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On Living in Cold Water: *K*-Strategies in Antarctic Benthos

A. Clarke

British Antarctic Survey, Natural Environment Research Council; Madingley Road, Cambridge CB3 OET, England

Abstract

Comparison of the life-histories of two species pairs of caridean decapods, each pair containing a polar and a more temperate-water species (*Chorismus antarcticus* (Pfeffer, 1887)/*Pandalus montagui* Leach, 1814 and *Notocrangon antarcticus* (Pfeffer, 1887)/ *Crangon crangon* (Linnaeus, 1758), suggested that in each case the polar species was more of a *K*-strategist than was the temperate species. In particular there were striking differences in brood size, egg weight and maturity of the newly hatched larvae. Measurements of individual annual reproductive effort, RE, as g fresh weight eggs per g fresh weight female indicated that in both species pairs the RE of the polar *K*-strategist was significantly less than that of the comparable temperate water *r*-strategist. Results expressing RE as g total egg lipid per g fresh weight female were equivocal. These data are discussed in relation to available autecological information for Antarctic marine invertebrates and it is concluded that many features of the polar benthos are explicable in terms of a general evolution of typical *K*-strategies. The role of low temperature in the widespread evolution of *K*-strategies may be crucial; consideration of this leads to a re-appraisal of "cold-adaptation".

Introduction

It has long been known that the eggs of many polar marine invertebrates are large and rich in yolk (Thorson, 1950), suggesting that reproduction in polar waters is expensive and requires a large energy store (Dunbar, 1970). So marked is this tendency for an increase in the incidence of large yolky eggs and associated non-pelagic development towards high latitudes that it has become known as Thorson's rule.

The question of whether it is more efficient for a marine invertebrate to breed by producing a large number of small eggs or a smaller number of large eggs has been examined mathematically by Vance (1973a, b). Although Vance's equations contain variables which it is not presently feasible to measure, for example the rate of larval predation in the plankton, they may be used to derive predictions which can be matched against observation. Specifically, Vance suggests that it is more efficient to produce many small eggs when food availability for planktonic young is patchy or unpredictable, and a smaller number of larger eggs when the environment for the newly hatched larvae is uniform or predictable (efficiency being defined as the number of metamorphosing larvae per unit investment of reproductive effort).

An alternative approach to reproductive adaptation is the concept of *r*- and *K*-strategies. The terms *r*-selection and *K*-selection were coined originally by MacArthur and Wilson (1967) as convenient labels for the extreme ends of a range of types of selection. Simplistically, *r*-selection is selection for maximum rate of population increase and *K*-selection is selection for maximum competitive ability in a saturated environment. Since few, if any, organisms are completely *r*- or *K*-selected, the terms are useful only in a comparative sense and Pianka (1970) has visualised an *r*-*K* continuum along which organisms can be arranged. A key prediction of this approach is that organisms exhibiting *K*-strategies (slow growth, deferred maturity, greater longevity, iteroparity, low fecundity, large yolky eggs) have a lower individual annual reproductive ef-

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fort than organisms exhibiting *r*-strategies (fast growth, shorter longevity, semelparity, high fecundity, small eggs).

In this study, two pairs of marine benthic invertebrates were chosen, each pair containing a related polar and temperate-water species. The relative positions of these species on the *r*-*K* continuum were assessed by investigation of their life-histories, and then their reproductive efforts were compared.

The polar species chosen were the shrimps *Chorismus antarcticus* (Pfeffer, 1887) and *Notocrangon antarcticus* (Pfeffer, 1887); these are the only two common or widely distributed caridean decapods in the Antarctic.

Pandalus montagui Leach, 1814 (family Pandalidae) was chosen for comparison with *Chorismus antarcticus* (family Hippolytidae) because, although from different families, these shrimps have many similarities in their biology. They are of similar size and shape, both are protandrous hermaphrodites and brood a clutch of eggs in a brood chamber formed beneath the front of the abdomen by specially extended sclerites. Female shrimps breed only once each year, although in both species at least some females go on to breed in succeeding years. Both species are probably opportunist omnivores, but there are differences in growth rate (Clarke and Lakhani, 1979), habitat, and the degree of environmental variability to which they are subject.

