m	0.000
18.9	5.5	m	0.007
15.9	3.0	m	0.057
15.0	2.6	m	0.004
13.6	2.2	m	0.012
13.3	1.8	m	0.008
14.0	2.3	m	0.003
20.0	6.6	f	0.129
14.4	2.2	m	0.003
14.1	2.1	m	0.003
14.0	2.1	m	0.001
15.1	2.7	m	0.005
14.7	2.3	m	0.012
13.1	1.8	m	0.016
9.8	0.8	m	0.000
9.7	0.6	f	0.002
7.9	0.3	j	0.001
7.5	0.3	j	0.001
7.6	0.4	j	0.001
7.2	0.5	j	0.000
7.9		j	0.001
14.9	2.9	m	0.016
15	3.1	m	0.000
22.9	9.6	f	0.038
24.4	12	f	0.086
21.4	7.4	f	0.066
19.4	5.4	f	
15.7	3.7	m	
18.8	5.2	f	
22.0	6.4	f	
19.0	5.9	f	
19.5	5.4	f	
21.0	6.6	f	
18.8	7.3	f+	
18.7	4.6	f	
16.8	3.2		
20.5	6.2	f	
20.2	6.0	f	
20.7	6.3	f	
17.2	4.6	f	
17.2	3.8	f	
14.3	2.6		

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
19.5	5.8	f	
22.4	8.8	f	
19.3	6.1	f	
24.7	9.7	f	
20.7	6.4	f	
21.1	5.9	f+	
18.5	3.8	f	
20.5		f	
22.2	7.1	f	
21.3	8.1	f	
20.9	7.3	f	
15.9	2.9	m	
15.7	2.5		
22.1	8.2	f	
15.7	3.2	f	
19.4	5.2	f	
19.4	6.0	f+	
19.7	5.5	f	
19.8	6.0	f	
13.7	1.8		
20.8	7.6	f+	
19.9	5.7	f	
20.1	6.6	f	
21.4	7.8	f	
20.6	8.2	f	
20.0	7.2	f	
21.8	7.3	f	
18.8	4.0	f +	
20.6	7.4	f	
17.4	4.0	f	
18.7	4.6	f	
15.2	2.9	m	
19.2	5.6	f	
19.6	5.6	f	
21.6	8.0	f	
20.1	7.6	f	
21.5	7.1	f	
18.6	6.0	f	
18.3	4.8	f	
18.9	4.6	f	
20.6	6.4	f	
18.0	5.6	f	
15.2	3.0	m	
11.3			
21.5	7.5	f	
18.6	5.8	f	
20.1	6.8	f	
20.7	7.6	f	
17.2	4.3	f	
18.3	5.3	f+	
15.9	3.2	m	

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
17.1	4.1		
16.4	3.6		
20.0	6.4	f	
18.7	5.3	f	
22.7	8.6	f	
22.3	7.8	f	
20.6	6.0	f	
18.3	4.8	f	
21.0	7.0	f	
23.2	10.7	f	
21.0	7.6	f+	
25.0	12.2	f +	
20.4	6.8	f	
16.1	4.2	m	
20.2	6.1	f	
17.6	4.3	m	
20.0	5.4	f	
20.1	5.6	f	
20.6	7.5	f	
23.0	7.8	f	
18.6	4.4	f	
19.5	5.0	f	
22.6	10.5	f +	
22.7	8.9	f	
21.0	8.1	f	
23.0	9.5	f	
20.8	7.3	f +	
20.2	7.3	f	
20.5	6.8	f	
21.6	6.7	f	
17.5	4.6	f	
19.9	7.0	f	
21.9	8.0	f	
15.0	3.0	f	
19.1	5.1	f	
19.9	6.3	f	
21.2		f+	
20.7	6.4	f	
21.1	7.1	f	
16.1	4.0	m	
17.0	4.9	f	
14.9	3.2	m	
17.2	5.9	f	
19.9	6.4	f	
18.4	5.5	f	
20.8	6.2	f	
19.1	5.3	f	
19.5	5.7	f	
17.4	4.1	f	
22.1	7.5	f	
14.9	2.6	f	

Table A2 continued

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
23.3	9.2	f	
17.1	4.5	f	
17.9	4.6	f	
19.7	6.4	f	
19.3	5.0	f	
18.1	4.5	f	
11.3	1.3	f	
17.9	4.4	f	
16.4	3.9	f	
17.3	4.9	f	
13.2	2.1	m	
16.9	3.5	m	
14.6	2.6	f	
11.3	1.1	m	
12.8	1.8	f	
15.1	2.6	f	
14.1	2.7	m	
14.1	2.5	m	
14.3	2.3	m	
16.0	2.9	f	
17.9	4.1	f	
14.0	2.4	m	
15.2	3.1	f	
14.4	2.0	m	
15.9	3.0	f	
12.3	1.5	f	
12.3	1.6	f	
16.2	3.7	f	
15.1	3.0	f	
15.8	3.1	f	
16.0	2.9	f	
15.1	2.5	f	
13.2	1.9	f	
18.2	4.7	f	
17.3	4.4	f	
20.1	6.4	f+	
19.2	6.2	f	
19.3	6.3	f	
18.3	5.8	f+	
16.4	3.4	f	
19.1	6.2	f	
19.5	5.6	f	
18.0	4.5	f	
16.7	4.2	m	
18.3	4.2	f	
17.2	4.6	f	
18.7	5.8	f	
12.0	1.4	f	
12.6	1.7	f	
12.6	1.7	f	
11.8	1.2	m	
13.1	1.7	m	
11.7	1.3	m	
10.6	1.1		
12.3	1.5	f	
11.6	1.3	m	

