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Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica

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Abstract Population dynamics of *Sterechinus neumayeri* were investigated at four sites in McMurdo Sound: Cape Evans, McMurdo Station, East Cape Armitage and New Harbor. The annual formation of natural growth bands in the jaws of the Aristotle's lantern was verified by a tagging-recapture experiment. Growth functions based on natural growth bands indicated differences among stations but showed *S. neumayeri* to be a slow growing species, reaching its maximum diameter of 70 mm at an age of about 40 yr. Annual production ranged between 2.4 (C. Evans) and 0.65 g ash free dry mass m⁻² (New Harbor) and was related to differences in food conditions. More than 95% of total production was invested in reproduction, and less than 5% was invested in somatic growth. Consumption estimates for *S. neumayeri* showed this species to play a significant role in the benthic trophic web of McMurdo Sound.

Introduction

Sterechinus neumayeri is the most abundant regular sea urchin in shallow Antarctic waters, being circum-

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arctic and subantarctic (to Kerguelen Island), and extending from the shore down to about 400 m water depth (Pawson 1969; Brey and Gutt 1991). Below this depth, the closely related species *S. antarcticus* is more abundant, which was found to show extremely slow growth (60 mm diameter at about 70 yr of age, see Brey 1991).

Sterechinus neumayeri is common on the western shores of Ross Island in McMurdo Sound, where it feeds mainly on benthic diatoms (reviewed by McClintock 1994) as well as on red algae and seal faeces (Dearborn 1965; Pearse and Giese 1966; Basch and Slattery unpublished). In deeper waters below the euphotic zone organic surface deposits are the primary food (observations from the Weddell Sea shelf, Brey unpublished). Predators of *S. neumayeri* include the starfish *Odontaster validus*, *Macroptychaster accrescens* and *Porania antarctica glabra* (McClintock 1994), and the sea anemone *Urticinaopsis antarcticus* (Dayton et al. 1970). It is likely that *S. neumayeri* is also preyed upon by other invertebrates as well as vertebrate predators. Spawning occurs in late austral spring to early summer (Pearse and Giese 1966; Yakovlev 1983), after an extended period of gametogenesis, with oogenesis requiring nearly 2 yr (Pearse and Bosch 1991). Development takes place in the water column and includes a typical pluteus larva; settlement and metamorphosis occur nearly 4 mo after fertilization (Bosch et al. 1987).

It is well established that individual sea urchin growth is strongly affected by habitat variability, especially food conditions (e.g. Ebert 1968). Hence, the purpose of this paper is to analyze the effects of contrasting environmental conditions at four sites in McMurdo Sound, Antarctica, on individual growth and population production of *Sterechinus neumayeri*. Moreover, we evaluate the significance of this sea urchin in the trophic web and energy flow of this high-Antarctic shallow water ecosystem.

Methods

Sampling sites and sampling

Populations of *S. neumayeri* were investigated at four different sites within McMurdo Sound: Cape Evans, McMurdo Station and East Cape Armitage located on the eastern side of the Sound, and New Harbor located on the western side (Fig. 1). The four sites have been described extensively by Dayton et al. (1974), Dayton and Oliver (1977), Dayton et al. (1986), McClintock et al. (1988), Knox (1990), Miller and Pearse (1991) and references therein. Table 1 summarizes the main physical and biological characteristics of these sites. Although strong year-to-year variations have to be considered, there are marked differences among the four sites: C. Evans and McMurdo Station are situated on the eastern side of the Sound, which is characterized by a tidally affected current regime, with a net water movement of about 6.8 km d^{-1} from north to south. New Harbor, on the western side of the Sound, as well as E. C. Armitage are exposed to currents moving northward from under the ice shelf. On the eastern side of the Sound there is an ice free period of about 3 to 5 mo yr^{-1} . The sea is ice free along the western side and at E. C. Armitage for only a short period in late summer, or not at all.

Correlated with the southerly current regime is a high level of pelagic primary production, as most of the pelagic production in McMurdo Sound results from advection of phytoplankton blooms from the open Ross Sea (Dayton and Oliver 1977; Knox 1990; Rivkin 1991). Pelagic primary production on the western side (New Harbor) is lower, and may be even lower at E. C. Armitage which does not benefit from this advection process at all. Sea-ice primary production depends mainly on the thickness of the snow layer on top of the ice, and may exhibit a small scale spatial distribution not related to the current regime in the Sound. Benthic microalgal production has not been measured directly, but, from differences in standing stock during the austral summer, Knox (1990) estimated minimum production on the eastern side to be about nine times higher than on the western side of the Sound. At C. Evans, dense standing stocks of red algae (*Iridaea cordata* and *Phyllophora antarctica*, Miller and Pearse 1991) occur, but their contribution to primary production is not known. Macrozoobenthic abundance is much higher on the eastern side than on the western side of the Sound, and presumably lowest at E. C. Armitage.

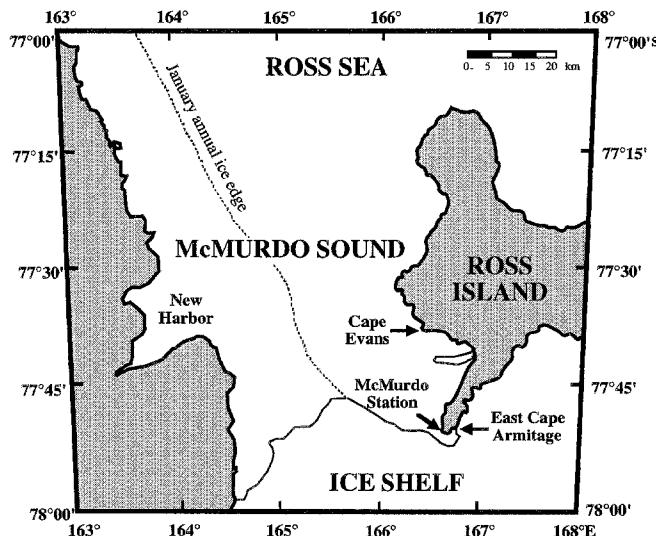


Fig. 1 Map of McMurdo Sound, Antarctica, showing the location of the four sampling sites

Abundance estimates

All counting, sampling and experimental work at the four sites was carried out using SCUBA. In Jan/Feb 1991 the abundance of *Sterechinus neumayeri* was estimated at C. Evans, McMurdo Station and New Harbor. At each station, three transects were run parallel to the shore between 20 and 25 m water depth, and ten quadrates (1 m^2) placed randomly along the transects were counted. In Sep 1993 divers estimated average abundance of *S. neumayeri* at C. Evans counting sea urchins along seven transects of 1 m width and 25 m length situated between 3 and 21 m water depth.

Tagging and recapture at McMurdo Station

More than 260 *Sterechinus neumayeri* were collected on 5 Dec 1989 in 15 to 18 m depth. About 110 specimens were transferred to the laboratory, the remaining 150 were held in mesh bags in sea water until the following day. These specimens were then injected with 1 to 3 ml (depending on sea urchin size) solution of tetracycline in filtered sea water (10 mg ml^{-1}). Tetracycline binds to sites of calcification, producing a fluorescent mark visible in ultra-violet light (Kobayashi and Taki 1969; Pearse and Pearse 1975). A total of 15 ind were placed in each of two cages ($122 \times 122 \times 15 \text{ cm}$) made of plastic coated mesh (2.5 cm) hardware cloth in about 15 m water depth in front of McMurdo Station. The remaining 120 ind were placed in three additional cages nearby and released a few days later. The time lag between tagging and release was conducted to allow sea urchins to recover from possible negative effects of handling and treatment with tetracycline. (During a previous experiment in 1984 all specimens were released directly after tetracycline injection and were killed within a few days by the starfish *Odontaster validus*.) On 6 Dec 1990, the two cages were removed from the sea bottom, and the surviving 26 ind were dried for later analysis. On the same day 104 free ranging specimens were collected from the release site and also dried. Of these, 34 turned out to be tagged (i.e., recovery rate = 28%).

