USING ARTIFICIAL SUBSTRATA TO MONITOR HOW CRYPTOFAUNAL ACARI COLONIZE LITTORAL ALGAE ON SUB-ANTARCTIC SOUTH GEORGIA

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ACARI
COLONIZATION
CRYPTOFAUNA
LITTORAL
MODELLING
SUB-ANTARCTIC

ABSTRACT: The colonization of littoral macroalgae by meiofaunal Acari on the sub-Antarctic island of South Georgia was studied using spun-Nylon pan scourers as artificial substrata. A total of twelve species of littoral Acari, including two Rhodacaridae, four Halacaridae, three Podacaridae and three Hyadesiidae, were collected from the scourers. *Rhombognathus auster, R. plumifer* (Halacaridae), *Halozetes littoralis, H. marinus* (Podacaridae) and *Hyadesia subantarctica* (Hyadesiidae) rapidly establish their dominance in spring and remain ascendant throughout the summer. Predation and competition have minimal impact on the mite populations compared with abiotic (climatic) influences. Low winter temperatures exert an indirect pressure by killing most of the algal substrata, while storms have a more direct effect by removing both mites and algae from the shore. Surviving mites over-winter in the shelter afforded by crevices and among the basal portions of enduring algae.

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RÉSUMÉ : La colonisation des algues microscopiques littorales par les acariens de la meiofaune dans l'île subantarctique de Géorgie du Sud a été étudiée avec pour substrat artificiel des écumoires en fil de Nylon. Au total, douze espèces d'acariens littoraux, comprenant deux Rhodacaridae, quatre Halacaridae, trois Podacaridae et trois Hyadesiidae ont été récoltées dans ces écumoires. *Rhombognathus auster, R. plumifer* (Halacaridae), *Halozetes littoralis, H. marinus* (Podacaridae) et *Hyadesia subantarctica* (Hyadesiidae) établirent rapidement leur domination au printemps et demeurèrent ascendants tout au long de l'été. La prédation et la compétition ont un impact minime sur les populations d'acariens par rapport aux influences abiotiques (climatiques). Les basses températures de l'hiver exercent une pression indirecte en tuant les algues du substrat, tandis que les tempêtes ont un effet plus direct en enlevant du rivage à la fois les populations d'acariens et les algues. Les acariens survivant passent l'hiver à l'abri des crevasses et au sein des parties basales endurcies des algues.

INTRODUCTION

In the Arctic and sub-Antarctic, littoral macroalgae are confined to areas free of sea-ice scouring (DAYTON *et al.*, 1970; WESLAWSKI *et al.*, 1993). Similarly, on some sub-Arctic shores, periodic sea-ice scouring may obliterate the well-developed algal canopy (McCOOK & CHAPMAN, 1991, 1993). In contrast, sea ice formation is normally limited to a thin crust or isolated plates of drift ice on the sub-Antarctic island of South Georgia (HEADLAND, 1984), where extensive algal communities are esta-

blished during the spring, but are eradicated in the winter by the combined effects of exposure to frost and storms (PUGH & BARTSCH, 1993).

The littoral macroalgae of polar, temperate and tropical regions are associated with a rich cryptofauna of small free-living invertebrates, including a diversity of mites or Acari (SCHUSTER, 1962; GRESSITT, 1967; SCHULTE, 1979; ROTH & BROWN, 1976; PUGH & KING, 1985a, 1985b; TIKHONOVA & PETROVA, 1987; LUXTON, 1990). Littoral mites are benthic crawlers, have a generally low productivity and undergo direct development to dioeceous adults via a free-living larva and one to three nymphs, though some species may be larviparous (LOHMANN, 1893; SCHUSTER, 1962; STRAARUP, 1968; BARTSCH, 1972; SCHUBART, 1975; PUGH & KING, 1986). The Rhombognathinae (Halacaridae: Prostigmata), Cryptostigmata and Astigmata graze microphytes off macroalgae, rocks and other surfaces, while the other halacarids, Mesostigmata and Prostigmata are predators of other meiofauna (MACQUITTY, 1984; PUGH & KING, 1985c).

The shores of sub-Antarctic islands contain relatively few potential habitats for the littoral meiofauna, compared with those of temperate regions, yet mites dominate the littoral fauna on Kerguelen and South Georgia, where they are particularly associated with littoral macroalgae and lichens (TRAVÉ, 1981, 1986: BELLIDO, 1982; PUGH & BARTSCH, 1993; PUGH, 1995). How mites colonize the seasonally abundant algae is amenable to study using artificial substrata.

Artificial substrata have been extensively used to study the development of marine animal and plant communities, including marine algal cryptofauna (FAGER, 1971; MYERS & SOUTHGATE, 1980; McGUINNESS & UNDERWOOD, 1986). Their principal advantages are uniformity of size and surface characteristics; while their utilization allows the development of complex sampling regimes and reduces, or even negates, the removal of possibly scarce natural substrata (MYERS & SOUTHGATE, 1980; TURNER & TODD, 1993).