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
15.7	3.3	f	
14.0	2.3	m	
14.4	2.2	m	
13.7	2.2	m	
13.6	2.1	m	
15.3	2.6	f	
13.5	2.1	m	
14.1	2.2	m	
12.5	1.6	f	
13.0	1.6	m	
11.5	1.3	f	
11.3	1.3	m	
15.7	2.8	f	
18.5	5.2	f+	
20.9	7.6	f+	
18.5	5.1	f+	
14.2	2.5	m	
18.3	4.9	f	
18.7		f+	
18.1	4.7	f	
17.6	4.3	f	
16.4	2.9	m	
13.4	2.1	f	
12.6	2.1	f	
12.4	1.6		
13.6	1.9	m	
11.8	1.4	f	
13.6	1.9	m	
12.4	1.5	m	
14.8	2.8	m	
13.6	2.1	m	
11.1		m	
13.2	1.7	m	
11.3	1.2	f	
11.9	1.3	f	
11.4	1.1	f	
11.6	1.1	m	
9.2	0.7	m	
7.8	0.4	m	
8.6	0.5	m	
21.7	7.8	f	
20.3	6.1	f	
21.4	7.2	f	
20.1	5.9	f	
21.7	7.3	f	
19.5	5.9	f	
18.8	5.2	f	
6.4	0.2	j	
6.0	0.1	j	
21.4	8.0	f	
18.0	4.7	f	
19.9	6.0	f	
17.7	4.6	f	
16.1	4.0	f	
18.3	4.5	f+	
18.0	4.1	f	

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
18.0	4.5	f	
15.5	3.3	m	
14.6	2.6	f	
15.2	2.7	f	
17.2	4.2	f	
16.8	2.9	f	
17.8	4.4	f	
18.1	4.8	f	
16.6	3.4	m	
16.7	3.5	f	
14.5	2.6	m	
13.4	2.1	m	
21.9	6.8	f	
14.7	2.4	m	
15.4	2.5	f	
16.8	3.6		
15.2	2.6	f	
14.7	2.7	m	
13.9	2.1	m	
13.3	1.8	m	
13.6	1.9	m	
15.2	2.6	f	
15.4	2.8	f	
13.7	2.3	m	
13.9	2.2	m	
13.3	1.8	f	
13.8	2.3	f	
13.4	2.0	f	
13.9	2.1	m	
12.4	1.6	m	
13.0	1.6	f	
14.1	2.3	f	
14.0	2.1	f	
12.9	1.7	f	
13.5	2.0	m	
10.7	1.1		
15.1	2.5	f	
14.7	2.5		
12.2	1.5	f	
12.7	1.5	m	
13.2	2.1	f	
12.4	1.6	f	
11.6	1.3	m	
11.6	1.3	m	
10.5	0.9		
12.0	1.3	m	
11.0	1.1	f	
12.7	1.7	m	
11.7	1.4	m	
24.5	11.4	f	
22.2	8.0	f	
17.4	4.6	m	
22.0	8.0	f	
18.6	5.8	f	
20.5	6.2	f	
20.0	6.6	f	

Table A2 continued

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
10.6	1.1		
10.1	0.8		
13.2	1.5	f	
9.5	0.8	f	
20.0	5.6	f	
15.1	3.2	f	
19.0	6.6	f+	
19.2	5.5	f	
17.7	4.3	f	
18.2	4.3	f+	
15.0	2.9	f	
14.7	2.9	f	
13.8	2.2	f	
12.7	2.2	m	
12.7	1.9	m	
8.7	0.5	j	
10.4	1.0	m	
6.3	0.2	j	
15.2	3.0	f	
12.3	1.7	m	
13.0	2.0	m	
5.0	0.3	j	
6.4	0.2	j	
16.9	3.8	f	
12.6		m	
12.2	1.7	f	
6.3	0.2	j	
6.8	0.3	j	
6.7	0.2	j	
7.4	0.4	j	
12.7	1.7	m	
13.6	2.3	m	
9.8	0.6	f	
6.1	0.2	j	
6.0	0.1	j	
10.3	0.9	m	
6.0	0.1	j	
6.5	0.2	j	
6.4	0.2	j	
6.1	0.2	j	
6.1	0.1	j	
20.5	4.9	f	
21.8	5.9	f	
22.2	7.0	f	
20.1		f	
20.7	6.0	f	
22.4	7.6	f	
22.6	7.8	f	
22.2	7.7	f	
21.5	7.8	f	
20.4	7.3	f	
21.8	7.5	f	
21.8	7.7	f	
21.6	7.2	f	
23.6	10.8	f	
22.1	8.4	f	