Sampling at Cape Evans

On 4 Dec 1992, 487 ind of *Sterechinus neumayeri* were haphazardly collected from 6 to 8 m depth. Based on 40 specimens of various body size, relations between dry body mass, dry gonad mass and size were established. The lanterns of 150 ind were removed and preserved in ethanol for later growth analysis.

Sampling at East Cape Armitage and New Harbor

Abundance of *Sterechinus neumayeri* is very low at these two sites. A total of 16 and 7 specimens were collected and dried in 1991 from New Harbor and E. C. Armitage, respectively.

Growth analysis

Growth was estimated from annual growth increments identifiable in the tetracycline-tagged individuals (McMurdo Station) as well as from natural growth bands (McMurdo Station, Cape Evans, New Harbor, E.C. Armitage). For growth analysis we used the jaws (i.e. half pyramids) of Aristotle's lantern, in which growth bands are more conspicuous than in other skeletal elements (Brey 1991). After measuring the horizontal diameter of the test, the lantern was removed, cleaned of attached organic matter and separated into its elements by treatment in hot 5% NaOCl solution. The jaws were subsequently washed in 95% ethanol and dried. Jaw size was

Table 1 Characteristics of the four sites investigated at Cape Evans, McMurdo Station, East Cape Armitage and New Harbor. Data based on Barry (1988), Barry and Dayton (1988), Barry et al. (1994), Dayton and Oliver (1977), Dayton et al. (1974), Dayton et al. (1986), Knox (1990), McClintock et al. (1988), Miller and Pearse (1991), Rivkin (1991) and references therein

Characteristics	Cape Evans	McMurdo Station	East Cape Armitage	New Harbor
Currents	tidal, southerly trend	tidal, southerly trend	mostly westwards	constant & slow northwards
Sea ice				
Max. thickness	2 m	2 m	3 m	3 m
Snow cover	little snow cover	snow cover	heavy snow cover	heavy snow cover
Maximum ice-free period	Dec–Apr every year	Jan/Feb–Mar every year	Mar most years	Mar not every year
Primary production				
Phytoplankton	44–100	44–100	No data	22–50 ^a
Sea ice algae	12	< 12	No data	No data
Benthic macroalgae	No data	No data	No data	No data
Benthic microalgae (g C m ⁻² yr ⁻¹)	± 32 ^b	± 12 ^b	No data	± 4 ^b
Sedimentation (g C m ⁻² yr ⁻¹)	21	21	No data	6
Sampling site				
Depth (m)	6–8	15–18	15–20	20
Slope	45°	10–25°	45°	10–25°
Sediments	sand & gravel	mud & gravel	cobbles	mud & silt
Seal faeces	abundant	abundant	very rare	none
Benthos				
Microalgae ^c (g C m ⁻²)	7.7–24.0	4.1–8.6	No data	0.5–3.8
Macroalgae	dense stands in 3.5 m & below 12 m depth	distinctly less abundant than at Cape Evans	distinctly less abundant than at Cape Evans	very rare
Zoobenthos				
Abundance (ind m ⁻²)	No data	120000 (20–40 m depth)	No data	10000 (20–40 m depth)
Dominant taxa	Nemertini, Echinoidea, Gastropoda, Asteroidea,	Cnidaria, Nemertini, Polychaeta, Bivalvia, Gastropoda, Echinoidea, Asteroidea,	Cnidaria, Pygmonida, Ophiuroidea	Ophiuroidea, Crinoidea, Echinoidea, Asteroidea, Bivalvia

^a Estimate based on biomass differences between western and eastern Sound

^b Minimum estimates of Knox (1990)

^c In austral summer

measured from the tip to the upper inner edge. The position of the tetracycline mark was determined using a 350 nm UV-B lamp. To analyze natural growth bands, jaws were ground smooth to a thickness of ≤ 1 mm (Brey 1991), submerged in tert-butyl-methyl-ether and examined using a stereo microscope.

Tetracycline growth bands of individuals from McMurdo Station were treated as size-increment data (SID), i.e. data pairs of size S_1 at time of tagging t_1 and size S_2 at time of recapture t_2 (one year later). Natural growth band readings were treated as size-at-age data (SAD). The hypothesis that natural growth bands are produced annually was tested by comparing growth curves derived from SID and SAD based on the same set of specimens. Asymptotic size (S_∞) and the growth constant (K) of the Gompertz growth function,

$$S_t = S_\infty \times e^{-e^{-K(t-t_0)}}, \quad (1)$$

which was algebraically re-arranged for use with SID

$$\ln(S_2) = \ln(S_\infty) \times (1 - e^{-K(t_2 - t_1)}) + \ln(S_1) \times (e^{-K(t_2 - t_1)}), \quad (2)$$

were estimated using the SIMPLEX algorithm (see Press et al. 1986).

In all the other cases, the general growth model of Schnute (1981) was employed to establish growth functions:

$$S_t = \left\{ Y_1^B + (Y_2^B - Y_1^B) \times \left[\frac{1 - e^{-A(t - \tau_1)}}{1 - e^{-A(\tau_2 - \tau_1)}} \right] \right\} 1/B. \quad (3)$$

The model includes four parameters, two constants A (time⁻¹) and B (dimensionless) and the size Y_1 and Y_2 . The two age values τ_1 , τ_2 are chosen by the user, e.g. youngest and oldest individual in sample. The starting values of Y_1 and Y_2 are set accordingly. Special cases of this general model resemble historical growth models such as the von Bertalanffy, Richards, or Gompertz models.

Differences in growth among different sites were checked by analysis of variance of the residuals of the common growth function.

Productivity and production

Somatic production was computed by the mass-specific growth rate method according to Crisp (1984) from (i) the size-frequency

distribution, (ii) the size-growth function and (iii) the size-body mass relation derived from C. Evans specimens. Production per "total catch" P_S was computed by:

$$P_S = \sum N_i \times M_i \times G_i, \quad (4)$$

where N_i is the number of individuals in size class i , M_i is the mean individual body mass in size class i , and G_i is the corresponding annual mass-specific growth rate, computed by:

$$G_i = b \times (1/S_i) \times (A/B) \times S_i^{1-B} \times \left[Y_1^B - \frac{Y_2^B - Y_1^B}{e^{-A(\tau_2 - \tau_1)}} - S_i^B \right] \quad (5)$$

b is the slope of the size-mass regression (see below), S_i is mean size in size class i and A , B , Y_1 , Y_2 , τ_1 and τ_2 are parameters of Schnute's generalized growth model (Eq. 3).

