Proc. NIPR Symp. Polar Biol., **1**, 56–62, 1987

LONGEVITY OF THE ANTARCTIC KRILL (*EUPHAUSIA SUPERBA* DANA) BASED ON A LABORATORY EXPERIMENT

Tsutomu IKEDA* and P. G. THOMAS

Antarctic Division, Department of Science, Channel Highway, Kingston, Tasmania 7150, Australia

Abstract: Laboratory observations over a 6-year period were made on the intermoult period (IP), changes in body length (BL) and maturity of 3 female and 3 male krill brought from Antarctic water to Australia. While the IP was stable over the period (range of individual means; 25.6–29.6 days), both BL and maturity changed greatly from one specimen to the next. Reversible modes shown in BL and maturity suggest that neither parameter is a good indicator of chronological age in this animal. Considering the age of krill at the beginning of this experiment (least 1–2 year old) krill lived for 7–8 years, which is considerably longer than the previously hypothesized 2–5 year life span of this animal.

1. Introduction

Controversy surrounds the growth and longevity of the Antarctic krill (*Euphausia superba* DANA). Modal size analysis of samples collected from Antarctic waters suggested a 2-year (RUUD, 1932; BARGMANN, 1945; MARR, 1962; MACKINTOSH, 1972) or 4-year (IVANOV, 1970) life cycle of this animal, depending on the number of peaks that appeared on the size frequency histogram. Recent computer analysis of the distribution mixtures of size frequency data identified up to 5-year old krill (SIEGEL, 1986). As noted by MAUCHLINE (1980), conclusions drawn from these size frequency analysis are subject to possible error due to the difficulty in ensuring that samples are taken from the same discrete krill population. To resolve this problem, MACKINTOSH (1972) proposed the need to rear krill under controlled experimental conditions to determine their growth rate.

Despite a long study history of krill dating back to the 1930's, experimental work on live krill began quite recently. Pioneer work made on board the ELTANIN by MCWHINNIE and MARCINIAK (1964) indicated extreme difficulty in keeping this animal alive for prolonged period in captivity. Following studies at the Antarctic stations (U.S. Palmer, South Georgia) however suggested that prolonged maintenance of krill in the laboratory was feasible (MACKINTOSH, 1967; CLARKE, 1976; MCWHINNIE *et al.*, 1979).

MURANO *et al.* (1979) was the first in successfully transport live krill outside Antarctic to enable continuation of long observation of growth and moulting of this animal. We adopted the same approach of remote transportion of live krill from

* Present address: Japan Sea Regional Fisheries Research Laboratory, 5939–22, Suido-cho 1-chome, Niigata 951.

Antarctic waters to Australia (IKEDA *et al.*, 1980). Preliminary results on intermoult period, growth and maturity of krill maintained in captivity for 3 years in Australia were reported elsewhere (IKEDA *et al.*, 1985). Reported here are the results gained from the extension of this experiment (IKEDA *et al.*, 1985) to a 6-year period.

2. Materials and Methods

Krill were collected during KAIYO MARU cruise to an area off Wilkes Land, Antarctica, in January 1980, and transported to a laboratory coldroom in Australia. Transportation procedures are detailed in IKEDA *et al.* (1980). Specimens (body length; 25 to 47 mm) were maintained individually (although some were paired male and female in the course of the experiment) in 1–4 litre glass bottles. Only 4 litre bottles were used after 1982.

Various food types (diatoms, frozen copepods, Tetra Marin) were used at the beginning of this experiment (1980 through 1982), but after 1982, the pennate diatom *Phaeodactylum tricornutum* (20 μm cell size) cultured in F-2 media at 10°C was used as the staple food at a concentration of 10^5–10^6 cells ml^{-1} (equivalent to 1–10 μg carbon ml^{-1}). The maximum phytoplankton concentration which krill encounter in the field is 0.5 μg carbon ml^{-1} (*cf.* IKEDA, 1985) which is a half the minimum food concentration employed in this study. Seawater (*ca.* 34‰) was changed weekly (twice weekly for paired individuals) at which the fresh food was provided (IKEDA and DIXON, 1982).