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
14.7	2.6	f	
18.2	4.2	f	
16.3	3.3	f	
11.5	1.3	m	
14.7	2.7	m	
14.0	2.2	m	
14.3	2.3	f	
13.8	2.2	m	
13.3	1.9	m	
12.7	1.7	f	
12.7	1.8	f	
12.2	1.5	m	
12.9	1.6	f	
12.7	1.5	f	
12.1	1.5	f	
12.8	1.8	f	
11.6		m	
11.0		m	
23.3	8.5	f+	
22.7	7.6	f	
23.2	8.1	f	
19.5	5.4	f+	
20.8	6.5	f	
20.6	6.6	f+	
21.4	6.0	f	
21.1	6.7	f	
19.4	4.9	f+	
17.7	4.2	f	
19.1	4.7	f	
20.5	6.5	f	
20.5	5.6	f	
18.5	5.0	f+	
21.2	6.6	f	
21.9	6.4	f	
19.9	5.9	f+	
18.0	3.6	f	
17.7	4.4	f+	
13.8	2.0	m	
13.0	1.8	m	
13.6	2.3	m	
11.4	1.1	m	
22.0	7.8	f	
22.6	7.8	f	
19.8	4.9	f	
16.2	3.1	f	
20.0	5.4	f	
20.1	6.2	f	
22.3	7.1	f	
23.9	9.2	f	
20.4	5.3	f	
21.8	5.8	f	
21.3	5.2	f	
19.6	4.8	f	
21.8	5.8	f	
22.0	5.4	f	
15.4	3.9	m	

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
19.1	5.0	f	
22.9	9.2	f	
21.4	7.1	f	
19.7	5.5	f	
19.6	5.1	f	
21.1	7.6	f	
19.7	5.4	f	
19.7	6.3	f	
20.4	5.5	f	
15.2	2.5	m	
19.3	5.2	f	
22.4	7.4	f	
21.3	5.4	f	
20.5	6.1	f	
22.9	8.8	f	
15.5	2.9	m	
20.5	5.2	f	
21.1	7.1	f	
21.9	6.3	f	
23.9	7.1	f	
22.0	6.9	f	
21.6	5.6	f	
20.2	5.8	f	
19.6	4.6	f	
19.1	5.1	f	
20.3	6.3	f	
19.4	5.1	f	
20.3	6.6	f	
18.7	5.3	f	
17.1	3.9	m	
17.9	4.2	f	
21.2	6.6	f	
22.9	7.9	f	
20.4	6.1	f	
21.6	6.7	f	
22.3	7.0	f	
14.2	2.4	m	
21.5	6.4	f	
22.9	8.3	f	
21.0	8.0	f	
20.7	6.0	f	
17.0	3.8	f	
15.2	2.5	m	
15.9	2.9	f	
21.9	6.6	f	
14.8	2.1	m	
20.4	6.9	f	
20.9	5.9	f	
14.8	2.5	m	
22.5	8.3	f	
22.2	8.5	f	
22.5	8.1	f	
20.9	5.5	f	
20.3	4.6	f	
19.3	5.5	f	
18.4	4.7	f	

Table A2 continued

L_{CL} (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Notocrangon antarcticus			
20.8	4.6	f	
19.1	5.0	f	
22.1	8.8	f	
20.6	6.0	f	
20.0	5.5	f	
20.2	5.7	f	
22.0	6.8	f	
22.1	8.6	f	
19.3	5.8	f	
19.3	5.2	f	
18.6	5.3	f	
21.3	5.9	f	
16.4	3.5	m	
15.1	3.0	m	
20.3	6.0	f	
20.9	7.5	f	
21.2	6.8	f	
23.5	8.5	f	
20.0	7.2	f	
14.7	2.7	m	
20.5	5.2	f	
21.2	7.0	f	
15.1	2.5	m	
20.7	5.3	f	
18.6	4.3	f	
20.0	6.4	f	
21.1	5.8	f	
18.4	5.0	f	
19.1	4.7	f	
20.8	6.0	f	
15.5	3.1	f	
18.2	5.1	f	
17.9	4.7	f	
19.9	6.2	f	
21.3	6.8	f	
19.7	4.9	f	
20.1	7.4	f	
20.1	5.8	f	
15.6	2.0	m	
16.6	2.9	f	
22.0	7.5	f	
21.5	6.7	f	
23.0	8.1	f	
21.9	5.7	f	
14.4		f	
21.4	6.4	f	
20.4	5.9	f	
23.0	8.3	f	
19.9		f	
20.7	4.8	f	
20.8		f	
22.2	7.5	f	
14.7	2.4	m	
19.1	3.9	f	
23.8	7.2	f	
20.9	5.6	f	