Gonad mass was computed from the size-frequency distribution and the size-gonad mass relation established at C. Evans, which was used for all sites. Gonad production was computed from abundance, gonad mass and an annual gonad output of 60% of maximum gonad mass (see Pearse and Giese 1966):

$$P_G = \sum N_i \times M_{G,i} \times 0.6. \quad (6)$$

The annual somatic production/biomass ratio P_S/B_S was calculated from production P_S and somatic biomass per total catch B_S :

$$B_S = \sum N_i \times M_i, \quad (7)$$

and total biomass was computed by:

$$B = B_S + B_G = B_S + \sum N_i \times M_{G,i}. \quad (8)$$

Annual production of *Sterechinus neumayeri* per square meter was computed by multiplying the P/B ratio with an estimate of average biomass derived from mean body mass per total catch M_{mean} and abundance counts in the field, N_{field} :

$$P = P/B \times M_{mean} \times N_{field} [\text{g m}^{-2} \text{ yr}^{-1}]. \quad (9)$$

Dry mass (DM) was converted to ash free dry mass (AFDM) by the following factors (Brey unpublished)

Body: AFDM = 0.13 × DM

Gonads: AFDM = 0.90 × DM.

Results

Morphometrics

Mean jaw size/test diameter ratio varied between 0.200 (McMurdo Station free ranging specimens) and 0.247

(E. C. Armitage). The ratio was significantly different between all sites except between C. Evans and New Harbor (Table 2), no difference was found between caged and free ranging specimens at McMurdo Station. Therefore three different regression lines were fitted for the jaw size-test diameter relation (Fig. 2).

At C. Evans the relations between dry mass (DM) and test diameter (D) were found to be

Somatic: $\log(g \text{ DM}) = -3.804 + 2.769 \times \log(\text{mm D})$; $N = 40$; $r^2 = 0.944$

Gonad: $\log(g \text{ DM}) = -5.510 + 3.497 \times \log(\text{mm D})$; $N = 40$; $r^2 = 0.817$.

No significant differences in intercept or slope ($\alpha = 0.05$) were found between the regressions for male ($N = 15$) and female ($N = 25$) individuals.

Abundance and size distribution

In 1991, mean abundance of *Sterechinus neumayeri* in the 20 to 25 m depth range was found to be 0.40 ind m^{-2} ($SD = 0.10$) at McMurdo Station and 0.77 ind m^{-2} ($SD = 0.21$) at C. Evans. In 1993 average abundance at C. Evans was 2.70 ind m^{-2} ($SD = 2.30$) between 3 and 21 m water depth (0.6, 1.4, 1.0, 6.6, 4.9, 3.3 and 1.2 ind m^{-2} in 3, 6, 9, 12, 15, 18 and 21 m depth, respectively). At both stations the majority of individuals (68% at McMurdo Station and 95% at C. Evans) ranged between 40 and 60 mm in diameter (Fig. 3). No specimens < 30 mm diameter were found. At New Harbor, mean abundance was computed to be 0.27 ind m^{-2} ($SD = 0.12$) in 1991. The 16 specimens collected ranged from 45 to 68 mm in diameter ($mean = 56.5$, $SD = 6.7$). No abundance estimates were made at E. C. Armitage. However, during the 1991 sampling only seven specimens were found, despite the same diving time as at New Harbor and a much more careful search for sea urchins. The specimens collected from this site were also distinctly smaller, ranging from 28 to 39 mm in diameter ($mean = 31.9$, $SD = 3.8$).

Table 2 *Sterechinus neumayeri*.

Analysis of variance (ANOVA) of differences in the jaw size/test diameter (J/D) ratio among sites and Bonferroni/Dunn post-hoc test on differences between means

ANOVA, Source	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	
Site	4	0.028	0.007	23.037	< 0.001	
Residual	228	0.071	0.0003			
Bonferroni/Dunn, Site		Mean J/D	SD	McM. free	C. Evans	N. Harbor
McMurdo caged	0.205	0.017	—	*	*	*
McMurdo free	0.200	0.018		*	*	*
C. Evans	0.219	0.019			—	*
New Harbor	0.219	0.011				*
E.C. Armitage	0.247	0.014				

* Significant difference at $\alpha = 0.05$; – no significant difference

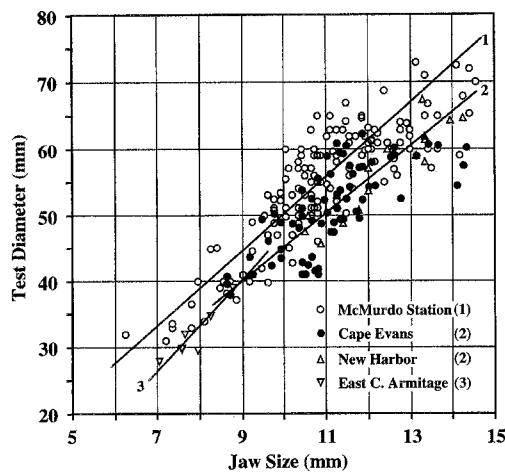


Fig. 2 *Sterechinus neumayeri*. Regression between test diameter D (mm) and jaw size J (mm), geometric mean regression model according to Ricker (1973). McMurdo Station: $D = -6.149 + 5.565 \times J$; $N = 137$, $r^2 = 0.748$; Cape Evans and New Harbor: $D = -6.865 + 5.185 \times J$; $N = 89$, $r^2 = 0.629$; Cape Armitage: $D = -22.121 + 6.892 \times J$; $N = 7$, $r^2 = 0.844$

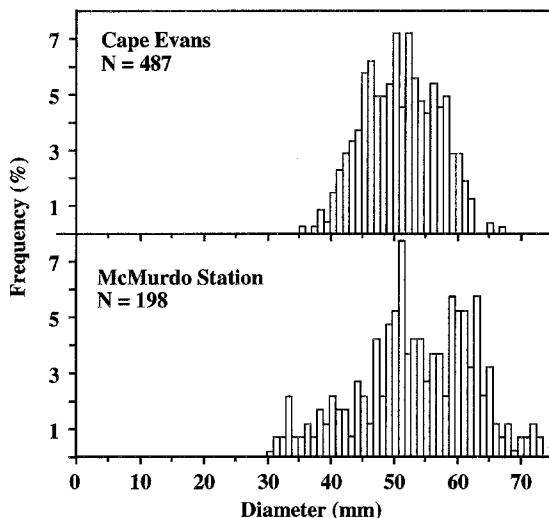


Fig. 3 *Sterechinus neumayeri*. Size-frequency distribution at Cape Evans in December 1992 and at McMurdo Station in December (composed of the 130 specimens collected in 1990 and 68 specimens collected in 1989 and remaining from laboratory experiments)

Growth

Natural growth lines in the jaws consisted of alternating opaque zones (light in reflected light, dark in transmitted light) and translucent zones (dark in reflected light, light in transmitted light, Fig. 4), as observed in other parts of echinoid skeletons by Pearse and Pearse (1975) and others. On the leading edge of most jaws a very narrow opaque zone was visible, preceded by alternating broader translucent and opaque zones. The tetracycline marks were clearly visible in the UV light

as distinct green lines in 59 of the 60 tagged individuals. The mark was situated at the transition from the second to last translucent zone to the following opaque zone (Fig. 4b, c). One specimen showed a very weak and less distinct mark and was excluded from further analysis.

Evaluation of natural growth line formation

The 59 specimens recovered from McMurdo Station that showed distinct tetracycline labels were used to compare growth estimates based on tagging-recapture data and natural growth line counts. The size-increment data were fitted best by a Gompertz growth function

$$J_t = 14.02 \text{ mm} \times e^{-e^{-0.107t}}; R^2 = 0.994.$$

No significant difference ($P = 0.129$) was found between caged and free ranging specimens. The function fitted to size-at-age data derived from natural growth line readings of the same 59 specimens was very similar

$$J_t = 14.13 \text{ mm} \times e^{-e^{-0.093(t-2.411)}}; R^2 = 0.747.$$

Individual age inferred from this function is linearly related to age inferred from the above growth function based on size-increment data. The slope of the regression does not differ significantly from 1.0 ($\alpha = 0.05$; Fig. 5), indicating natural growth lines are formed annually.