A variety of man-made materials have been used as models of different natural habitats, and small branching algae (= 'scrub algae') may be simulated by domestic pan scourers because their plastic filaments mimic the morphology of the algal fronds, adsorb similar surface microfloral films and recruit similar meiofauna (MYERS & SOUTHGATE, 1980; KING et al., 1990). The present study used two types of pan scourer to study the colonization of rocky shore macroalgae by meiofaunal Acari on South Georgia.

MATERIALS AND METHODS

The study was carried out at Husvik Harbour (54°11'S, 36°40'W), on the relatively sheltered north-east coast of South Georgia. Husvik Harbour is free of glacial activity, ice-scouring and silt-deposition, comprises small rocky shores separated by coarse sand or gravel beaches and has a tidal range of c. 1.2 ± 0.1 m (PUGH & BARTSCH, 1993).

Two sites were selected on the basis of accessibility and the probable absence of seal haul-out activity, at 'Karrakatta' on the north side of the Harbour, which was slightly more exposed than the other at Kanin Point on the south side (Fig. 1). There were no major differences in the algal communities on the two shores (JOHN et al., 1994), both of which were necessary because not all of the scourers could be accommodated on either one and it was seen as a necessary 'insurance' against possible catastrophic events.

Two levels on each shore were studied, designated as 'high' (CD + 0.8 ± 0.1 m), where the dominant algae were Iridaea cordata (Turner) Bory de Saint-Vincent and Nothogenia fastigiata (Bory de Saint-Vincent) Parkinson, and 'low' (CD + 0.3 ± 0.1 m) dominated by Palmaria georgica (Reinsch) R.W. Ricker and Schizoseris condensata (Reinsch) R.W. Ricker (JOHN et al., 1994).

The two types of spun-Nylon domestic pan-scourer, referred to as 'mats' and 'buns' (MYERS & SOUTHGATE, 1980), were deployed as artificial scrub algae at each level of both sites. The rectangular mats were made from 'Scotchbrite' scourers cut to c. 110 × 150 × 9 mm and folded in half, while the round buns were c. 76 mm diameter, 25 mm thick, 'Nyleska' scouring pads. Both scourers had a similar volume of c. 150 ml but different pore sizes, of 1-3 mm in the mats and 3-5 mm in the buns.
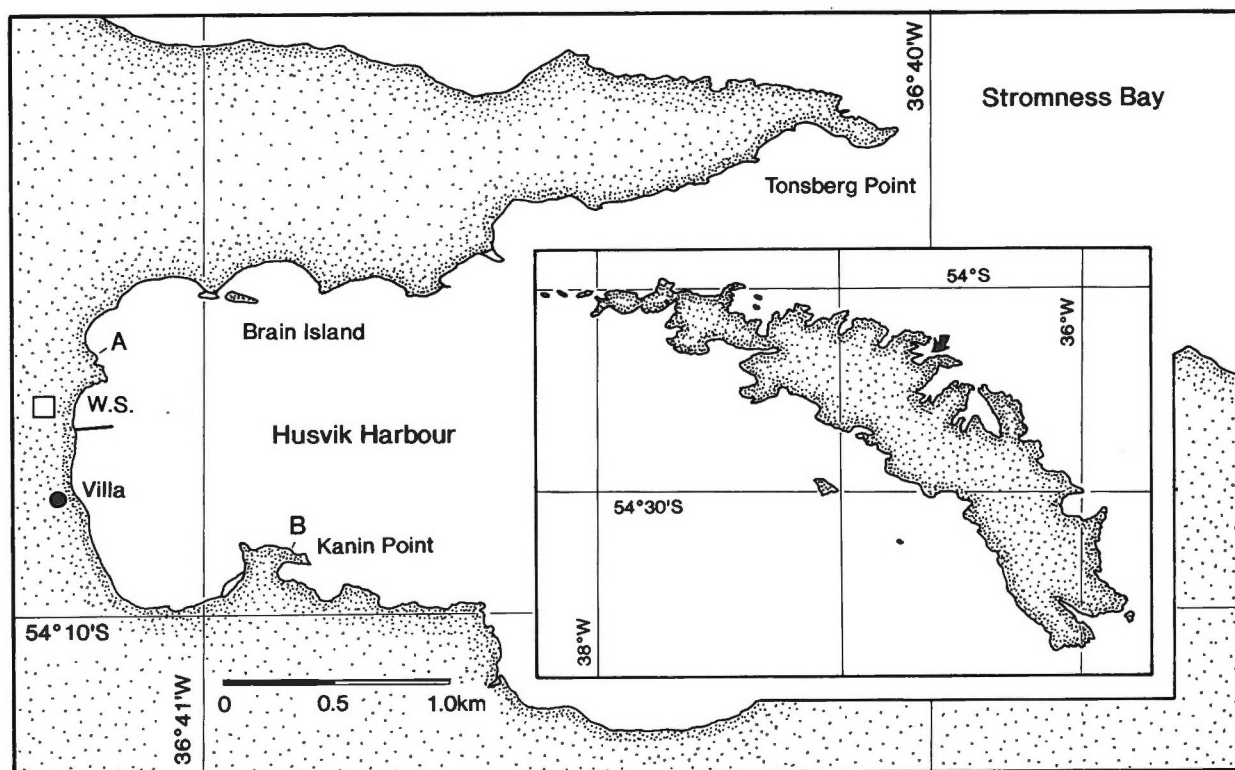
FIG. 1: The study sites at Husvik Harbour, South Georgia. Inset: South Georgia showing the location of Husvik Harbour, the southern arm of Stromness Bay (arrowed). Main map: The two study sites, adjacent to the 'Karrakatta' (A) and at Kanin Point (B) are indicated.W.S. marks Husvik Whaling Station.