L_{CL} (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Notocrangon antarcticus			
24.1	10.2	f	
21.8	7.2	f	
15.5	3.0	m	
21.2	5.5	f	
23.6	9.5	f	
15.6	2.9	m	
19.5	5.0	f	
15.4	2.6	m	
20.1	6.1	f	
15.3	3.0	m	
15.8	3.0	m	
22.3	7.7	f	
21.0	8.4	f	
23.0	8.1	f	
21.6	6.5	f	
20.9	7.8	f	
22.2	7.7	f	
21.7	7.3	f	
22.7	8.2	f	
19.2	5.8	f	
20.3	5.4	f	
20.3	6.2	f	
19.5	5.2	f	
21.3	6.8	f	
20.1	4.5	f	
19.7	5.6	f	
23.3	9.1	f	
21.6	6.9	f	
20.5	6.2	f	
21.3	7.5	f	
20.1	6.3	f	
17.2	3.5	f	
17.1	3.9	f	
20.0	5.9	f	
21.8	6.8	f	
20.1	5.0	f	
20.3	6.4	f	
16.3	2.7	f	
19.4	4.1	f	
19.0	3.9	f	
17.1	3.8	f	
20.2	5.7	f	
14.5	2.3	m	
15.0	2.4	m	
18.0	4.5	f	
14.3	2.2	m	
16.2	2.6	m	
21.9	6.6	f	
13.6	1.9	m	
19.6	6.6	f	
16.0	2.8	m	
18.9	3.6	f	
13.3	2.0	f	
20.8	5.3	f	
20.2	5.6	f	
20.4	5.8	f	

L_{CL} (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Notocrangon antarcticus			
21.6		f	
19.8	5.5	f	
21.1	6.3	f	
20.5	6.6	f	
19.7	5.7	f	
20.6	4.1	f	
22.1	7.4	f	
21.3	7.5	f	
19.8	6.2	f	
15.5	2.7	m	
22.5	8.6	f	
23.3	8.8	f	
20.7	6.0	f	
20.8	6.6	f	
21.1	6.3	f	
18.8	4.6	f	
21.4	7.3	f	
15.3	2.5	m	
21.4	7.5	f	
20.0	5.9	f	
21.7	5.2	f	
20.5	4.9	f	
18.2	4.0	f	
21.0	6.5	f	
21.1	6.0	f	
21.1	6.7	f	
20.2	6.3	f	
21.0	5.5	f	
15.5	2.9	m	
17.2	3.6	f	
18.8	4.2	f	
21.4	4.8	f	
21.4	7.4	f	
22.6	7.9	f	
16.1	3.2	m	
21.3	6.0	f	
18.1	3.7	f	
15.8	2.9	f	
15.7	2.4	m	
13.3	1.5	f	
18.0	3.9	f	
8.8	0.4	m	
9.3	0.5	f	
13.1	1.6	m	
13.7	1.8	m	
14.3	1.8	f	
17.2	3.0	f	
14.0	2.0	f	
17.2	3.6	f	
18.0	4.0	f	
10.7	0.8	m	
19.5	5.0	f	
13.7	1.6	m	
19.4	4.4	f	
13.6	1.8	f	
18.4	3.8	f	