Size-at-age data from all sites

Natural growth lines were counted in 83 specimens from McMurdo Station, 73 specimens from C. Evans, 16 specimens from New Harbor and 7 specimens from E. C. Armitage. Schnute's generalized growth model was fitted to these 179 data pairs of jaw size J-at-age data as well as test diameter S-at-age data (Fig. 6). The resulting growth curves corresponded to generalized von Bertalanffy functions (Table 3)

$$J_t = 30.98 \text{ mm} \times [1 - e^{-0.001(t-1.628)}]^{0.238}$$

$$S_t = 70.23 \text{ mm} \times [1 - e^{-0.031(t-1.651)}]^{0.267}.$$

A subsequent analysis of the residuals of the jaw size growth functions showed significant differences between E. C. Armitage and the other three sites (Table 4), whereas the residuals of the test diameter growth function also showed a significant difference between McMurdo Station and C. Evans and New Harbor (Table 5). Consequently, the test diameter growth functions fitted separately to the data from McMurdo Station (generalized von Bertalanffy function)

$$S_t = 68.17 \text{ mm} \times [1 - e^{-0.100(t+2.481)}]^{0.880}$$

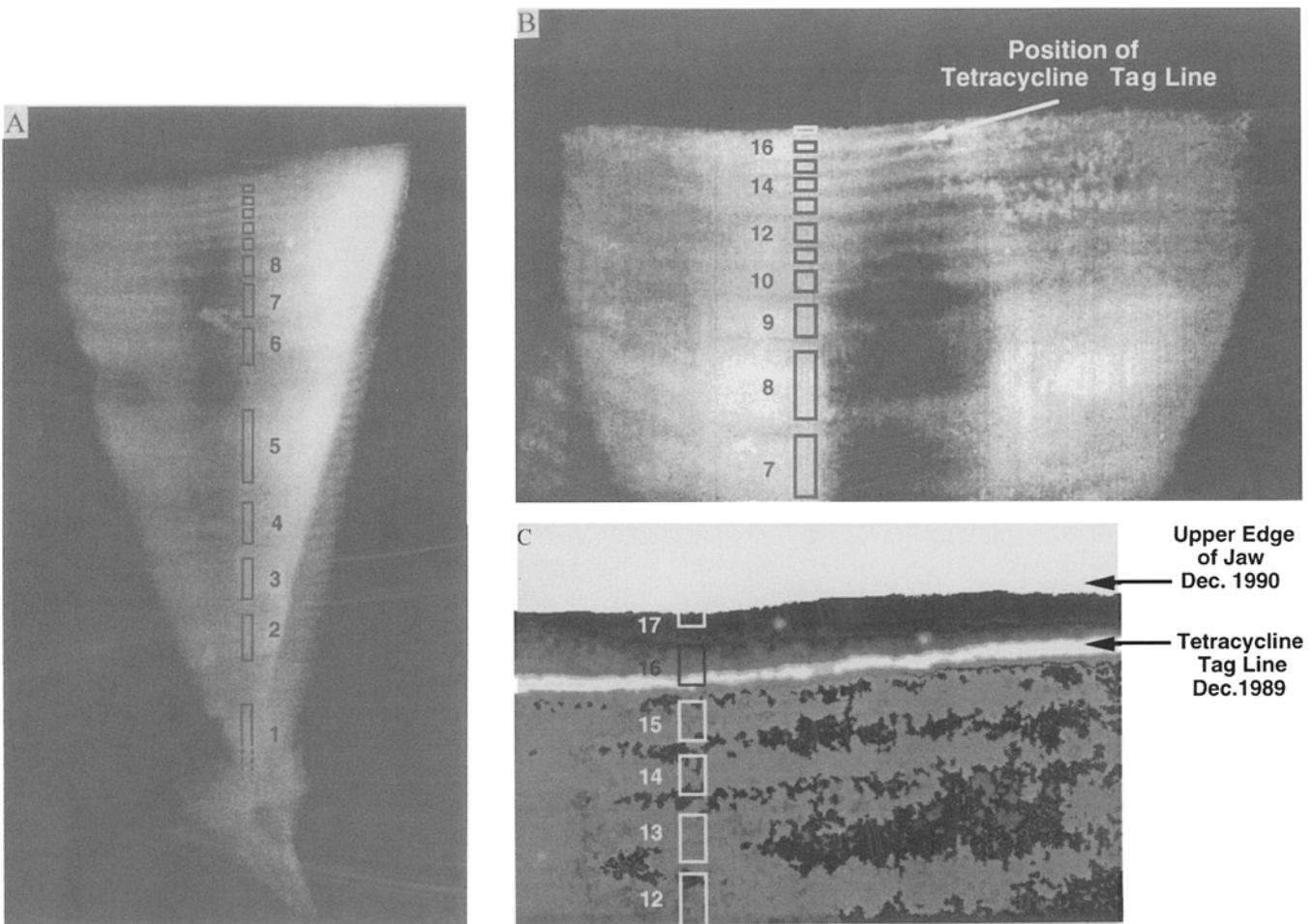


Fig. 4 *Sterechinus neumayeri*. Growth bands in the jaw. Tetracycline labelled free ranging specimen from McMurdo Station (test diameter 62.0 mm, jaw size 11.9 mm, 17 growth bands). Photographs taken by either stereo microscope or compound microscope and subsequently digitized. **A** View of total jaw in reflected light. Bars indicate the first 13 growth bands. The unusual width of light band No. 5 and the subsequent dark band may indicate a difficult to identify intermittent growth band. **B** Enlarged view of upper jaw edge. Original photograph was taken in transmitting light, but was electronically inverted, i.e. zones of rapid growth appear light. Brightness, brilliance and contrast have been modified to show most recent growth lines. Arrow indicates tetracycline tag line running parallel to the natural dark growth line. **C** Detailed microscopic view ($\times 100$) of upper jaw edge in reflected UV light. Brightness, brilliance and contrast have been modified to show both the tetracycline label (bright line) and preceding natural growth lines

and from C. Evans and New Harbor (Richards function)

$$S_t = 66.49 \times [1 - (1/0.446) \times e^{-0.072(t-2.597)}]^{-0.446}$$

were distinctly different (Fig. 7). The limited number and range of data did not allow for the computation of a separate growth curve for E. C. Armitage.

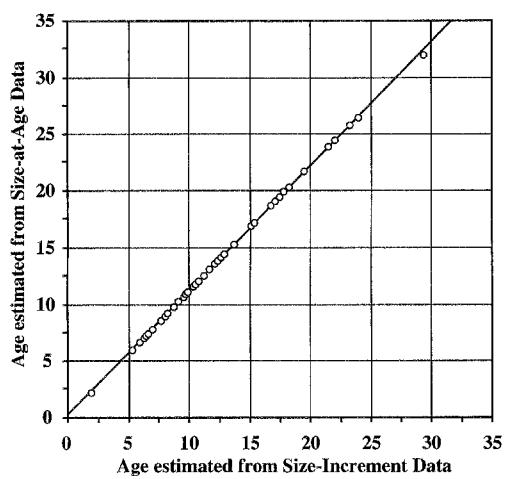


Fig. 5 *Sterechinus neumayeri*. Relation between age estimated from size-at-age data (SAD, natural growth band counts) and age estimated from size-increment data (SID, tetracycline tagging) at McMurdo Station. Age_{SID} and Age_{SAD} were computed from size J_t using Gompertz growth functions fitted to the size-increment data and to the size-at-age data (setting t_0 from 2.411 to zero for comparability), respectively. SID: $J_t = 14.02 \text{ mm} \times e^{-e^{-0.107t}}$; SAD: $J_t = 14.13 \text{ mm} \times e^{-e^{-0.093t}}$; Age_{SAD} = $0.243 + 1.098 \text{ Age}_{\text{SID}}$; $N = 57$; $r^2 = 0.999$. Two of the 59 tagged specimens are not included in the regression because $J_t > J_\infty$ for one or both growth functions