The most easily sampled British hippolytids, *Spirontocaris lilljeborgii* and *Hippolyte varians*, were rejected because both species are dioecious. Size for size they both produce more eggs of smaller size than *Chorismus antarcticus*, but since the evolution of protandrous hermaphroditism affects reproductive effort (Calow, 1978), a comparison of *C. antarcticus* with either species was considered invalid.

Notocrangon antarcticus and *Crangon crangon* (Linnaeus, 1758) are from the same family (Crangonidae) and are very similar in size and shape. Both are shallow-burrowing active predators, dorso-ventrally flattened, dioecious, and brood eggs beneath the abdomen. *N. antarcticus* breeds only once each year, but those *C. crangon* which breed early will produce two or more broods per season (Lloyd and Yonge, 1947). It is likely that this species pair show differences in growth rate and environmental temperature range similar to the first pair.

Material and Methods

Ovigerous female shrimps were removed from samples taken as follows:

Polar Species

Chorismus antarcticus: 0.5 m Agassiz trawl, sandy bottom, 10 m, King Edward Cove, South Georgia (54°17'S; 30°36'W); February to October, 1972 and 1973.

Notocrangon antarcticus: 1 m Agassiz trawl, mud, 120 m, Cumberland East Bay, South Georgia; 27 February, 1978.

Both polar species were analysed immediately after capture.

Temperate Species

Pandalus montagui: subsample from a commercial catch, 6 m beam trawl, mud, 20 m, Lynn Well, the Wash, UK; 21 December, 1976.

Crangon crangon: subsample from catch with a 2 m push-net, 0.5 m at low tide, sand, Littlestone, Kent, UK; March, 1977.

Both temperate species were preserved in 4% neutralised formal-saline and analysed within 2 months.

Eggs were removed from the pleopods by gentle scraping with a small spatula and then counted directly under a stereomicroscope (polar species), or from photographs of the whole brood spread one egg thick (temperate species). The eggs were then weighed and analysed for lipid. Female shrimps were measured to 0.1 mm with vernier calipers, from the rear of the eye socket to the rear edge of the carapace in the dorsal median line (carapace length), and weighed fresh to the nearest 0.1 mg. Unless otherwise specified, all text references to female weight refer to this egg-free wet weight. The methods are described in detail in Clarke (1979).

Reproductive effort was measured both on a fresh weight basis (fresh weight total egg batch÷fresh weight female excluding eggs) and as total lipid in eggs÷female fresh weight. In all species, corrections were applied where necessary to allow for changes in weight or lipid content of eggs during embryonic development, and for the effects of formalin preservation (Clarke, 1979).

All statistical procedures were performed using the Frequencies, Scattergram and Regression subprograms of the Statistical Package for the Social Sciences (SPSS).

Results

Brood Size and Egg Weight

In all 4 species of shrimp (*Chorismus antarcticus*, *Pandalus montagui*, *Notocrangon antarc-*

ticus, Crangon crangon) the relationship between brood size and female weight could reasonably be described by a straight line (Figs. 1 and 2; least-squares fits are given in Table 1). Only in *C. crangon* did a scattergram suggest a possible non-linear relationship (Fig. 2), and in addition the relationship between brood size and carapace length (fitted as a least-squares regression after logarithmic transformation) differed significantly ($P < 0.05$) from the expected cubic. The sample of *C. crangon* contained females with egg batches at various stages of development; since eggs are not protected from abrasion during burrowing, differential egg loss will explain at least part of this variation.