Table A2 continued

L_{CL} (mm)	WM (g)	Sex	Lipof. (% AF)
Notocrangon antarcticus			
20.0	6.0	f	
19.3	5.2	f	
23.4	7.3	f	
20.7	6.6	f	
19.4	5.0	f	
15.2	2.5	m	
21.3	5.6	f	
21.5	6.4	f	
15.9	2.7	m	
21.4	5.2	f	
20.9	4.6	f	
20.2	5.0	f	
16.1	3.1	m	
18.9	4.9	f	
22.0	6.7	f	
21.7	8.0	f	
16.5	3.6	m	
20.0	6.0	f	
22.0	7.2	f	
19.1	4.7	f	
20.0	6.1	f	
21.8	7.6	f	
20.8	6.5	f	
19.1	3.8	f	
20.2		f	
20.5	4.9	f	
20.6	5.9	f	
22.4	7.8	f	
21.0	6.0	f	
8.6	0.5	f	
9.2	0.7	m	
12.0	1.3	m	
7.4	0.3	f	
7.5	0.4	m	
20.6	7.1	f+	
9.5	0.6	f	
12.9	1.5	f	
14.3	2.3	f	
21.9	8.2	f+	
9.3	0.6	f	
10.1	0.9	m	
11.5	1.2	f	
10.3	0.9	m	
16.0	3.1	m	
14.5	2.8	f	
8.2	0.6	f	
8.3	0.5	f	
6.8	0.3	j	
9.5	0.7	j	
8.0	0.3	m	
9.1	0.6	j	
Notocrangon antarcticus			
19.5	4.8	f	
14.9	2.6	f	
17.2	4.2	f	
22.9	7.5	f	
21.1	6.4	f	
13.1	1.7	f	
13.9	2.0		
11.4	1.2	m	
14.0	2.1	m	
13.3	1.9		
17.5	3.8	f	
14.9	2.4	f	
12.5	1.6	m	
20.5	5.2	f	
12.7	1.5	f	
13.8	2.2	m	
15.4	2.8	m	
18.8		f	
11.4	1.2	m	
13.4	1.8	m	
17.4	3.5	f	
19.0	5.0	f	
18.0	4.1	f	
22.8	8.1	f	
13.1	1.6	f	
16.9	3.7	f	
16.4	3.0	f	
13.2	1.7	f	
18.9	4.9	f	
10.0	0.8	m	
10.5	0.9	m	
9.0	0.6	m	
16.2	3.1	f	
17.7	3.7	f	
10.0	1.0	m	
9.9	0.5	f	
12.1	1.3	m	
20.0	5.3	f	
24.3	11.6	f+	
18.3	5.5	f+	
22.5	9.6	f+	
11.4	1.1	f	
8.8	0.6	j	
22.5	6.9	f	
10.5	0.9	m	
10.8	0.9	f	
12.5	1.6	m	
8.8	0.5	f	
15.5	2.5	f	
17.4	4.6	f+	
18.5	6.2	f+	
Notocrangon antarcticus			
17.7	3.9	f	
19.6	4.8	f	
14.2	2.1	f	
17.1	3.7	f	
18.4	4.2	f	
12.3	1.5	f	
22.1	8.5	f+	
12.2	1.5	f	
9.2	0.7	m	
8.0	0.4	m	
8.0	0.4	m	
8.0	0.4	f	
9.5	0.9	m	
11.2	1.1	m	
20.6	5.9	f	
9.5	0.7	f	
15.7	3.0	f	
21.1	6.7	f+	
20.5	7.7	f+	
19.5	6.1	f	
12.7	1.6	m	
13.1	1.5	f	
13.4	2.0	f	
8.0	0.5	m	
19.6	5.2		
10.3	0.7	f	
9.3		f	
12.0	1.3	m	
12.2	1.7	m	
20.8	6.5	f+	
18.8	4.6	f	
16.0	2.8	m	
17.0	3.8	f	
12.0	1.3	m	
12.8	1.6	m	
12.0	1.3	m	
11.5	1.1	m	
8.7	0.4	j	
10.1	0.8	m	
17.9	3.7	f	
13.1	1.8	f	
13.0	1.4	f	
14.1	1.7	f	
11.1	1.0	f	
10.3	0.8	m	
13.0	1.8	f	
8.6	0.5	f	
10.8	1.0	f	
14.0	2.2	m	
19.5	6.6	f+	

Table A2 continued

L_t	L_{cox}	WM	Sex	Lipof.
(mm)	(mm)	(g)		(% AF)
Waldeckia obesa				
27	6.4	0.50	f	1.088
23	5.5	0.35	f	0.244
25	5.7	0.31	m	1.185
25	5.7	0.34	m	0.625
27	5.7	0.43	m	0.743
23	5.3	0.34	f	0.614
27	6.1	0.42	f	0.295
24	5.8	0.39	f	0.356
26	5.7	0.37	m	1.668
20	4.7	0.22	f	1.080
25	5.7		m	0.587
28	6.5		f	1.098
26	6.1		m	0.483
23	5.4		m	0.493
26	6.4		f	0.860
27	6.6		f	0.937
21	4.5		f	0.185
23	5.3		m	0.377
24	5.6		f	0.424
27	6.4		f	1.069
25	6.0		m	0.193
19	4.8		f	0.129
24	5.6	0.31	f	0.655
25	5.8	0.31	m	0.543
26	6.1	0.39	m	0.952
26	5.9	0.37	m	0.555
26	5.7	0.33	m	0.636
23	5.5	0.30	m	0.405
22	5.3	0.25	f	0.696
23	6.1	0.35	f	2.003
26	5.9	0.40	m	1.013
22	5.9	0.33	f	0.851
26	6.2	0.38	m	0.932
27	6.0	0.36	m	1.151
27	6.4	0.44	f	1.522
26	6.2	0.43	f	0.712
22	5.5	0.28	f	0.412
27	6.3	0.40	m	1.905
26	6.0	0.39	m	0.729
25	6.0	0.35	f	0.560
25	5.8	0.32	m	0.441
24	5.9	0.37	f	2.055
19	5.2	0.21	f	0.520
21	5.2	0.22	f	0.297
22	5.2	0.27	f	0.351
23	5.5	0.31	f	0.583