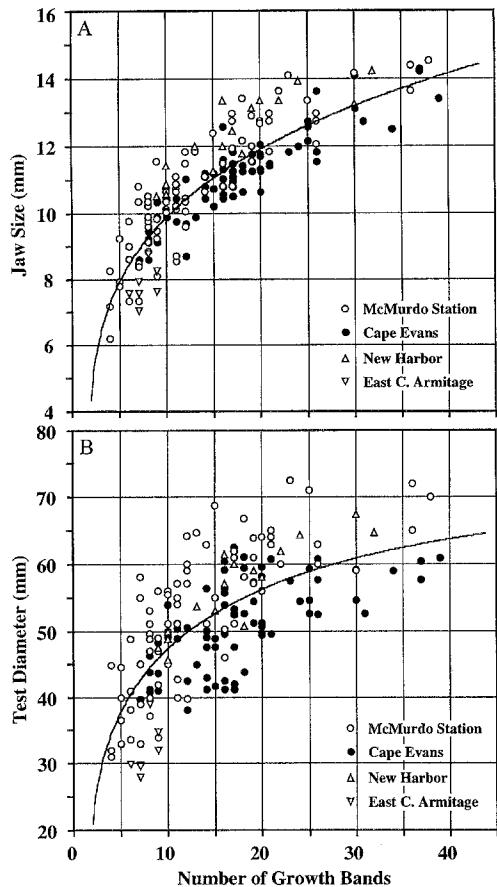


Fig. 6 *Sterechinus neumayeri*. Schnute's growth model fitted to 179 size-at-age data pairs. **A** Size = Jaw size: generalized von Bertalanffy function, $J_t = 30.98 \text{ mm} \times (1 - e^{-0.001(t-1.628)})^{0.238}$; **B** Size = Test diameter: generalized von Bertalanffy function, $D_t = 70.23 \text{ mm} \times (1 - e^{-0.031(t-1.651)})^{0.267}$

Productivity and production

Individual production

The relation between test diameter and individual production of *Sterechinus neumayeri* is shown in Fig. 8A (DM) and B (AFDM). Somatic production increased with diameter up to 43 and 52 mm at McMurdo Station and C. Evans and New Harbor, respectively, and then decreased again. At McMurdo Station the slope of this curve was much steeper, and the maximum was about 2.6 times higher than at C. Evans and New Harbor. Gonad production increased exponentially with increasing diameter. In terms of AFDM, gonad production exceeded peak somatic production by factors of 5.7 (McMurdo Station, 43 mm size class) and 36.7 (C. Evans and New Harbor, 52 mm size class).

Population production

At McMurdo Station, the annual P/B ratio was 0.208 and 0.450 when based on DM and AFDM, respectively

Table 3 *Sterechinus neumayeri*. Parameters of Schnute's general growth model fitted to different data sets. The parameters τ_1 and τ_2 were set to $\tau_1 = 7$ and $\tau_2 = 40$ in all cases. (S size; K , D , growth constants; t_0 , age at size zero.) Generalized von Bertalanffy model: $S_t = S_\infty \times (1 - e^{-K(t-t_0)})^D$; Richards function: $S_t = S_\infty \times (1 + D/(e^{K(t-t_0)} - 1))^{-D}$

Data set	<i>N</i>	Dependent variable	Y_1 (mm)	Y_2 (mm)	$A \cdot yr^{-1}$	B	R^2	Corresponding historical model	S_∞	K	D	t_0
All sites	179	Jaw size	8.903	14.172	0.001	4.194	0.787	von Bertalanffy	30.98	0.001	0.238	1.628
All sites	179	Test diam.	42.540	63.738	0.031	3.748	0.481	von Bertalanffy	70.23	0.031	0.267	1.651
McMurdo Station	83	Test diam.	44.276	67.308	0.100	1.136	0.634	von Bertalanffy	68.17	0.100	0.880	-2.481
C. Evans & N. Harbor	89	Test diam.	43.173	62.431	0.072	-2.241	0.498	Richards	66.49	0.072	0.446	2.597

Table 4 *Sterechinus neumayeri*. Growth of jaw: analysis of variance (ANOVA) of differences in the residuals of the common growth function among sites and Bonferroni/Dunn post-hoc test on differences between means

ANOVA, Source	df	SS	MS	F	P
Site	3	29.847	9.949	19.965	< 0.001
Residual	175	87.207	0.499		
Bonferroni/Dunn, Site					
	Mean Residual	C. Evans	N. Harbor	E. C. Armit.	
McMurdo Stat.	0.205	—	—	*	
C. Evans	0.219	—	—	*	
New Harbor	0.219	—	—	*	
E.C. Armitage	0.247	—	—	*	

* Significant difference at $\alpha = 0.05$; — no significant difference

Table 5 *Sterechinus neumayeri*. Growth of test: analysis of variance (ANOVA) of differences in the residuals of the common growth function among sites and Bonferroni/Dunn post-hoc test on differences between means

ANOVA, Source	df	SS	MS	F	P
Site	3	2230.524	910.175	27.128	< 0.001
Residual	175	5871.446	33.551		
Bonferroni/Dunn, Site					
	Mean Residual	C. Evans	N. Harbor	E. C. Armit.	
McMurdo Stat.	3.595	*	*	*	
C. Evans	— 2.457	—	—	*	
New Harbor	— 1.793	—	—	*	
E.C. Armitage	— 12.906	—	—	*	

* Significant difference at $\alpha = 0.05$; — no significant difference

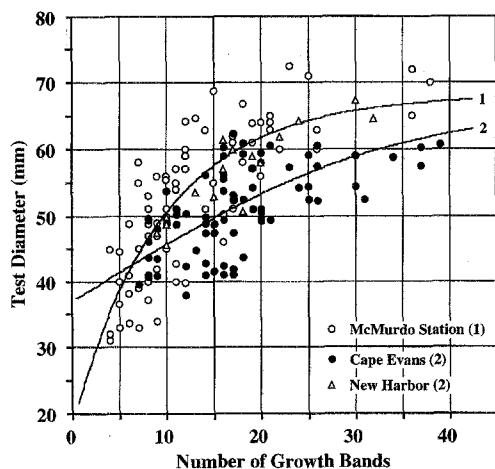


Fig. 7 *Sterechinus neumayeri*. Schnute's growth model fitted to 83 diameter-at-age data pairs from McMurdo Station and to 89 diameter-at-age data pairs from C. Evans and New Harbor. McMurdo Station: generalized von Bertalanffy function, $S_t = 68.17 \text{ mm} \times (1 - e^{-0.100(t+2.481)})^{0.880}$, C. Evans and New Harbor: Richards function, $S_t = 66.49 \times (1 + 1/D \times e^{-0.072(t-2.597)})^{-0.449}$ (Open circles McMurdo Station; filled circles C. Evans; open triangles New Harbor).