Scourers were deployed over a c. 1 × 2 m area at each level of each site among the scrub algae by hammering hardened steel masonry nails (53 mm long × 3.5 mm diameter) into natural fissures within the parent rock of volcanoclastic sandstone-shale turbidite (MACDONALD et al., 1987). The scourers were secured to the nails with numbered square plastic 'washers' made from 1.5 mm thick polythene cut into 30 × 30 mm squares and drilled with a 3 mm central hole.

Deployment was initiated at the beginning of the austral spring shortly before the 'bloom' of macroalgae (PUGH & BARTSCH, 1993), during the low spring tide of 7/8 November, 1990. Twenty to thirty mats and buns were attached at both high and low levels and at both sites. Then at intervals of 14, 28, 56, 84 and 112 (± 1) days during periods of spring tides, two or three mats and buns were collected from each shore level of each site by randomly drawing the washer numbers from the eight site/level/scourer combination sets. A storm

prevented collection from the low site at Karrakatta on day 28.

In the laboratory, surface growths of macroalgae were picked off the scourers, but material within the mesh was not removed. Cryptofauna were extracted from the scourers using a two-phase flotation process using hypersaline made from cooking salt to a specific gravity of 1.2 at 15° C. The first extraction was conducted on whole scourers and the second on buns which were cut in half then unravelled, and mats shredded into narrow strips. Although flotation is not suitable for all meiofauna it is efficacious for mites (PUGH & KING, 1985a). Furthermore, repeated washing of some alcohol fixed scourers yielded few additional mites and suggested that the extraction process was >94% effective.

All samples of Acari were fixed in GAW, a mixture of 10% v/v glacial acetic acid, 50% glycerol and 40% distilled water, which was subsequently replaced with 40 % aqueous lactic acid and evapo-

rated to approximately 80% at 50° C, when the samples were sealed and cleared for up to 28 days. The mites were identified in glycerine jelly or lactic acid temporary mounts and stored in 70% aqueous ethanol with 5% glycerol, when the presence and number of eggs and/or larvae were counted within adult females.

To test the suitability of the scourers as models of the natural scrub algae a ranked sample incidence of the ten most frequently collected mites on both natural (N) and artificial (A) substrata were compared. Identical ranks scored 10 points and differences in rank were scored as 10-(|A-S|) and summed. The end result is a percentage similarity of rank score, between natural and artificial substrata, which are independent of both sample number and sample size. Additional data regarding the occurrence of mites on the native algae were obtained from PUGH & BARTSCH (1993) and PUGH (1995).

The number of each mite species on each scourer at each level at each of the two sites and at each time interval, were input into a 'Minitab' statistical software package (Minitab Inc., Pennsylvania, U.S.A.) (RYAN, et al., 1985). The data were transformed using a $y = \log_n (n+1)$ correction, where n is the number of specimens at each count, a correction which accommodates zero values. These data were used to identify any evidence of species preference for either site, level and/or scourer as well as interactive effects between any two of these parameters. The four factors, i.e. scourer, level, shore and time interval were tested using a 4-factor ANOVA with unequal size samples to account for variation in sample number (SOKAL & ROHLF, 1981).

.OBSERVATIONS

(1) ACARI COLLECTED

Mites were the most numerous animals collected from the scourers, comprising over 92 % of the total specimens. Twelve species of Acari were collected during the experiment, including *Parasitiphis aurora* Lee and *P. brunneus* (Kramer) (Rhodacaridae: Mesostigmata); *Rhombognathus auster*

Bartsch, *R. multisetosus* Newell, *R. plumifer* Trouessart and *Lohmannella bihamata* Viets (Halacaridae: Prostigmata); *Halozetes belgicae* (Michael), *H. littoralis* Wallwork and *H. marinus* (Lohmann) (Podacaridae: Cryptostigmata); *Hyadesia halophila* Fain, *H. maxima* Fain, Sømme & Block and *H. subantarctica* Fain (Hyadesiidae: Astigmata). The spatial distribution of each species with respect to substrata, level on shore and sites are outlined in Table I.