L_t	L_{cox}	WM	Sex	Lipof.
(mm)	(mm)	(g)		(% AF)
Waldeckia obesa				
29	7.3	0.45	f	2.881
23	5.5	0.29	f	0.592
25	5.7	0.33	m	1.017
26	5.6	0.37	m	1.090
27	6.0	0.38	m	1.837
23	5.7	0.34	m	0.520
23	5.3	0.29	m	0.508
26	6.2	0.40	m	0.733
27	6.3	0.38	f	1.507
22	5.1	0.28	f	0.481
27	6.3	0.33	f	2.006
27	6.2	0.40	f	1.845
24	5.8	0.35	f	1.167
27	6.1	0.36	m	1.156
26	5.9	0.35	m	0.493
26	5.6	0.35	m	1.253
24	5.5	0.33	m	0.582
22	5.0	0.31	f	0.569
24	5.4	0.34	m	0.904
24	5.9	0.32	m	0.528
25	5.6	0.37	m	0.772
23	5.4	0.20	f	0.418
24	5.8	0.31	f	1.484
27	5.6	0.38	m	0.551
26	5.6	0.32	m	1.552
22	5.3	0.26	m	0.664
21	5.1	0.25	f	0.402
29	7.1	0.54	f	1.263
29	6.8	0.53	f	1.438
29	6.7	0.52	f	1.598
28	6.5	0.44	m	1.018
27	6.4	0.46	f	1.338
28	6.6	0.52	f	1.547
26	5.7	0.41	m	1.015
30	6.9	0.54	f	2.570
28	6.6	0.46	f	3.043
28	6.9	0.50	f	1.587
28	6.4	0.49	f	1.053
30	7.0	0.70	f	2.231
24	6.1	0.37	f	0.957
26	5.6	0.36	m	0.606
27	6.8	0.46	f	1.421
25	5.8	0.36	m	1.547
27	6.9	0.57	f	1.073
26	6.3	0.41	f	0.956
25	5.8	0.37	m	0.381

L_t	L_{cox}	WM	Sex	Lipof.
(mm)	(mm)	(g)		(% AF)
Waldeckia obesa				
25	5.9	0.37	m	0.225
26	5.9	0.37	m	0.196
28	6.8	0.49	f	1.165
24	6.1	0.30	f	0.532
29	7.0	0.54	f	2.798
24	5.4	0.36	m	0.733
28	6.3	0.57	m	1.314
25	6.0	0.34	f	0.362
24	5.6	0.34	m	0.643
28	6.6	0.59	f	1.634
25	5.9	0.41	m	0.453
26	6.5	0.49	f	1.105
28	7.7	0.64	f	3.439
26	6.3	0.39	f	0.400
26	6.1	0.45	f	0.597
26	6.0	0.39	m	0.611
26	6.1	0.46	f	1.130
24	5.5	0.32	m	0.366
26	6.0	0.44	m	0.359
26	6.4	0.41	f	0.359
25	5.7	0.34	m	0.146
29	7.0	0.55	f	0.995
24	5.4	0.30	m	0.443
25	5.5	0.38	m	0.478
27	6.3	0.43	m	0.346
27	6.3	0.44	f	0.514
28	6.4	0.46	m	0.968
30	7.2	0.62	f	2.013
26	5.9	0.40	m	0.822
26	6.2	0.44	m	0.509
25	5.8	0.37	m	0.667
22	5.7	0.35	f	0.528
25	5.6	0.35	m	0.632
28	6.7	0.50	f	0.877
25	5.9	0.37	f	1.076
28	7.3	0.63	f	1.134
28	7.2	0.53	f	1.069
8	1.9	0.02	j	0.004
13	3.1	0.05	j	0.023
12	3.0	0.05	j	0.011
12	3.0	0.04	j	0.018
11	2.8	0.02	j	0.039
8	2.1	0.02	j	0.010
8	1.9	0.02	j	0.011
9	2.1	0.02	j	0.014
6	1.2	0.01	j	0.000

Table A2 continued

L_t (mm)	L_{cox} (mm)	WM (g)	Sex	Lipof. (% AF)
Waldeckia obesa				
28	6.5	0.44	f	1.929
12	2.8	0.04	j	0.002
9	2.1	0.02	j	0.006
10	2.3	0.02	j	0.005
10	2.4	0.03	j	0.024
12	2.7	0.05	j	0.023
10	2.4	0.03	j	0.000
16	3.7	0.10	j	0.059
8	1.7	0.01	j	0.038
9	2.0	0.02	j	0.000
10	2.3	0.02	j	0.005
10	2.2	0.02	j	0.010
12	2.6	0.04	j	0.000
17	4.0	0.15	j	0.072
7	1.6	0.01	j	0.000
6	1.2	0.01	j	0.007
6	1.2	0.00	j	0.006
5	1.2	0.00	j	0.002
6	1.2	0.01	j	0.004
27	5.8	0.51	f	0.873
11	2.6	0.04	j	0.017
25	5.8	0.40	f	
23	5.4	0.34	m	
26	6.0	0.36	m	
27	6.3	0.42	m	
25	5.8	0.37	m	
21	5.2	0.31	f	
22	5.1	0.29	m	
28	6.5	0.47	f	
27	6.4	0.43	m	
23	5.5	0.34	f	
26	6.3	0.41	f	
24	5.7	0.36	m	
22	5.2	0.26	f	
28	6.3	0.44	f	
26	5.8	0.37	f	
26	5.7	0.33	m	
23	5.6	0.33	f	
20	4.9	0.20	f	
27	6.3	0.43	m	
20	4.8	0.19	m	
22	5.3	0.25	f	
21	4.7	0.19	f	
24	5.6	0.32	m	
22	5.3	0.27	m	