Bottles were placed on a bench or on a roller system, both installed in a coldroom maintained at −0.5 to 0.0°C. In Prydz Bay, Antarctica, where the krill were collected, annual water temperature variation rarely exceeds the range of −2.0 to 1.5°C. The experiment was run under subdued light (<0.6 W m^{-2}) or complete darkness. Bottles were examined daily for the presence of moults, from which intermoult period (IP) was determined. Collected moults were preserved in a buffered formalin-seawater for later measurement of the uropod exopodite length (UL) and the determination of maturity stages. Maturity of each individual was assessed from the morphology of the secondary sexual characters (petasma for males, thelycum for females) using MAKAROV and DENYS's (1980) system. From the UL, body length (BL, from the tip of the rostrum to the distal end of the telson) was estimated using the equation $BL=2.65+7.36UL$ (IKEDA and DIXON, 1982).

3. Results and Discussion

Of the 22 specimens initially selected in early 1980, 6 specimens (3 males, 3 females) survived through to 1986. This maintenance period of 6 years is considerably longer than any other previous study. Previous studies were of one year duration (MCWHINNIE *et al.*, 1979; MURANO *et al.*, 1979).

Prior to the present analysis, data obtained under different conditions from those specified in "Materials and methods" were omitted., *i.e.* data collected during periods of no food (specimen S-S2) in 1980, and higher temperature (2°C) in 1980–early 1982 (specimen H-M1) were omitted.

IP observed on these 6 specimens was rather stable over 6 years (Figs. 1a, 1b),

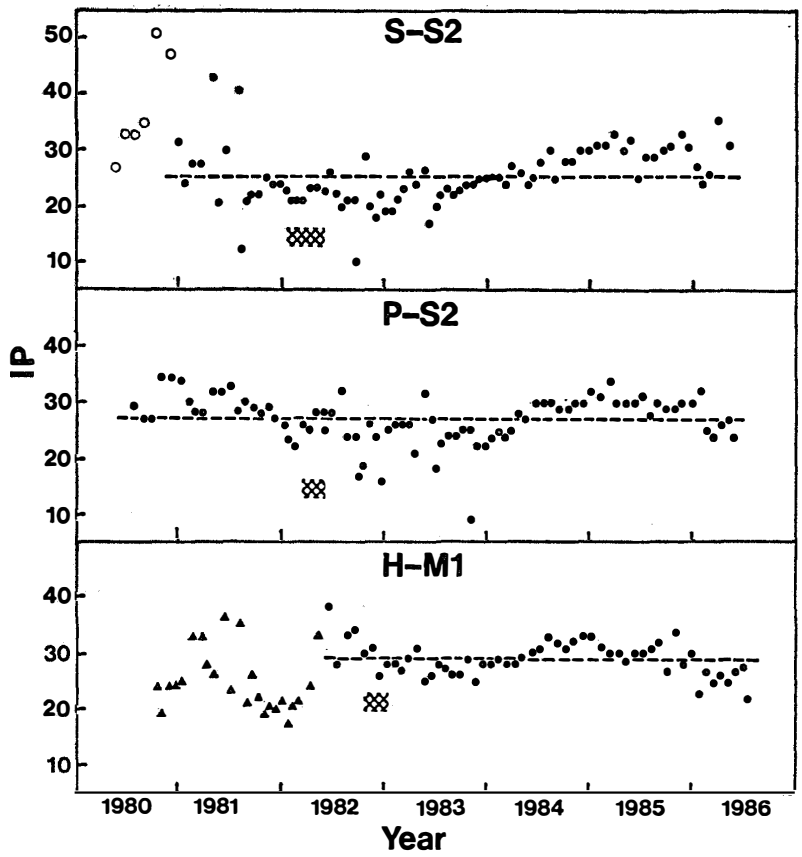

Fig. 1a. Changes in intermoult period (IP, days) over a 6-year period of 3 female krill. Open circle of S-S2 and solid triangle of H-M1 indicate data during a period of starvation and higher experimental temperature, respectively. Both these data are therefore omitted in Table 1. Horizontal hatched lines denote overall mean IP of each specimen. Meshed rectangles indicate the period when the maximum growth was seen (cf. Fig. 2a).