The remaining non-mite fauna consisted of small gastropod molluscs of the family Rissoidae, bivalve molluscs of the genera *Kidderia*, *Lasaea*, and/or *Lissarca* and amphipods of the family Gammaridae, none of which were found **within** the scourers, but associated with/attached to their surfaces. Only some small oligochaetes and nematodes were collected from within the mesh.

(2) COMPARABILITY OF DATA

(2a) Species Rank (Table II)

The most common mites recorded amongst the algae (equivalent to 99.2 % of all records) were the same as those collected from the scourers, furthermore their ranked order was very similar at 78 %. The differences between the mats (82 %) and buns (79 %), is not significant. Similar comparisons of the five most abundant species (82 % of records) raised the similarities to between 90 and 98 %. With regard to the density of individual species, *Rhombognathus auster* and *Halozetes marinus* were recorded at densities of 103 < 471 and 109 < 498 dm^{-2} respectively on both scourers.

(2b) Individual Parameter Effects (Table III)

i. Scourer: Both *Parasitiphis brunneus* (P < 0.01) and *Halozetes marinus* (P < 0.01) were more abundant in the buns than the mats. All other species were indifferent to either substrata.

ii. Level: *Parasitiphis brunneus*, *Halozetes belgicae* and *Halozetes littoralis* clearly show a preference for the upper level sites (P < 0.01), while *Rhombognathus plumifer* was more abundant at the lower level sites (P < 0.01). All other species showed no preference for either shore level.

TABLE 1: Spatial occurrence of littoral Acari on artificial substrata. (Data show number of specimens collected/number of samples.)

| shore level | Karrakatta | | | | Kanin Point | | | | |
| Acari | High | | Low | | High | | Low | | Totals |
scourers	mat	bun	mat	bun	mat	bun	mat	bun	
Parasitiphis aurora	1/1	6/1	—	—	—	—	—	—	7/2
Paraitiphis brunneus	19/7	478/7	—	1/1	8/5	46/11**	—	15/1	276/32
Rhombagnathus auster	29/6	74/6	14/4	12/6	47/10	190/11	185/13*	23/10	574/66
R. multisetosus	—	—	4/1	1/1	—	—	—	—	5/2
R. plumifer	2/2	17/1	47/1	52/9*	10/2	1/	14/6	9/6	145/34
Lohmannella bihamata	—	—	—	3/1	—	—	—	—	3/1
Halozetes belgicae	7/2	3/1	—	—	—	—	—	2/1	12/4
H. littoralis	15/5	26/9**	—	1/1	9/2	1/1	1/1	7/4	60/23
H. marinus	35/7	82/10	3/2	3/3	285/12	560/13	47/12	22/6	1037/65
Hyadesia halophila	—	—	—	—	—	—	1/1	—	1/1
H. maxima	—	1/1	—	—	4/1	2/1	—	—	7/3
H. subantartica	1/1	4/3	3/3	—	31/8	26/3	6/5	16/6	87/29
Total samples	13	13	11	11	13	13	13	12	99

Significance of correlations between species and substratum/level/sitecombinations are indicated as follows: * = $p < 0.05$; ** = $p < 0.01$ (YATES, 1934) Chi^2.

TABLE 2: Comparability of natural and artificial substrata.

| mite | sample counts* | | | | rank | | | | score 10-(IA-NI) | | |
	alga	M+B	Mat	Bun	alga	M+B	Mat	Bun	M+B	Mat	Bun
Rhombognathus auster	82	66	33	33	1=	1	1=	1	10	10	10
Halozetes marinus	82	65	33	32	1=	2	1=	2	9	10	9
Hyadesia subantartica	46	29	17	12	3	5	3=	6	8	10	7
Rhombognathus plumifer	22	34	17	17	4	3	3=	4	9	9	10
Halozetes littoralis	19	23	8	15	5	6	5	5	9	10	10
Hyadesia maxima	18	3	1	2	6	8	7=	7=	8	9	9
Parasitiphis brunneus	16	32	12	20	7	4	4	3	7	7	6
Rhombognathus multisetosus	1	1	2	1	8	9=	7=	9=	9	9	9
Halozetes belgicae	1	2	4	2	8	7	6	7=	9	8	9
Parasitiphis aurora	0	2	1	1	0	9=	7=	9=	0	0	0
	sum of ranked scores				based on top ten species				78 %	82 %	79 %
	—				based on top five species				90 %	98 %	92 %

Note: (*) counts based on 150 algal samples (PUGH & BARTSCH, 1993; PUGH, 1995) and 99 scourer (50 mat and 49 bun) samples.