The range of brood sizes observed varied widely both within and between species (Figs. 1 and 2), although within none of the 4 species was egg weight related to brood size (all $P > 0.05$). Species with larger brood sizes, however, had smaller eggs (Table 2), and associated with this were differences in the type of embryonic development. The temperate species with smaller eggs hatch relatively immature larvae, whereas the polar species hatch into more advanced larvae. This relationship between egg size and maturity of the newly hatched larva holds for many carideans and penaeids (Wickins, 1976). Although the rate of embryonic development in crustaceans is slower at low temperatures (Wear, 1974), these polar larvae are more advanced than might be expected because several stages within the egg are shortened or suppressed (abbreviated development: Gurney, 1937; Makarov, 1968, 1973). Very few newly hatched larvae of

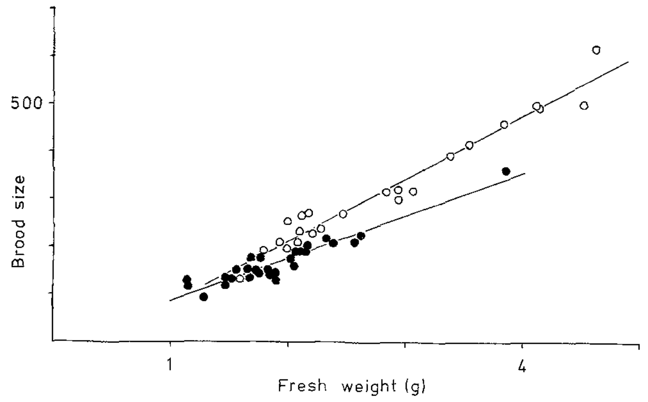

Fig. 1. *Chorismus antarcticus* (filled circles) and *Notocrangon antarcticus* (open circles). Least-squares regression of brood size (number of eggs) on female fresh weight for polar shrimps. *C. antarcticus*, $y_i = 90.04\ x_i - 2.86$; *N. antarcticus*, $y_i = 131.84\ x_i - 52.64$

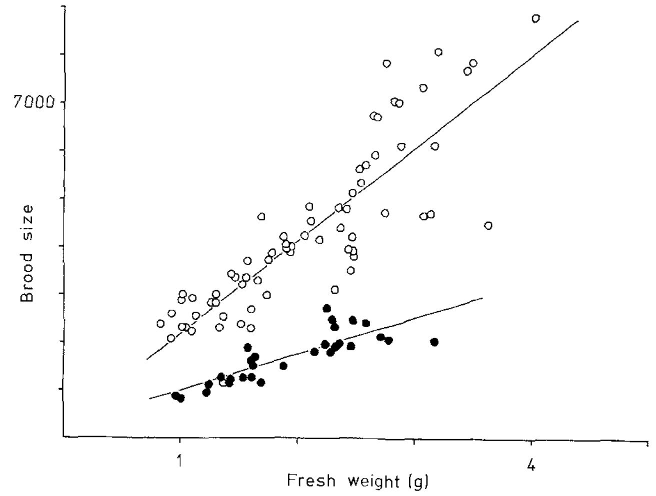

Fig. 2. *Pandalus montagui* (filled circles) and *Crangon crangon* (open circles). Least-squares regression of brood size (number of eggs) on female fresh weight for temperature-water shrimps. *P. montagui*, $y_i = 759.79\ x_i + 226.07$; *C. crangon*, $y_i = 131.59\ x_i + 257.84$

Table 1. Relationship between brood size (no. of eggs) and female weight (g) or size (mm) for 4 species of caridean decapod

Species	Regression coefficient, *b*	Standard error of *b*	Intercept	r^2	*F*	*n*
Regression of brood size on female weight						
Chorismus antarcticus	90.04	6.30	-2.86	0.89	204.5	28
Notocrangon antarcticus	131.84	5.98	-52.64	0.96	486.8	23
Pandalus montagui	759.79	96.81	226.07	0.70	61.60	29
Crangon crangon	1936.59	140.35	257.84	0.74	191.38	68
Regression of $\log_e$ brood size on $\log_e$ carapace length						
Chorismus antarcticus			- no data -			
Notocrangon antarcticus	3.17	0.25	-2.55	0.88	155.10	23
Pandalus montagui	2.59	0.28	0.72	0.76	85.34	29
Crangon crangon	2.23	0.19	2.79	0.68	133.95	65