Table 1. Summary data of intermoult period (IP), change in body length (BL), the maximum growth rates in BL seen during the experiment, and correlation coefficient between IP and BL.

Specimen		IP (days)		BL (mm)				Max growth rate (mm day^{-1})	Correlation coefficient IP *vs.* BL (significance level)
		N	X (±1 SD)	Initial	Final	Max	Min		
Female	S-S2	81	25.6 (5.8)	28.9	38.9	45.5	24.4	0.053	0.180 (NS)
	P-S2	80	27.7 (4.4)	26.9	45.5	48.5	24.7	0.070	−0.125 (NS)
	H-M1	54	29.0 (3.0)	36.8	42.4	45.5	33.9	0.037	−0.071 (NS)
Male	P-L3	75	29.6 (2.9)	47.5	47.3	48.2	39.4	0.033	0.118 (NS)
	F-L1	74	28.2 (2.5)	46.8	42.7	48.5	40.7	0.031	0.363 ($p<0.01$)
	No. 1	60	29.2 (4.0)	34.4	40.9	45.5	34.4	0.033	0.280 ($p<0.05$)

and individual means ranged 25.6–29.0 days in females and 28.2–29.6 days in males. The regression analyses revealed that variations in IP were little correlated with those of BL in each specimen (Table 1). The general range of IPs obtained in this study is similar to those of IKEDA and DIXON (1982), IKEDA *et al.* (1985) and MAIHARA and ENDO (1986), but much longer than those of MACKINTOSH (1967) (13.5 days), MURANO

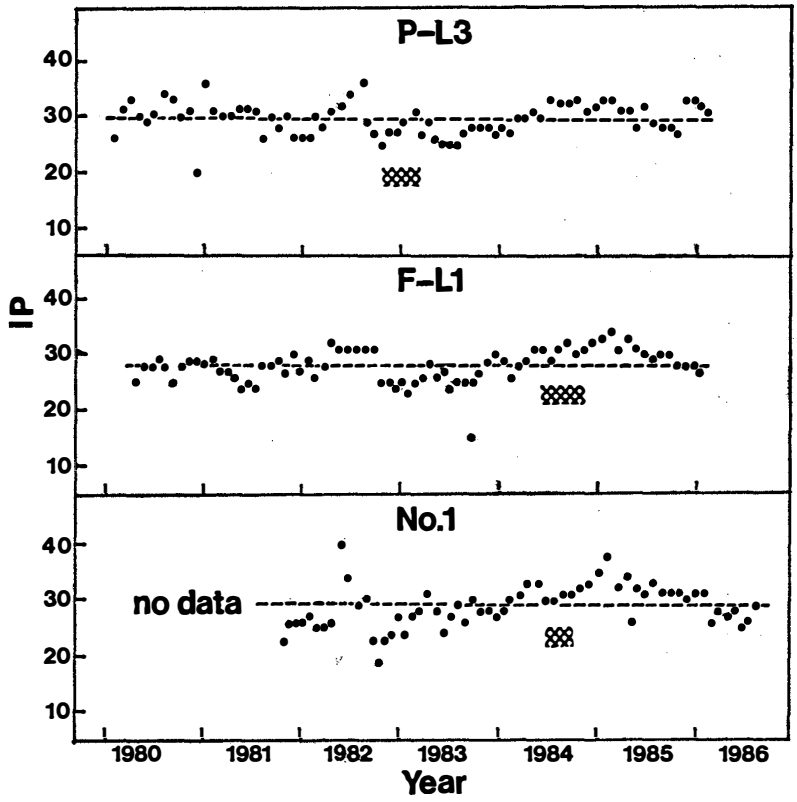

Fig. 1b. Changes in intermould period (IP, days) over a 6-year period of 3 male krill. For the specimen No. 1, data are available from late 1981. Horizontal hatched lines denote overall mean IP of each specimen. Meshed rectangles indicate the period when the maximum growth was seen (cf. Fig. 2b).

et al. (1979) (20.9 days), POLECK and DENYS (1982) (12.5–20.1 days) and MORRIS and KECK (1984) (14.3 days). IKEDA *et al.* (1985) discussed the possible cause(s) of this inconsistent result between workers, and concluded that differences in specimen body size, experimental conditions such as temperature, food or light can not be considered alone to be the major cause. Due to the diverse experimental design between workers and our present lack of knowledge about the effect of each different condition on IP, direct comparison of IP between studies is not possible.