TABLE 3: Effects of different factors as estimated using ANOVA

| Acari | Individual Parameters | | | 2-parameter interaction | | |
	scourer	level	site	Ps/Lv	Ps/Si	Si/Lv
Parasitiphis brunneus	B**	U**	—	—	—	—
Rhombognathus auster	—	—	P*	—	—	PL/KH*
R. plumifer	—	L**	—	—	—	KL*
Halozetes belgicae	—	—	P**	—	—	KH*
H. littoralis	—	U**	—	—	—	KH**
H. marinus	B**	—	P**	HB/LM**	—	PH**
Hyadesia subantartica	—	—	P**	—	—	—

Note : Species with less than 10 specimens collected have been omitted.
Lv = level. Ps = scourer; Si = Site.
Significance of correlation: * = $p < 0.05$; ** = $p < 0.01$
The correlation of individual species with different parameters are indicated as follows :
  scourers : B = buns   M = mats
  shore levels : L = lower   U = upper
  shore : K = Karrakatta   P = Kanin Point.
  — = no significant correlation at $P < 0.05$.

iii. Site: Four species show evidence of site preference, with *Rhombognathus auster* (P < 0.05), *Hyadesia subantarctica* (P < 0.01), *Halozetes belgicae* (P < 0.01) and *Halozetes marinus* (P < 0.01) being more abundant at Kanin Point. The other species were equally abundant on both shores.

(2c) Two-Parameter Interactions (Table III)

iv. Scourer and level: Only *Halozetes marinus* showed possible interactive effects, in that it was more common at Karrakatta in high buns and low mats (P < 0.01).

v. Scourer and site: None.

vi. Shore level and site: *Rhombognathus auster* was more abundant at Kanin Point on the low level and at Karrakatta on the high site, *Rhombognathus plumifer* was biased towards the Karrakatta low site (P < 0.05), *Halozetes littoralis* to the Karrakatta high site and *Halozetes marinus* to the Kanin Point high site (both at P < 0.01).

(3) TEMPORAL CHANGES

The artificial substrata showed a succession of surface growth, for example lower level scourers were initially coated/filled with (green?) algal films (days 14 to 28), followed by green filamentous algae (days 28 to 56), surface growths of *Ulva* and *Porphyra* (days 56 to 112), and finally *Adenocystis*, *Nothogenia* and *Schizoseris* (day 112).

The mites collected from the artificial substrata may be divided into three groups based upon their abundance and time of collection (Fig. 2). The most abundant species (*Rhombognathus auster*, *R. plumifer*, *Halozetes littoralis*, *H. marinus*, *Hyadesia subantarctica* and *Parasitiphis brunneus*), were collected throughout the study, though *P. brunneus* was not found amongst the day 14 scourers. The remaining species may be divided into early colonists, found between days 14 and 56 (*Parasitiphis aurora*, *Halozetes belgicae* and *Hyadesia halophila*), and late colonists which were present between days 56 and 112 (*Rhombognathus multisetosus*, *Lohmannella bihamata* and *H. maxima*). There were no correlations between any mite species and algae

covering the artificial substrata, despite any apparent temporal coincidence.

The total number of mites collected throughout the study increased to day 56 (Fig. 3A), followed by a substantial loss on day 84 and a second subsequent number increase on day 112. This pattern of increase, loss and increase was apparent in all of the most abundant species (Figs. 2 & 3), among both artificial substrata, at both shore levels and on both shores (Fig. 3B-3D). The rate increase in the numbers of mites recorded (measured as mean per scourer) was initially rapid at 0.82 day^{-1} (to day 14), but declined through 0.72 day^{-1} (days 14 to 28) to 0.30 day^{-1} (days 28 to 56). After the loss between days 56 and 84, the recovery measured between days 84 and 112 was high at 1.08 day^{-1}.

Rhombognathus auster females were observed to contain between 0 and 4 (usually 1 or 2) developing eggs, while the population included 3.7 to 16.0 % larvae and protonymphs. Similarly, the *H. marinus* females contained 0 to 4 (usually 2 or 3) developing eggs and the populations 11 to 25 % larvae and protonymphs. Females of both species were observed to contain fully developed larvae.

DISCUSSION

(1) EFFICACY OF ARTIFICIAL SUBSTRATA

The species of mites collected on the artificial substrata and their ranked abundance are similar to those of the native algae, confirming that both scourers are adequate models of the scrub algae. The complete lack of any correlation between particular mite and algal species clothing the artificial substrata mirrors the generalist colonization pattern observed on shore algae (PUGH & BARTSCH, 1993; PUGH, 1995), and justifies using the occurrence of mites among the littoral algae as a whole. But the numbers of mites recovered from the native algae (250 < 1500 dm^{-2} for *Rhombognathus auster* and 250 < 950 dm^{-2} for *Halozetes marinus* among rocky shore algae (PUGH & BARTSCH, 1993; PUGH, 1995)) were higher than those recovered from the artificial substrata (100 < 500 dm^{-2} in both species).