Table 2. Egg size, brood size (no. of eggs) and breeding biology of 4 species of caridean decapod

Species	Brood size	Fresh weight per egg (μg)	Lipid per egg (μg)	Egg lipid (% fresh weight)	Remarks
Polar					
Chorismus antarcticus	100-300	1920	126	6.6	Protandrous hermaphrodite, broods eggs for 9-10 months, hatches into demersal schizopod larva, single brood per year, iteroparous.
Notocrangon antarcticus	130-500	1066	157	14.7	Dioecious, broods eggs for 9-10 months, hatches into demersal schizopod larva, single brood per year, iteroparous.
Temperate					
Pandalus montagui	150-4000	276	23.2	8.3	Protandrous hermaphrodite, broods eggs for 4-5 months, hatches into planktonic zoea larva, single brood per year, iteroparous.
Crangon crangon	1000-14000	79	5.3	6.3	Dioecious, broods eggs for 8-10 weeks, hatches into zoea larva, 2-3 broods per year, iteroparous.

Table 3. Annual individual reproductive effort (RE) in 4 species of caridean decapod. SE: Standard error

Species	$\bar{x}$ ± SE	Regression (least-squares) of egg fresh weight (mg) on female fresh weight (g):					
		b	SE	Intercept	r^2	*F*	*n*
RE expressed as fresh weight eggs/ fresh weight female (g/g)							
Chorismus antarcticus	0.171 ± 0.003	170.67	10.97	-0.70	0.90	241.3	28
Pandalus montagui	0.243 ± 0.006	222.02	21.76	37.37	0.74	104.07	39
Notocrangon antarcticus	0.118 ± 0.003	153.91	5.04	-91.45	0.98	934.35	23
Crangon crangon	0.165 ± 0.004	151.08	10.96	22.61	0.74	190.13	68
RE expressed as total egg lipid/ fresh weight female (g/g)							
Chorismus antarcticus	0.012 ± 0.001	13.49	1.33	-3.26	0.80	102.2	28
Pandalus montagui	0.020 ± 0.001	18.42	2.16	3.70	0.66	72.65	39
Notocrangon antarcticus	0.017 ± 0.001	19.82	0.80	-6.00	0.97	614.5	23
Crangon crangon	0.011 ± 0.001	10.47	0.75	1.25	0.75	196.01	68

the polar species have been taken in plankton samples, and it is likely that these feed demersally (benthic larvae: Mileikovsky, 1971), possibly leading a partly lecithotrophic existence for a while (Clarke, 1977).

Reproductive Effort

When measured on a fresh weight basis, the mean individual annual reproductive effort (RE) of the polar species was significantly less than that of the temperate species (both P <0.05; Table 3); the degree of individual variability within species can be seen from the scattergrams (Figs. 3 and 4). Tinkle and Hadley (1975) have pointed out that the only true measure of RE is that fraction of the total energy budget diverted into reproduction; this will include energy used in collecting extra food, any territorial or mating behaviour, and the energy expended in carrying a brood of eggs weighing up to 20% of the female's own weight. The latter is very difficult to estimate, but since all 4 species brood (albeit for differing periods of time), it has here been ignored. Menge (1974) estimated this cost in the seastar *Leptasterias invicta* (which does not feed whilst brooding eggs) as the decrease in pyloric caecae reserves during the brooding period. This decrease amounted to about 70% of the reproductive output, and thus constituted a significant energy drain.