In juvenile western rock lobsters (*Panulirus longipes*), isolation of individuals caused the extension of IP (CHITTLEBOROUGH, 1975). In our experiment, the male P-L3 and female P-S2 were paired since July 1983. IP of P-L3 before and after pairing remained unchanged (29.4±3.2 days *vs.* 29.9±1.6 days, $t=0.80$, $df=73$, $p>0.4$), and the same is true for the IP of P-S2 (27.3±5.5 days *vs.* 28.0±2.8 days, $t=0.70$, $df=78$, $p>0.4$). Thus, this effect is not obvious in krill.

In contrast with IP, the BL of these 6 specimens varied greatly from one specimen to the next, with each specimen showing phases of shrinkage and growth. The maximum BL reached during the 6-year period was 45.5–48.5 mm in females and 45.5–48.5 mm in males (Table 1). Progression and regression of maturity accompanied with the increase and decrease in BL, respectively, but this pattern became obscure after 1984 (see 1984–1985 data of S-S2, 1985 data of P-L3, Fig. 2a, 2b). The maximum growth rate range seen in the course of this experiment (0.033–0.070 mm

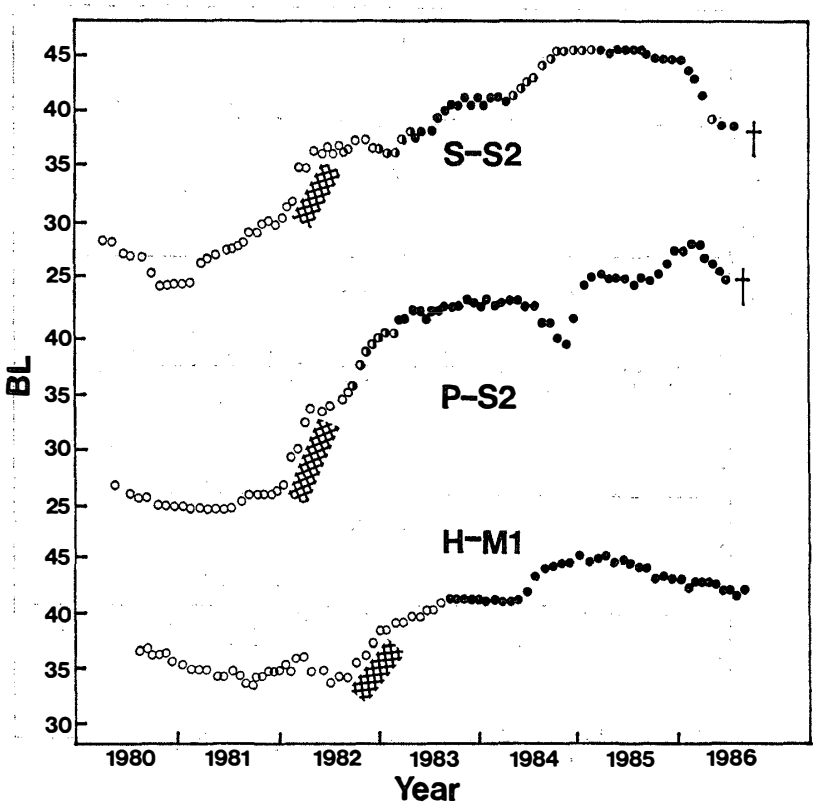

Fig. 2a. Changes in body length (BL, mm) and maturity stage over a 6-year period of 3 female krill. Open circles; juvenile stage, half-solid circles; sub-adult stage, solid circles; adult stage as determined from the morphology of the thelycum. Meshed rectangles indicate the period when the maximum growth was seen, crosses, the death of specimens.

day^{-1}) overlaps with the maximum rate observed by MURANO *et al.* (1979) (0.051 mm day^{-1}) and MAIHARA and ENDO (1986) (0.053 mm day^{-1}), and is similar to the range reported by POLECK and DENYS (1982) (0.037–0.068 mm day^{-1}).