The effects of the individual parameters were variable, for example with regard to scourer type:
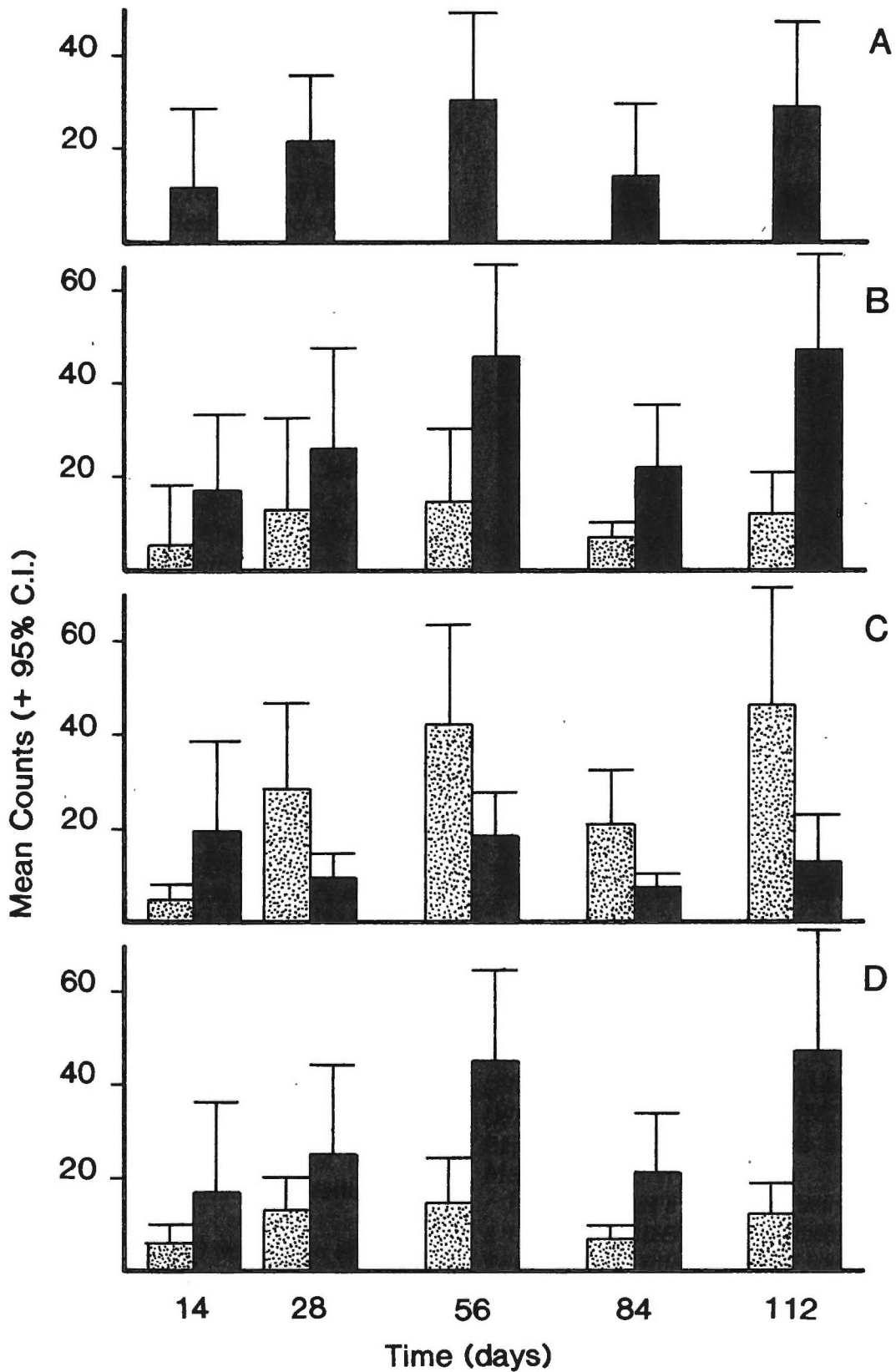
FIG. 2: Temporal abundance of individual mite species. Bars show changes in abundance of each species during the experiment, with the solid areas showing mean counts per scourer, expressed as $\log_n (n+1)$ and stippled areas the 95 % confidence intervals.
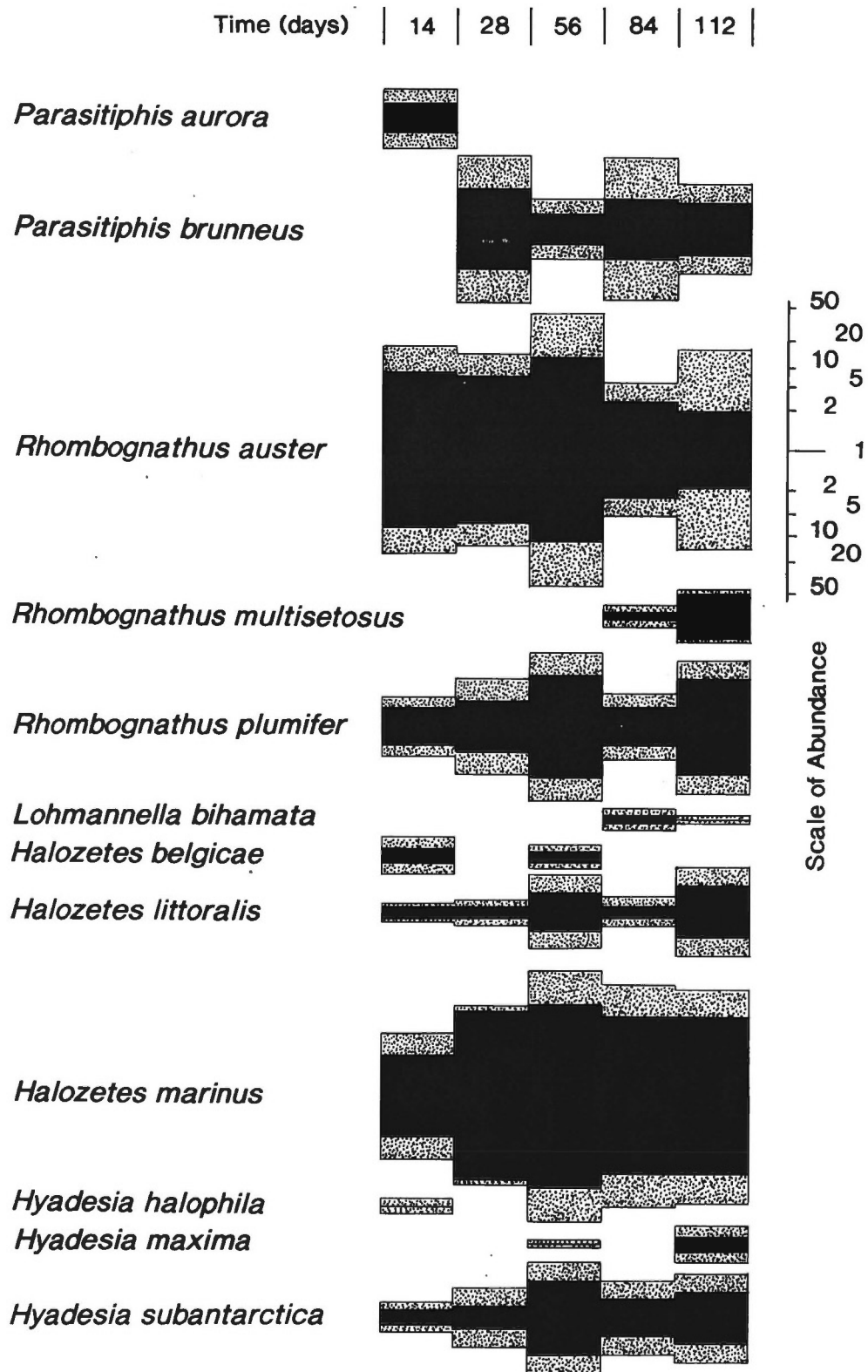
FIG. 3: Temporal abundance of mites relative to experimental parameters. Bars show mean the number of mites collected per scourer and lines the 95 % confidence intervals. A: Total numbers of mites collected. B: Numbers collected on mats (stippled) v. buns (solid). C: Numbers collected at high (stippled) v. low (solid) levels. D: Numbers collected at Karrakatta (stippled) v Kanin Point (solid) sites.