An alternative approach to using egg biomass is to examine RE in terms of lipid, on the frequently used assumption that this is a relatively expensive re-

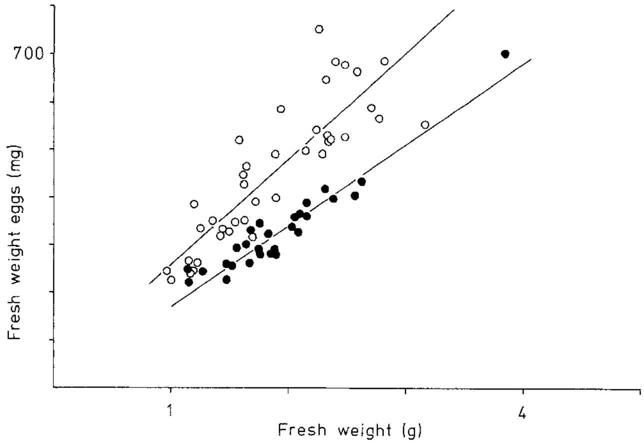

Fig. 3. *Chorismus antarcticus* (filled circles) and *Pandalus montagui* (open circles) reproductive effort. Least-squares regression of fresh weight total egg batch on female fresh weight. *C. antarcticus*, $y_i = 170.67\ x_i - 0.70$; *P. montagui*, $y_i = 222.02\ x_i + 37.37$

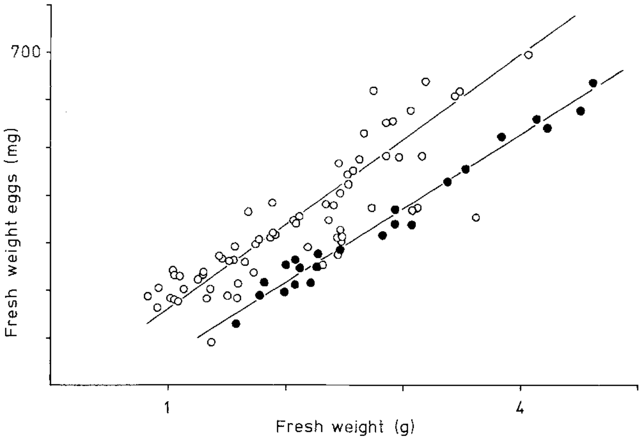

Fig. 4. *Notocrangon antarcticus* (filled circles) and *Crangon crangon* (open circles) reproductive effort. Least-squares regression of fresh weight total egg batch on female fresh weight. *N. antarcticus*, $y_i = 153.91\ x_i - 91.45$; *C. crangon*, $y_i = 151.08\ x_i + 22.61$

serve material to synthesize. Since the lipid contents of ovigerous female shrimps (analysed without their eggs) are fairly similar, RE was measured as g egg lipid per g female weight. These analyses gave opposite results for the two species pairs, namely *Chorismus antarcticus* RE $<$ *Pandalus montagui* RE, but *Notocrangon antarcticus* RE $>$ *Crangon crangon* RE (Table 3). The latter comparison is based on the assumption that female *C. crangon* spawn only once per year; allowing for 2 or more spawning periods (Lloyd and Yonge, 1947) reverses the trend, but it is clear that these comparisons do not give as clear-cut a result as those based on egg fresh weight.

Discussion

RE in Caridean Decapods

When RE is expressed in terms of fresh weight biomass, the results of the comparisons undertaken here match the predictions of *r*-*K* theory, for in both species pairs (*Chorismus antarcticus*/*Pandalus montagui* and *Notocrangon antarcticus*/*Crangon crangon*) the RE of the (polar) *K*-strategist was less than that of the comparable (temperate) *r*-strategist. The results also match the qualitative predictions of Vance (1973a, b; see discussion of the environment below), although Vance was analysing RE in terms of number of metamorphosing larvae per unit female investment, whereas these data refer to changes in the overall annual investment by the parent.

Investment in reproduction over the total life span of each of the 4 species is more difficult to judge. All 4 species are iteroparous, but only in *Crangon crangon* do females produce more than one brood per year. It is not possible to be definitive, but it seems likely that the total life RE of *C. crangon* is greater than that of *Notocrangon antarcticus*, and also that that of *Pandalus montagui* is greater than that of *Chorismus antarcticus* (assuming a similar reproductive span once fully mature); more data are needed.