Overall results obtained in this study indicate a complex nature of growth and maturation in krill. While their IP was rather stable under the present experimental conditions, both BL and maturity were not. The ability of adult krill to regress to the immature form was reported by MCWHINNIE *et al.* (1979) and POLECK and DENYS (1982). Maturity regression and progression is often accompanied with BL reduction and increment respectively (IKEDA *et al.*, 1985; THOMAS and IKEDA, 1987), however this is not always the case as mentioned earlier. The reversible growth and maturation modes seen in this species suggest that neither BL nor maturity stage is a good indicator of chronological age of juvenile and adult krill.

From the BL, the age of krill used in this experiment was estimated to be at least 1–2 years old at the beginning of this experiment. Then, the minimum age of these animals reached at the completion of this experiment in 1986 is 7–8 years old. This observed >7–8 year life span of krill is considerably longer than any previous estimates based on field samples (2–6 year life span), but supports the hypothetical longevity of 7.5–11.3 years proposed by IKEDA (1985). It can be argued, however, that since temperature, light and food supply were maintained at constant levels during this experi-

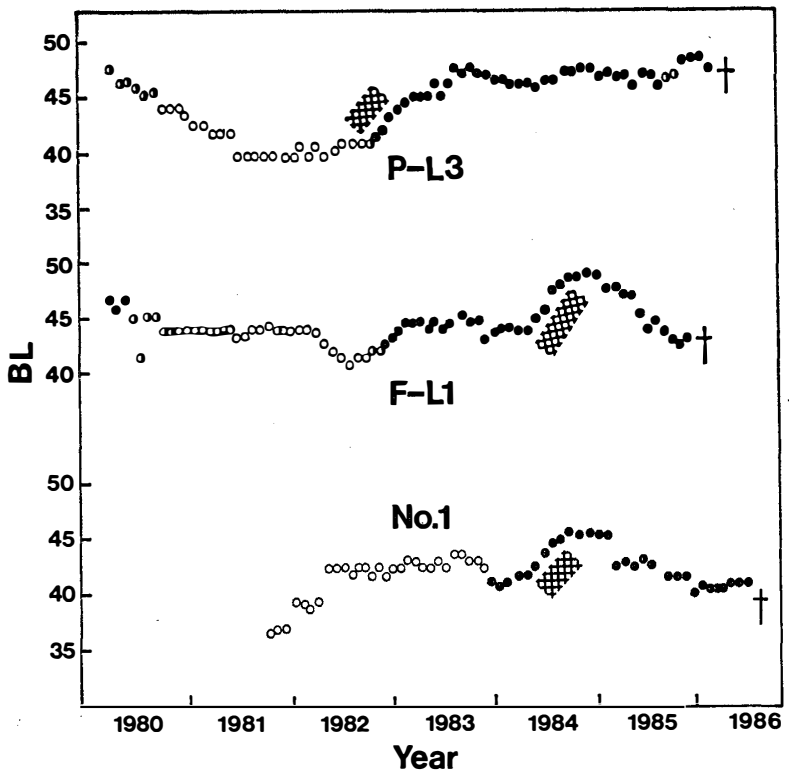

Fig. 2b. Changes in body length (BL, mm) and maturity stage over a 6-year period of 3 male krill. Open circles; sub-adult A stage, half-solid circles; sub-adult B-C stages, solid circles; adult stage as determined from the morphology of the petasma. Meshed rectangles indicate the duration when the maximum growth was seen, crosses, the death of specimens.

ment, the extrapolation of the present results to naturally living krill population requires caution. However, because of the difficulties associated in tracing the same discrete population of krill for years in the field, the evaluation of our conclusion of an extremely long life cycle of krill must await the refinement of age pigment technique which is recently developed (ETTERSHANK, 1984; NICOL, 1987).

Acknowledgment

We would like to thank Mr. M. STOLP for his assistance with this manuscript.

References

BARGMANN, H. E. (1945): The development and life-history of adolescent and adult krill, *Euphausia superba*. Discovery Rep., **23**, 103–176.

CHITTLEBOROUGH, R. G. (1975): Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res., **26**, 177–196.