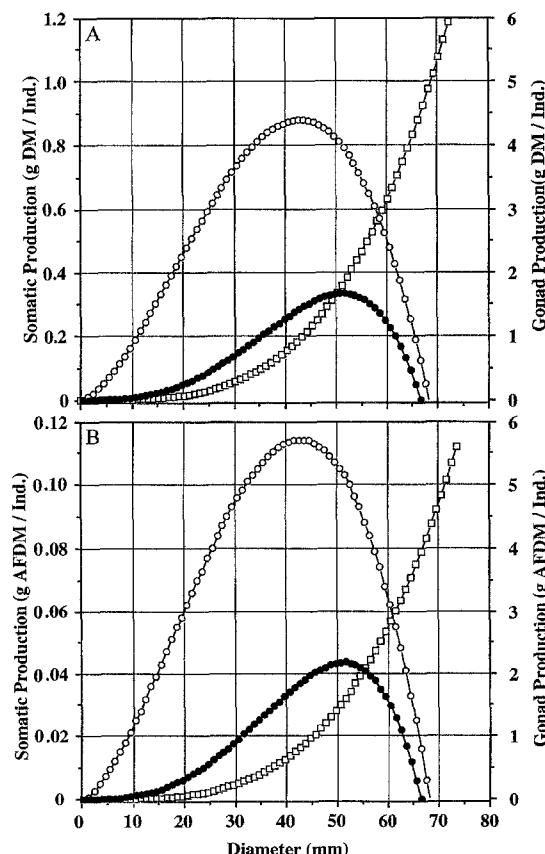


Fig. 8 *Sterechinus neumayeri*. Relation between test diameter and individual production at McMurdo Station and C. Evans (also New Harbor). A Dry mass (DM), B ash free dry mass (AFDM). (Open circles somatic production at McMurdo Station; filled circles somatic production at C. Evans; open squares gonad production at both stations)

(Table 6). Total production amounted to $1.19 \text{ g DM m}^{-2} \text{ yr}^{-1}$ ($0.88 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$). 79% (DM) or 96% (AFDM) of this total was comprised of gonad production. At C. Evans, the annual P/B ratio was slightly lower, 0.183 (DM) and 0.436 (AFDM), respectively (Table 6). Because of the higher abundance, total production was much higher at this site, $3.01 \text{ g DM m}^{-2} \text{ yr}^{-1}$ ($2.40 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) in 6 to 8 m depth and $5.86 \text{ g DM m}^{-2} \text{ yr}^{-1}$ ($4.63 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) for the whole depth range (3 to 21 m). 86% (DM) or 98% (AFDM) of this total was comprised of gonad production. At New Harbor, the annual P/B ratio was estimated to be 0.182 (DM) and 0.436 (AFDM), whereas production was estimated to be $0.78 \text{ g DM m}^{-2} \text{ yr}^{-1}$ ($0.65 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$).

For E. C. Armitage, insufficient data do not allow estimates of productivity and production, but the low growth rate (Table 6), the small average size (Fig. 6) and the very low abundance should result in population production values much lower than at the other sites.

Discussion

Growth band formation

Patterns of alternating translucent and opaque zones in skeletal elements of echinoids have been reported for many species (Birkeland and Chia 1971; Miller and Mann 1973; Crapp and Wills 1975; Pearse and Pearse 1975; Gage and Tyler 1985; Gage 1992 and others). However, feeding experiments showed that these bands

are not necessarily formed annually (Pearse and Pearse 1975). Only in a few cases an annual rhythm of band formation could be demonstrated by controlled growth experiments in aquaria (Miller and Mann 1973) or by labelling experiments (Gage 1992). The similarity of growth parameter values and of age estimates derived from size-increment data and from natural growth bands in *Sterechinus neumayeri* at McMurdo Station (Fig. 5) provide some of the most convincing data indicating annual formation of growth bands in any echinoid. Such annual patterns might be expected for an environment with extreme seasonal variation.

The position of the tetracycline mark at the transition from the second to last translucent to the subsequent opaque zone (Fig. 4b, c) indicates that two growth bands are formed per year. These are comprised of a translucent band formed before December and an opaque band formed after December. Pearse and Pearse (1975) found translucent bands to be formed during periods of slow growth, and opaque bands during periods of rapid growth. Therefore, *Sterechinus neumayeri* seems to grow slowly during the austral winter/spring until December and then rapidly during the austral summer/fall. The narrow opaque band observed at the edge of most jaws indicates rapid growth initiated slightly before sampling in December. Onset of growth may be triggered by the influx of phytoplankton into McMurdo Sound, beginning at the end of November (Knox 1990; Rivkin 1991). Alternatively, it could be a response to increasing photoperiod. Pearse et al. (1986) found in a temperate sea urchin that somatic growth was enhanced, and gametogenesis suppressed during increasing day-lengths. In *S. neumayeri*

Table 6 *Sterechinus neumayeri*.

Productivity and production at McMurdo Station (20 to 25 m), C. Evans (6 to 8 m) and New Harbor (20 to 25 m). (N abundance; M mean body mass; S somatic; G gonad; DM dry mass; $AFDM$ ash free dry mass).

Conversion factors (Brey unpublished)—Body: $AFDM = 0.13 \times DM$; Gonads: $AFDM = 0.90 \times DM$

	McMurdo Station		Cape Evans ^b		New Harbor	
	DM	AFDM	DM	AFDM	DM	AFDM
$P_S/B_S (\text{yr}^{-1})$	0.060	0.060	0.035	0.035	0.021	0.021
$P_G/B_G (\text{yr}^{-1})^a$	0.600	0.600	0.600	0.600	0.600	0.600
$P/B (\text{yr}^{-1})$	0.208	0.450	0.183	0.436	0.181	0.441
mean $N (\text{m}^{-2})$	0.40	0.40	1.40	1.40	0.27	0.27
mean $M_S (\text{g})$	10.405	1.353	8.769	1.140	11.553	1.502
mean $M_G (\text{g})$	3.904 ^c	3.514 ^c	3.103	2.793	4.397 ^c	3.959 ^c
mean $M (\text{g})$	14.309	4.867	11.872	3.932	15.950	5.460
$B_S (\text{g m}^{-2})$	4.162	0.541	12.276	1.596	3.119	0.406
$B_G (\text{g m}^{-2})$	1.562 ^c	1.406 ^c	4.344	3.910	1.187 ^c	1.069 ^c
$B (\text{g m}^{-2})$	5.724	1.947	16.620	5.505	4.307	1.474
$P_S (\text{g m}^{-2} \text{ yr}^{-1})$	0.250	0.033	0.430	0.056	0.065	0.009
$P_G (\text{g m}^{-2} \text{ yr}^{-1})$	0.937 ^c	0.844 ^c	2.606	2.346	0.712 ^c	0.641 ^c
$P (\text{g m}^{-2} \text{ yr}^{-1})$	1.191	0.876	3.006	2.402	0.778	0.650

^a Gonad Production/Biomass ratio P_S/B_S estimated from Pearse and Giese (1966)

^b Production for the total depth range (3 to 25 m, $N = 2.7 \text{ ind m}^{-2}$) can be estimated by $2.7/1.4 \times P_{(6-8 \text{ m})}$. Production in 20–25 m depth (1.0 ind m^{-2}) can be approximated by $0.7 \times P_{(6-8 \text{ m})}$

^c Based on size-gonad mass relation established at C. Evans

gametogenesis occurs mainly in austral autumn/winter during decreasing or zero day-length, and spawning occurs in austral spring/summer during 24 h day-length (Pearse and Giese 1966; Yakovlew 1983; Pearse and Bosch 1991).