No clear-cut result emerges when RE is expressed as g egg lipid per g female weight. To view reproductive output purely in terms of lipid (or calories) is simplistic, ignoring considerations such as N availability for yolk protein, availability of essential amino acids and fatty acids, or phosphorus balance. Thus, we have no idea of the relative cost to the shrimp of, say, synthesising egg lipid as against egg protein. We also lack knowledge of the metabolic rates of shrimps, although there are indications that *Chorismus antarcticus*, like other polar marine invertebrates, has a low basal metabolism (Everson, 1977). However, with no indications of the metabolic scope for activity, the cost of feeding activity, or overall level of energy intake, it is not yet possible to frame a coherent picture of energy balance. With all these difficulties in mind, this paper follows Pianka (1972) in approximating RE as biomass reproductive products per unit biomass female. On this basis it is therefore tentatively concluded that the comparisons undertaken here match the predictions of *r*-*K* theory.

Grahame (1977) found in a study of the reproductive effort of 2 sympatric prosobranch gastropods at Robin Hood's Bay (UK), that these animals also matched *r*-*K* theory, but no clear result came from a comparison of 2 species of intertidal seastar (Menge, 1974, 1975). The latter comparison, however, was complicated by the large difference in size of the 2 species, competitive effects, and intense density-independent selection. These factors confounded measures of RE and made equivocal any attempt to place the 2 species along an *r*-*K* continuum.

A potential confounding factor in the comparisons undertaken here is variation of brood size with sampling area - would samples of *Chorismus antarcticus* and *Pandalus montagui* from different areas have shown the opposite trend? There are no other data for *C. antarcticus*, but data are available for *P. montagui* from 2 other areas. The relationship between brood size and carapace length in Table 1 matches well the data of Mistakidis (1957) for *P. montagui* from the River Crouch (UK). However, in the deeper water off the Northumberland coast, for a given size of female, brood size is reduced to about half (Allen, 1963). Since growth rate is also reduced in these shrimps, it would seem that in this area food is probably severely limiting, and a comparison with *C. antarcticus* from South Georgia would not be valid.

Makarov (1970) has shown that the brood size of *Notocrangon antarcticus* in the South Orkney Islands (60°S, 45°W) is about half that at South Georgia for a given size of shrimp; the eggs are correspondingly larger and hatch into bigger larvae. Makarov gives no data to allow calculation of RE, but it is interesting that in this species there is a tendency for more marked *K*-strategist characters in higher latitudes.

K-strategies in Antarctic Benthos

Southwood (1977) and others have argued that *K*-strategies will evolve when either the environment is homogeneous, or when temporal variations in climate and resource availability are predictable. Selection will then favour the evolution of slow growth rates, deferred maturity and low fecundity, producing young of high competitive ability (Pianka, 1972).

The Antarctic environment is characterised by intense summer bursts of primary production which result in high food availability for both plankton and benthos, alternating with winter periods of low food availability. The summer burst of phytoplankton, although variable in intensity from year to year, is extremely predictable (Hart, 1942; Littlepage, 1965; Horne *et al.*, 1969; Whitaker, 1977); the Antarctic environment would thus appear to fit Southwood's criteria for selection favouring the evolution of *K*-strategies.

This is not to say that all polar marine invertebrates will be found to be *K*-strategists; the conclusions of Vance (1973a) and, for example, a recent study of molluscs by Clark and Goetzfried (1978) have demonstrated that sympatric organisms utilising different food sources with varying patterns of availability will evolve different strategies. Such variation is evident in the differing patterns of reproduction of Antarctic marine invertebrates in relation to the timing of the summer phytoplankton bloom (White, 1977). Nonetheless, although *r*- and *K*-strategists will exist together, it is suggested that an examination of the Antarctic benthos will indicate that most of the species have evolved *K*-, rather than *r*-, strategies.

Descriptive and anecdotal material on the life-histories of Antarctic organisms have long been available (see reviews by Dell, 1972; Arnaud, 1974, 1977), but only more recently have detailed autecological studies been undertaken; a number of these are summarised in Table 4.