CLARKE, A. (1976): Some observations on krill (*Euphausia superba* Dana) maintained alive in the laboratory. Br. Antarct. Surv. Bull., **43**, 111–118.

ETTERSHANK, G. (1984): A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*. J. Crust. Biol., **4** (Spec. No. 1), 295–305.

IKEDA, T. (1985): Life history of Antarctic krill *Euphausia superba*; A new look from an experimental approach. Bull. Mar. Sci., **37**, 599–608.

IKEDA, T. and DIXON, P. (1982): Observations on moulting in Antarctic krill (*Euphausia superba* Dana). Aust. J. Mar. Freshwater Res., **33**, 71–76.

IKEDA, T., MITCHELL, A. W., CARLETON, J. H. and DIXON, P. (1980): Transport of living Antarctic zooplankton to a tropical laboratory; A feasibility study. Aust. J. Mar. Freshwater Res., **31**, 271–274.

IKEDA, T., DIXON, P. and KIRKWOOD, J. (1985): Laboratory observations of moulting, growth and maturation in Antarctic krill (*Euphausia superba* Dana). Polar Biol., **4**, 1–18.

IVANOV, B. G. (1970): On the biology of the Antarctic krill *Euphausia superba*. Mar. Biol., **7**, 340–351.

MACKINTOSH, N. A. (1967): Maintenance of living *Euphausia superba* and frequency of moults. Nor. Hvalfangst-Tid., **56**, 97–102.

MACKINTOSH, N. A. (1972): Life cycle of Antarctic krill in relation to ice and water conditions. Discovery Rep., **36**, 1–94.

MAIHARA, Y. and ENDO, Y. (1986): Laboratory observations on molting and growth of Antarctic krill, *Euphausia superba* DANA (extended abstract). Mem. Natl Inst. Polar Res., Spec. Issue, **44**, 125–127.

MAKAROV, R. R. and DENYS, C. J. (1980): Stages of sexual maturity of *Euphausia superba* Dana. BIOMASS Handb. Ser., **11**, 1–11.

MARR, J. W. S. (1962): The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep., **32**, 33–464.

MAUCHLINE, J. (1980): The biology of mysids and euphausiids. Adv. Mar. Biol., **18**, 373–595.

MCWHINNIE, M. A. and MARCINIAK, P. (1964): Temperature responses and tissue respiration in Antarctic Crustacea with particular reference to the krill *Euphausia superba*. Biology of the Antarctic Seas, ed. by M. O. LEE. Washington, D. C., Am. Geophys. Union, 63–72 (Antarct. Res. Ser., Vol. 1).

MCWHINNIE, M. A., DENYS, C. J., PARKIN, R. and PARKIN, K. (1979): Biological investigation of *Euphausia superba* (krill). Antarct. J. U. S., **14**, 163–164.

MORRIS, D. J. and KECK, A. (1984): The time course of moult cycle and growth of *Euphausia superba* in the laboratory. A preliminary study. Meeresforschung, **30**, 94–100.

MURANO, M., SEGAWA, S. and KATO, M. (1979): Moult and growth of the Antarctic krill in laboratory. Trans. Tokyo Univ. Fish., **3**, 99–106.

NICOL, S. (1987): Some limitations on the use of the lipofuscin ageing technique. Mar. Biol., **93**, 609–614.

POLECK, T. P. and DENYS, C. J. (1982): Effect of temperature on molting, growth and maturation of the Antarctic krill *Euphausia superba* (Crustacea: Euphausiacea) under laboratory conditions. Mar. Biol., **70**, 255–265.

RUUD, J. T. (1932): On the biology of southern Euphausiidae. Hvalradets Skr., **2**, 1–105.

SIEGEL, V. (1986): Investigations on the biology of Antarctic krill, *Euphausia superba*, in the Bransfield Strait and adjacent areas. Mitt. Inst. Seefisch., Hamburg, **38**, 1–244 (in German).

THOMAS, P. G. and IKEDA, T. (1987): Sexual regression, shrinkage, re-maturation and growth of spent female *Euphausia superba* in the laboratory. Mar. Biol., **95**, 357–363.

(Received March 27, 1987; Revised manuscript received July 21, 1987)