Comparison among sites

Differences in population dynamics of *Sterechinus neumayeri* among the four sites are assumed to be related mainly to differences in food availability, although other factors such as differences in interspecific competition and predation should be considered. Since *S. neumayeri* feeds mainly on benthic diatoms and organic benthic deposits, the highly productive sites on the eastern side of the Sound should provide the best living conditions (see Table 1). The shallow (6 to 8 m) C. Evans site should allow for a higher microbenthic production than the deeper (15 to 18 m) site at McMurdo Station. The dense macroalgal stocks at C. Evans (Miller and Pearse 1991), as well as the numerous seal faeces at McMurdo Station and C. Evans (L. Basch personal observations) may also improve food conditions. New Harbor on the western side of the Sound has lower levels of pelagic and microbenthic primary production (Dayton and Oliver 1977; Barry et al. 1994), while E. C. Armitage is assumed to provide the poorest conditions with coarse sediments indicative of strong currents and low sedimentation, and an almost permanent snow laden sea-ice cover that inhibits sea-ice and benthic microalgal primary production (McClintock et al. 1988).

Differences in the amount of food available will cause differences in production of *Sterechinus neumayeri*. Production ($\text{g m}^{-2} \text{ yr}^{-1}$) depends primarily on two parameters, population size (abundance, biomass) and individual growth rate (somatic and gonad productivity). As discussed above, we should expect habitat-specific production in *S. neumayeri* to decrease according to the ranking C. Evans, McMurdo Station, New Harbor, E. C. Armitage. In the following sections we will evaluate this assumption and discuss the mode of "regulation" of production in response to different food levels in *S. neumayeri*.

Abundance and biomass

A comparatively high abundance and biomass of *Sterechinus neumayeri* was found in shallow water at C. Evans (6 m depth) with values of 1.4 ind m^{-2} and $5.51 \text{ g AFDM m}^{-2}$. Even below 20 m depth (0.77 ind m^{-2} in 1990 and 1.20 ind m^{-2} in 1993) abundance was higher than at the other sites. Abundance and biomass of *S. neumayeri* at McMurdo Station at 20 to 25 m depth, 0.40 ind m^{-2} and $1.95 \text{ g AFDM m}^{-2}$, is less than half the amount at C. Evans

in the same depth range. Divers did not recognize any distinct differences in abundance between the 20 to 25 m depth and the shallower experimental site (15 to 18 m) at McMurdo Station. The figures at New Harbor (20 to 25 m), 0.27 ind m^{-2} and $1.47 \text{ g AFDM m}^{-2}$, are slightly lower than at McMurdo Station, whereas at E. C. Armitage abundance was observed to be extremely low, and biomass would accordingly be low.

The ranking of abundance and biomass figures adheres to our proposed ranking of sites according to food level, suggesting that adaption to different food levels results in an "adjustment" of abundance and biomass in *Sterechinus neumayeri*. This sequence is paralleled by differences in abundance and nutritional condition of the common sea star *Odontaster validus* found by Pearse (1965) and McClintock et al. (1988). The exceptionally high values for *S. neumayeri* at C. Evans may be explained partially by higher than estimated microbenthic production (see below). Moreover, the abundant seal faeces (L. Basch personal observations) and macroalgal debris (Dearborn 1965; Pearse and Giese 1966) may be of more significance than thought previously, especially during periods when microbenthic standing stocks are low.

Individual growth

The validity of the growth curves computed for *Sterechinus neumayeri* suffers to a certain extent from the absence of smaller individuals. This is especially the case at C. Evans and New Harbor, where some urchins $< 35 \text{ mm}$ would have significantly altered the left portion of the growth functions. Nonetheless, it is unlikely that the addition of smaller individuals would distinctly change the shape of the growth functions which describe the present size range of individuals.

Among the four sites investigated, jaws and tests of *Sterechinus neumayeri* grew slowest at E.C. Armitage (Fig. 6, Tables 4 and 5), but the low number of specimens ($N = 7$) precluded the establishment of a separate growth curve. Growth, as measured in changes in jaw size, was not different among the remaining three sites, McMurdo Station, C. Evans and New Harbor (Table 4), but growth in test diameter was significantly higher at McMurdo Station (Table 5, Figs. 7 and 8). Interestingly, the jaw size/test diameter ratio (Table 2) is inversely related to test growth, and is lowest at McMurdo Station (mean: 0.201), intermediate at C. Evans and New Harbor (0.219) and highest at E. C. Armitage (0.247) (i.e. the slower the individuals grow, the larger is the jaw in relation to the test). There is evidence that both the differences in growth and the differences in jaw size/test diameter ratio are related to different food levels at the sites investigated. Ebert (1968) showed that growth in *Strongylocentrotus purpuratus* depends on the amount of food available, and Ebert (1980) as well as Levitan (1991) found the jaw

size/test diameter ratio in two sea urchins, *Strongylocentrotus purpuratus* and *Diadema antillarum*, to be inversely related to food availability. Therefore, individual growth and jaw size/test diameter ratios indicate food conditions for *S. neumayeri* are best at McMurdo Station, intermediate at C. Evans and New Harbor, and worst at E. C. Armitage.

Productivity and production

At E. C. Armitage, the low abundance of *Sterechinus neumayeri* did not allow for computation of productivity (P/B ratio) and production ($\text{g m}^{-2} \text{ yr}^{-1}$). However, it is obvious that, as with the asteroid *Odontaster validus* (McClintock et al. 1988), productivity, which is related to growth rate, is very low at E. C. Armitage. Low production is also reflected in the extremely low abundance and small average size of the individuals. The production computations for New Harbor should be interpreted cautiously, as they are based on a size-frequency distribution of only 16 individuals.

Provided the size-gonad mass relation established at C. Evans is valid for all sites, differences in productivity between C. Evans, McMurdo Station and New Harbor are slight; annual P/B is 0.436, 0.450 and 0.441 (based on AFDM), respectively. However, production is distinctly higher at C. Evans ($2.40 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) than at McMurdo Station ($0.88 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) and New Harbor ($0.65 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$, Table 6).

Population P/B ratios show no clear ranking among sites with the one likely exception of E. C. Armitage. Production of *Sterechinus neumayeri*, however, shows a similar ranking to both abundance and biomass, with the sequence C. Evans > McMurdo Station > New Harbor > E. C. Armitage.

In summary, food conditions seem to affect abundance and biomass of *Sterechinus neumayeri* more than individual growth rates, which are clearly affected only at the very poor E. C. Armitage site. Moreover, there is a contradiction between the number one ranking of the population at McMurdo Station according to individual growth and jaw size/test diameter ratios, while

the population at C. Evans had highest ranking according to abundance, biomass and production. This contradiction could be related to density-dependent intra-specific competition. The superior food conditions at C. Evans may increase recruitment success (but see below), or could constantly attract adult sea urchins to immigrate and remain in the area. Both processes would lead to increased abundance and subsequently to increased intraspecific competition for food. Hence, although absolute food supply per square meter is higher at C. Evans than at McMurdo Station, the lower amount of food per individual would cause decreased individual growth rates, as observed in other benthic invertebrates (see e.g. Peterson 1982, 1989).

Reproduction and recruitment

Sterechinus neumayeri reproduces by releasing large numbers of planktotrophic larvae (Bosch et al. 1987). Pearse and Giese (1966) calculated an average pre-spawning gonad index ($100 \times \text{gonad mass}/\text{body mass}$) of 32.5 between April and November (austral spring), and a decline to about 12 between December and February (austral summer) for *S. neumayeri* at C. Evans. The specimens we collected for gonad mass determination at C. Evans (4 Dec) had a gonad index of 34.6 ($SD = 10.2$, $N = 40$), indicative of a prespawning condition. Hence a gonad output of 60% of maximum gonad mass [$100 \times (32.5-12)/32.5$] is realistic.