L_t (mm)	L_{cox} (mm)	WM (g)	Sex	Lipof. (% AF)
Waldeckia obesa				
30		0.68		
28	6.7	0.51	f	
13	3.1		j	
28	6.2	0.42	m	
	5.6	0.37	m	
24	5.6	0.34	f	
27	6.7	0.42	f	
28	6.7	0.45	f	
27	5.7	0.39	m	
29	6.5	0.53	m	
28	6.8	0.55	f	
29	6.9	0.53	f	
27	6.5	0.51	f	
31	7.1	0.70	f	
23	5.4	0.32	m	
28	6.8	0.51	f	
26	6.2	0.45	f	
26	6.5	0.45	f	
30	7.3	0.55	f	
23	5.5	0.33	f	
26	5.8	0.42	m	
27	6.7	0.46	f	
26	5.8	0.37	m	
27	6.4	0.42	f	
26	6.4	0.41	f	
26	6.2	0.47	f	
29	7.5	0.55	f	
26	6.0	0.37	m	
24	5.5	0.34	f	
27	6.4	0.46	m	
28	6.8	0.48	f	
27	6.6	0.43	f	
22	5.8	0.33	m	
28	7.2	0.52	f	
28	7.0	0.54	f	
23	5.8	0.32	f	
27	6.3	0.43	f	
28	7.2	0.61	f	
29	6.9	0.55	m	
25	5.9	0.36	f	
28	7.0	0.62	f	
25	5.8	0.37	m	
25	5.9	0.38	m	
28	7.3	0.60	f	
28	7.1	0.56	f	
28	7.2	0.55	f	

L_t (mm)	L_{cox} (mm)	WM (g)	Sex	Lipof. (% AF)
Waldeckia obesa				
26	6.1	0.37	m	
27	7.0	0.50	f	
25	6.2	0.40	f	
26	6.4	0.38	m	
25	5.9	0.40	m	
26	6.1	0.50	f	
29	7.0	0.66	f	
24	5.9	0.41	f	
24	5.9	0.42	f	
28	7.0	0.58	f	
25	5.6	0.35	m	
26	6.2	0.40	m	
27	6.5	0.55	f	
25	6.0	0.38	f	
27	6.8	0.57	f	
27	6.8	0.50	f	
27	5.3	0.28	m	
29	7.5	0.62	f	
27	6.7	0.53	f	
29	7.6	0.56	f	
11	2.8	0.05	j	
13	3.2	0.07	j	
13	3.3	0.06	j	
15	3.5	0.10	j	
14	3.3	0.07	j	
14	3.4	0.08	j	
12	3.0	0.06	j	
13	3.5	0.08	j	
12	3.2	0.06	j	
10	2.6	0.04	j	
12	3.2	0.07	j	
13	3.4	0.08	j	
10	2.7	0.05	j	
12	3.1	0.05	j	
14	3.4	0.08	j	
7	1.9	0.01	j	
12	2.9	0.06	j	
14	3.5	0.08	j	
10	2.5	0.03	j	
14	3.4	0.04	j	
12	2.9	0.05	j	
14	3.5	0.09	j	
10	2.4	0.03	j	
9	2.3	0.02	j	
12	2.9	0.06	j	
9	2.1	0.02	j	

Table A2 continued

L_t (mm)	**L_{cox}** (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Waldeckia obesa				
24	5.8	0.35	m	
22	5.0	0.25	f	
11	3.0	0.05	j	
12	2.9	0.05	j	
11	2.8	0.04	j	
12	3.1	0.06	j	
13	3.3	0.07	j	
9	2.2	0.03	j	
15	3.6	0.11	j	
11	2.8	0.05	j	
11	2.8	0.05	j	
13	3.2	0.06	j	
11	2.7	0.05	j	
9	1.2	0.03	j	
11	2.9	0.05	j	
11	2.6	0.04	j	
8	2.2	0.02	j	
8	2.0	0.02	j	
9	2.1	0.03	j	
11	2.6	0.05	j	
12	3.0	0.05	j	
10	2.5	0.03	j	
7	1.7	0.02	j	
7	1.6	0.01	j	
11	2.7	0.04	j	
6	1.6	0.01	j	
9	2.2	0.03	j	
7	1.7	0.02	j	
6	1.5	0.01	j	
8	1.9	0.02	j	
6	1.4	0.01	j	
7	1.5	0.01	j	
		0.29		
19	4.9	0.20	f	
18	4.5	0.20	m	
20	5.0	0.24	f	
15	4.0	0.14	j	
13	3.5	0.08	j	