the correlation of both *Parasitiphis brunneus* and *Halozetes marinus* with buns and not mats is probably an effect of their size, in that both were relatively large at 780 < 820 μm, compared with the other mite species at < 700 μm. The large size may have prevented either species from penetrating the fine mesh of the mats, but not the more open mesh of the buns. A similar trend was noted for the non-acarine colonists most of which were larger than 1 mm and collected from *below* the scourers and not within them.

Substratum 'mesh size' exerts a powerful influence over cryptofauna which preferentially colonize densely tufted algae because these afford better protection from desiccation, temperature fluctuations and wave action (WIESER, 1952). In the present experiment however, the mesh of the buns was finer than that associated with all scrub algae observed on the shore. Indeed, as previously suggested, the mesh size is a limiting factor for two species, but the majority of mite species were small enough to penetrate both artificial substrata.

The effects of shore level suggest that although species of both aquatic and terrestrial mite groups (*sensu* PUGH & KING, 1985a), cohabit at both levels, the terrestrial species *Parasitiphis brunneus, Halozetes belgicae* and *H. littoralis* of the terrestrial moiety were more abundant at the upper levels, while the halacarids *Rhombognathus plumifer* of the aquatic moiety, was correlated with the lower level. Site preferences and two-parameter interactions, especially between shore level and site probably reflect local variation in exposure to wave action and other variables, but these proved difficult to relate to specific environmental factors.

(2) TEMPORAL CHANGES

The pattern of community development, observed amongst the algae colonizing the scourers, i.e. films followed by short and longer-lived macroalgae, has been observed in sub-Arctic, temperate and tropical latitudes (MOORE, 1939; BENEDETT-CECCHI & CINELLI, 1993; McCOOK & CHAPMAN, 1993).

Although the dominant mites, namely *Parasitiphis brunneus, Rhombognathus auster, R. plumifer, Halozetes marinus* and *Hyadesia subantarctica*

remain ascendant throughout the study, the rarer species are clearly divided into early terrestrial mites (*Parasitiphis aurora, Halozetes belgicae* and *Hyadesia halophila*) and late, largely aquatic, mite colonists (*Rhombognathus multisetosus, Lohmannella bihamata* (and *Hyadesia maxima*). This suggests a succession among the 'minor' species (*sensu* CLEMENTS, 1916), as the scourers gradually become filled and clothed with algae, better able to retain seawater during tidal emersion and so more 'marine' in nature.

The low proportion of larvae and protonymphs, together with the presence of larviparity in populations of both *Rhombognathus auster* and *Halozetes marinus*, are adaptations to the physical stresses caused by exposure to wave action, and are typical of littoral mites with annual life cycles (PUGH & KING, 1986). These contrast with the protracted life cycles and juvenile stages of Antarctic and sub-Antarctic Acari which are adaptations to the physiological stresses associated with a severe climate and a short growing season (CONVEY, 1994). Furthermore, the low egg counts indicate a low productivity and that the observed increases in mite numbers on the scourers is a result of colonization from adjacent algae and not *in situ* reproduction.

(3) FACTORS REGULATING LITTORAL MITE COMMUNITIES

Biological pressures within the littoral mite communities on South Georgia are thought to be low. For example there is considerable mutual co-habitation between species, suggesting that interspecific competition is low and that such mixed aggregations may form a common defence against being dislodged by wave action (PUGH, 1995).

Although juvenile 'fingerlings' of several fish species are recorded from the nearshore environment of South Georgian fjords and may feed upon algal epifauna including amphipods (BURCHETT, 1983a, 1983b), it is unlikely that these would enter the littoral zone to feed on the larger meiofauna (A. NORTH, personal communication), let alone the smaller mites. Possible invertebrate predators, other than mites, were not observed at any time and although there were numerous predatory gamasid

mites among the artificial substrata (predator: prey ratio = 1: 6.4), such mites do not feed very often (PUGH & KING, 1985c), and are thought not to limit the populations of grazing mites.

The decline in mite numbers between days 56 and 84 (January 2 and 30) is apparent in all of the 6 most abundant species, at both sites, both shore levels and on both scourers (Fig. 3), is not an effect of the experiment, but driven by external forces. The substantial recovery in numbers measured between days 84 and 112 suggests that the loss observed on day 84 occurred very soon after the day 56 (January 2) sample. During January 4/5, wind speed rose from a monthly mean of $3.9ms^{-1}$ to a sustained $10ms^{-1}$ (MACALISTER, personal communication), and storm-driven swells were recorded. These swells and their associated heavy breaking waves deposited algae as tidal debris in the supra-littoral adjacent to Kanin Point. Numerous dead and damaged specimens of both *Rhombognathus auster* and *Halozetes marinus* were recovered from tidal debris and littoral sediments on the shore adjacent to Kanin Point after the January 4/5 storm. As neither species are interstitial nor supra-littoral (PUGH & BARTSCH, 1993; PUGH & MAC ALISTER, 1994; PUGH, 1995), these specimens were undoubtedly dislodged from littoral algae or rock crevices by the storm.

These observations suggest that climatic events are the major limiting factors of littoral mite populations on South Georgia, especially wave action during storms, but not the direct effects of winter low temperatures because meiofaunal mites are sufficiently cold tolerant to survive them (DAHL, 1948; KIRCHNER, 1969; BARTSCH, 1974; PUGH, 1994).

The halacarids in the Elbe estuary of northern Europe shelter from winter freezing in protected niches (BARTSCH, personal communication) and it is suggested that the littoral mites on South Georgia adopt a similar strategy and over-winter crevices, small scrub algae and the basal portions of larger littoral algae which survive frost action. Indeed observations made during early spring before the 'bloom' of littoral algae and in late autumn, suggest there were large numbers of *Rhombognathus auster*, *Halozetes littoralis* and *H. marinus* among the turf-like alga *Iridaea* in shallow cracks in the rock surface.

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