The share of total production that is attributable to gonad production, 96% at McMurdo Station and 98% at C. Evans (in terms of AFDM), is extremely high compared to values available from boreal and subtropical echinoids, in which gonad production never exceeds 40% of total production (Table 7). Even in the Antarctic sea urchin *Sterechinus antarcticus* this figure is only 48% (recomputed from Brey 1991; see comment in Table 7). In contrast to the extremely high amount of energy directed into reproduction in *S. neumayeri* in McMurdo Sound, levels of successful recruitment seem to be quite low. The youngest specimens we found had an estimated age of 4 yr at McMurdo Station, 6 yr at

Table 7 *Sterechinus neumayeri*. Comparison of individual somatic (P_s) and gonad production (P_g) in *S. neumayeri* and other echinoid populations (g AFDM)

Species	Area	$P_s \text{ ind}^{-1}$	$P_g \text{ ind}^{-1}$	P_s/P_g	Source
<i>Mellita quinquesperforata</i>	Florida	0.779	0.402	0.34	Lane 1977
<i>Moira atropes</i>	Florida	0.235	0.102	0.30	Moore and Lopez 1966
<i>Parechinus angulosus</i>	S. Africa	0.385	0.089	0.18	Greenwood 1980
<i>Strongylocentrotus droebachiensis</i>	Canada	0.076	0.018	0.19	Miller and Mann 1973
<i>Sterechinus antarcticus</i> ^a	Weddell Sea	0.010	0.021	0.48	Brey 1991
<i>Sterechinus neumayeri</i>	McMurdo Station	0.082	2.108	0.96	present study
<i>Sterechinus neumayeri</i>	C. Evans	0.039	1.676	0.98	present study

^a Gonad mass M_g was determined in specimens collected in February by Brey and Gutt (1991), i.e. most likely after spawning. Pre-spawning gonad mass was estimated by $2 \times M_g$ in February

E. C. Armitage, 7 yr at C. Evans and 6 yr at New Harbor (Fig. 6). It is unlikely that divers collecting echinoids overlooked juveniles completely, hence we have to conclude that no successful recruitment had occurred since 1985/86. This is in sharp contrast to a *S. neumayeri* population sampled on the Weddell Sea shelf, where half of the population consisted of individuals <15 mm (Brey and Gutt 1991). Recruitment of echinoderms has been found to be quite sporadic in many cases (e.g. Ebert 1983), but additional studies suggest a common pattern of recruitment in McMurdo Sound benthos. McClintock et al. (1988) found no juveniles of the sea star *Odontaster validus* during 1.5 yr of regular sampling. Dayton (1979) found little or no recruitment in several sponge species over a 10 yr period. Dayton (1989) reported almost no recruitment of marine invertebrates to settling plates during 5 yr of exposure, but found a multi-species colonization of the same plates some years later. Similarly, Pearse and Pearse (1991) found very little recruitment on glass slides after 1 yr of exposure. Recruitment success of many species in McMurdo Sound is likely to be controlled by a common physical factor, as suggested by Dayton (1989). This factor may be the current regime, duration and extension of sea-ice cover or anchor ice formation, or time and amount of melt water discharge. Interannual variations in such factors may provide favourable conditions for recruitment only once every several years.

Comparison with *Sterechinus neumayeri* on the Weddell Sea shelf

Sterechinus neumayeri is the dominant echinoid species on the upper shelf and slope (100 to 450 m) of the Antarctic continent, whereas below 450 m the conspecific *S. antarcticus* is more abundant (Brey and Gutt 1991). Brey (1991) investigated the population dynamics of *S. antarcticus* in the Weddell Sea, but growth and production of *S. neumayeri* were not analyzed.

Abundance and biomass of *Sterechinus neumayeri* in the Weddell Sea, 0.121 ind m^{-2} and $0.007 \text{ g AFDM m}^{-2}$, are significantly lower than in McMurdo Sound. The mean jaw size/test diameter ratio of *S. neumayeri* on the Weddell Sea shelf, $0.267 (\text{SD} \pm 0.019; N = 163)$ is much higher than at any of the four sites in McMurdo Sound (0.201 to 0.247), indicating that living conditions for echinoids are even better at E. C. Armitage than on the shelf below 100 m. Since average temperature on the Weddell Sea shelf (about -1°C) is higher than the average temperature in McMurdo Sound (about -1.8°C), we assume food supply to be the major difference between the two systems. On the Weddell Sea shelf, sedimentation from the euphotic zone is the primary source of food. This shows great interannual and spatial variability, but on the average

does not exceed a few grams of carbon per year (Bodungen et al. 1988; Bathmann et al. 1991; Schalk et al. 1993). In eastern McMurdo Sound (C. Evans and McMurdo Station), potential food levels are comprised of at least $12 \text{ g C m}^{-2} \text{ yr}^{-1}$ benthic microalgae production, plus $21 \text{ g C m}^{-2} \text{ yr}^{-1}$ sedimentation, plus seal faeces and macroalgal production (Table 1). Food levels on the western side of the Sound (New Harbor) are lower (Table 1), but still above the sedimentation rates recorded on the Weddell Sea shelf.

Significance of *Sterechinus neumayeri* in the McMurdo system

Limited data on growth efficiency ($100 \times \text{production/consumption}$) for echinoids range between 5 and 30% (Miller and Mann 1973; Lane 1977; Propp 1977; Greenwood 1980). Based on an average growth efficiency of 11%, we estimated consumption by *Sterechinus neumayeri* in McMurdo Sound to be $10.9 \text{ g C m}^{-2} \text{ yr}^{-1}$ at C. Evans, $4.0 \text{ g C m}^{-2} \text{ yr}^{-1}$ at McMurdo Station and $3.0 \text{ g C m}^{-2} \text{ yr}^{-1}$ at New Harbor (assuming $1 \text{ g AFDM} = 0.5 \text{ g C}$). These figures correspond to 21% (C. Evans), 12% (McMurdo Station), and 30% (New Harbor) of the estimated sedimentation and benthic microalgal production (Dayton et al. 1986; Knox 1990; Barry et al. 1994; see also Table 1). Even if other potential food sources such as seal faeces and macroalgal debris are taken into account, *S. neumayeri* seems to consume a significant share of total food available to the benthos of McMurdo Sound.

If the populations of *Sterechinus neumayeri* in McMurdo Sound are assumed to be in a steady state, the amount of food consumed by predators of this sea urchin approximates somatic production, $0.03 \text{ g C m}^{-2} \text{ yr}^{-1}$ at C. Evans, $0.02 \text{ g C m}^{-2} \text{ yr}^{-1}$ at McMurdo Station and $< 0.01 \text{ g C m}^{-2} \text{ yr}^{-1}$ at New Harbor (Table 6). However, gonad production is much higher than somatic production, $1.17 \text{ g C m}^{-2} \text{ yr}^{-1}$ at C. Evans, $0.42 \text{ g C m}^{-2} \text{ yr}^{-1}$ at McMurdo Station and $0.32 \text{ g C m}^{-2} \text{ yr}^{-1}$ at New Harbor (Table 6). The obvious discrepancy between gonad output and recruitment success indicates most gonad production is lost. Since eggs and sperms are released into the water column and since pelagic larval development takes nearly 4 mo to complete (Bosch et al. 1987), a significant portion of gonad production may be consumed by pelagic organisms, indicating a strong "upward" coupling between benthic and pelagic components of the community food web.

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