L_t (mm)	**L_{cox}** (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Waldeckia obesa				
28	7.0	0.64	f	
27	6.6	0.45	f	
17	4.4	0.15	f	
14	3.5	0.09	j	
18	4.7	0.18	f	
18	5.0	0.19	f	
17	4.2	0.13	f	
18	4.8	0.17	f	
17	4.4	0.13	m	
17	4.2	0.16	f	
19	4.5	0.15	f	
18	4.4	0.15	m	
18	4.6	0.17	f	
20	4.6	0.19	f	
19	4.7	0.21	f	
18	4.4	0.16	m	
15	3.9	0.09	f	
18	4.4	0.14	f	
17	4.0	0.14	j	
19	4.5	0.19	m	
18	4.3	0.18	f	
20	4.7	0.19	m	
21	5.0	0.23	f	
15	3.7	0.08	j	
12	3.3	0.06	j	
12	2.9	0.05	j	
19	4.7	0.18	f	
14	3.5	0.07	j	
17	4.1	0.13	j	
20	5.0	0.19	m	
15	4.0	0.11	j	
19	5.3	0.22	f	
13	3.4	0.06	j	
19	4.6	0.19	f	
15	3.5	0.08	j	
18	4.7	0.17	f	
15	3.6	0.09	j	
10	2.6	0.03	j	

L_t (mm)	**L_{cox}** (mm)	**WM** (g)	**Sex**	**Lipof.** (% AF)
Waldeckia obesa				
10	2.4	0.03	j	
9	2.2	0.03	j	
10	2.4	0.03	j	
9	2.1	0.02	j	
9	2.0	0.02	j	
8	1.9	0.02	j	
6	1.3	0.01	j	
7	1.5	0.01	j	
8	1.8	0.02	j	
6	1.5	0.00	j	
9	2.2	0.03	j	
8	1.8	0.01	j	
7	1.6	0.01	j	
6	1.3	0.01	j	
6	1.2	0.01	j	
22	5.2	0.31	m	
18	4.3	0.18	f	
20	5.1	0.24	f	
16	4.2	0.12	f	
18	4.3	0.17	j	
18	4.7	0.18	f	
14	3.4	0.08	j	
18	4.7	0.19	f	
18	4.2	0.16	f	
18	4.6	0.19	m	
17	4.0	0.14	j	
18	4.6	0.17	m	
11	2.6	0.04	j	
11	2.6	0.04	j	
8	1.8	0.02	j	
8	1.8	0.01	j	
6	1.5	0.01	j	
9	2.0	0.02	j	
14	3.0	0.07	j	
10	2.3	0.03	j	
12	3.4	0.04	j	
15	3.8	0.10	j	

Table A3 Compilation of population parameters for *Notocrangon antarcticus* (Decapoda) and *Waldeckia obesa* (Amphipoda) (publications I-III, unpubl. results). For explanations of methods see chapter 2; *conversion factors from wet mass (g) to kJ by Salonen et al. (1976), Rumohr et al. (1987) and Brey et al. (1988). A_{max} = maximum age, AFDM = ash free dry mass, B = biomass, k = growth constant, L_∞ = asymptotic body length (cox = coxal plate length, CL = carapace length), M_{max} = maximum body mass, P = production, T_0 = age at which size is zero, VBGF = von Bertalanffy growth function, Z = mortality rate, ϕ ψ = growth performance parameters.

Parameter	**Method/ Reference**	***Waldeckia obesa***		***Notocrangon antarcticus***	
		Females	Males	Females	Males
a	log(gWM)	2.71		2.89	2.97
b	=a•log(mmL)-b	2.54		2.98	3.07
M_{max} (kJ)*		2.32	1.88	42.74	15.24
A_{max} (years)	Modal progression analysis	8	5	10	6
L_∞	Wetherall plot	•	•	22.27	16.93
W. obesa: L_{cox}	VBGF	7.35	6.92	22.34	16.93
N. antarcticus: L_{CL}	Gompertz	6.96	6.55	21.46	15.74
k (per year)	Wetherall plot	•	•	1.05	0.63
	VBGF	0.52	0.61	0.79	0.64
	Gompertz	0.89	1.02	1.62	1.22
t_0 (years)	VBGF	-0.49	-0.42	-0.76	-1.03
	Gompertz	-0.49	-0.39	0.04	-0.23
Z (per year)	Catch curve	0.27	0.43	0.44	0.92
	Brey (1995, 1999a)	•	•	0.41	0.85
B (g AFDM m^{-2})	based on 0.064 ind m^{-2}	•	•	0.039	0.004
P (g AFDM m^{-2})	(Gutt et al. 1991)	•	•	0.017	0.004
P/B (per year)	Z≈P/B	0.27	0.43	0.44	0.92
	MSGRM (VBGF)	0.41	0.58	0.30	0.39
	MSGRM (Gompertz)	0.41	0.58	0.44	0.46
		Juveniles	All		
	MSGRM (VBGF)	2.26	0.38	•	•
	MSGRM (Gompertz)	2.20	0.39	•	•
ϕ	(k from VBGF)	2.71	2.72	2.59	2.26
ψ	Brey (1995, 1999a)	-0.54	-0.42	0.63	0.40

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Bericht von den Fahrtabschnitten 1, 2 und 3, herausgegeben von D. Fütterer

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