It is clear from an examination of Table 4 (and the reviews listed above) that the Antarctic benthos is characterised by low fecundity coupled with large, yolk-rich eggs hatching into relatively advanced larvae (Clarke, 1977; Picken, 1979a), brooding and/or viviparity, slow growth rates (summarised by Everson, 1977), deferred maturity, and slow rates of ovarian maturation - that is, *K*-strategies. The high incidence of brooding and/or viviparity will result in low dispersal rates and thus the high degree of endemism characteristic of the Antarctic marine fauna (Dell, 1972).

Large size is also a moderately common feature of polar benthos (Dell, 1972; but see Arnaud, 1974). Horn (1978) has pointed out that once an animal has shifted towards the *K*-end of the *r*-*K* continuum, there will ensue a positive feedback loop which may lead to the evolution of very large species. Gigantism can thus been seen merely as a consequence of *K*-selection, rather than as a specific polar adaptation requiring an explanation in itself. The existence of *r*- and *K*-strategist self-augmenting feedback loops inevitably leads to the

Table 4. Life-history data for Antarctic benthos

Species	Remarks	Source
Mollusca		
Philine gibba	Slow growth, large eggs, non-pelagic development, low reproductive output, slow gametogenesis.	Seager (1979)
Laevilacunaria antarctica	Large eggs, non-pelagic direct development.	Picken (1979b)
Nacella (Patinigera) concinna	Slow growth, high longevity, low metabolic rate, high fecundity with small eggs, hatching into planktotrophic larvae, slow gametogenesis.	Picken (in press), Shabica (1976), Ralph and Maxwell (1977)
Lissarca miliaris	Slow growth, low fecundity, large eggs brooded in mantle cavity, direct development, iteroparous, low reproductive output, slow gametogenesis.	Richardson (1977)
Kidderia subquadratum	Low fecundity, large eggs brooded in mantle cavity, slow gametogenesis.	Shabica (1974)
Echinodermata		
Odontaster validus	Slow growth, demersal larvae, slow gametogenesis	Pearse (1965)
Crustacea		
Chorismus antarcticus	Slow growth, low metabolic rate, low fecundity, large yolk-rich eggs hatching into demersal schizopod larvae.	Clarke (1977), Clarke and Lakhani (1979), Everson (1977)
Pontogeneia antarctica	Slow growth, apparently elevated metabolism, low fecundity, large eggs.	Richardson (1977)

situation observed frequently in nature, namely that in a group of sympatric animals polarisation often occurs with all organisms shifted towards either the *r*-end or *K*-end of the spectrum, with relatively few in between. This is surely an analogous result to that of Vance (1973a) who, although arguing from an entirely different set of criteria, deduced that under a variety of environmental conditions, only very small planktotrophic eggs (i.e., *r*-strategies) or large yolk-rich lecithotrophic eggs (i.e., *K*-strategies) would maximise reproductive efficiency; populations would thus tend to show a varying proportion (depending on exact environmental conditions) of either extreme. It would appear from available data that most species in the Antarctic marine environment lie towards the *K*-extreme. It is, however, noticeable, that those species which do produce large numbers of small larvae [e.g. *Nacella concinna*, which Shabica (1976) regards as *K*-selected] are amongst the most successful (Mileikovsky, 1971; Picken, in press).

The role of low temperature in this widespread evolution of *K*-strategies may be crucial. It is now becoming clear that previous concepts of "metabolic cold adaptation" (*sensu* Scholander *et al.*, 1953), namely that polar ectotherms are adapted in exhibiting an elevated basal metabolism are, at least in the case of marine organisms, based on experimental artefact and difficulties of interpretation (Holeton, 1974; White, 1975; Everson, 1977). Rather, a low temperature will allow a low basal metabolic rate which, coupled with a decreased reproductive output and slow growth, means that individual energy requirements are greatly reduced, in turn allowing a greatly increased standing crop biomass for a given food input (see Dell, 1972). This is a fundamentally different view of "cold adaptation" to that of Scholander *et al.* (1953) or Dunbar (1970), and will be dealt with in more detail in a later paper (Clarke, in press).

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