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SIZE COMPOSITIONS OF LYSIANASSID AMPHIPODS IN COLD AND WARM WATER HABITATS

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SUMMARY

Since the family Lysianassidae is one of the largest and most diverse in the order Amphipoda it is suitable for the study of adaptations to different zoogeographic regions. The fauna is best known in regions of cold water (polar oceans and deep sea). Here most species are relatively small (6–13 mm) but a small number of large species are also found. In tropical waters such as the Indo-Pacific lysianassids are less well known and less conspicuous. The species are smaller and there is an apparent lack of large species. The problem is therefore not the occurrence of giants in cold water habitats but rather the small size of tropical species. While increased predation or competition could be responsible it is suggested here that the differences are probably due to shorter life spans at the higher temperatures in tropical waters. The species mature at a small size and produce small clutches of small eggs. In cold water survival is greater and the species mature at a larger size and infrequently produce large clutches of large eggs.

INTRODUCTION

One of the most striking features of marine amphipods is that they tend to be small in shallow tropical water but rather large in the Arctic, Antarctic and the deep sea. The reasons for these differences remain unknown but the apparent gigantism in the cold water habitats has been the subject of considerable speculation (Barnard, 1962, De Broyer, 1977 and Menzies, George and Rowe, 1973). The present contribution presents a different approach to this question by considering the size compositions of the faunas rather than just the occurrence of giants.

Species of the amphipod family Lysianassidae are suitable for making interhabitat comparisons since they are numerous at all depths in all oceans and many have the same life style—scavengers of freshly killed or wounded animals—and are either pelagic or benthic burrowers in soft sediments. Other lysianassids that are parasitic or commensal will not be considered here.

MATERIALS AND METHODS

In the present analysis the midpoint of the size range of mature females has been used as a measure of size. Mature females are readily recognised by the presence of setose oostegites and are usually reported in the literature. Mature males are typically smaller than females and can be recognised by their elongate calceolate antennae but are rarely reported in the literature. The midpoint of the size range is considered to be more representative of the size of mature animals than is the maximum. Since the maximum is determined by post-maturation survival it can be biased by an individual who survives longer than normal (personal observation) and is therefore not representative of the adult size of most individuals of the species. The maximum and the midpoint are similar in species with short reproductive lives. Size at maturity (Steele and Steele, 1975) and mean adult size would give a more precise measurement of size but neither is available for many lysianassid amphipods.

Total length was measured from the anterior margin of the head at the base of any rostrum, to the tip of the telson. Small individuals and hatched young from the brood pouch were measured with an eyepiece micrometer. Egg diameter is the average of the length and width of early (Stage A (Steele and

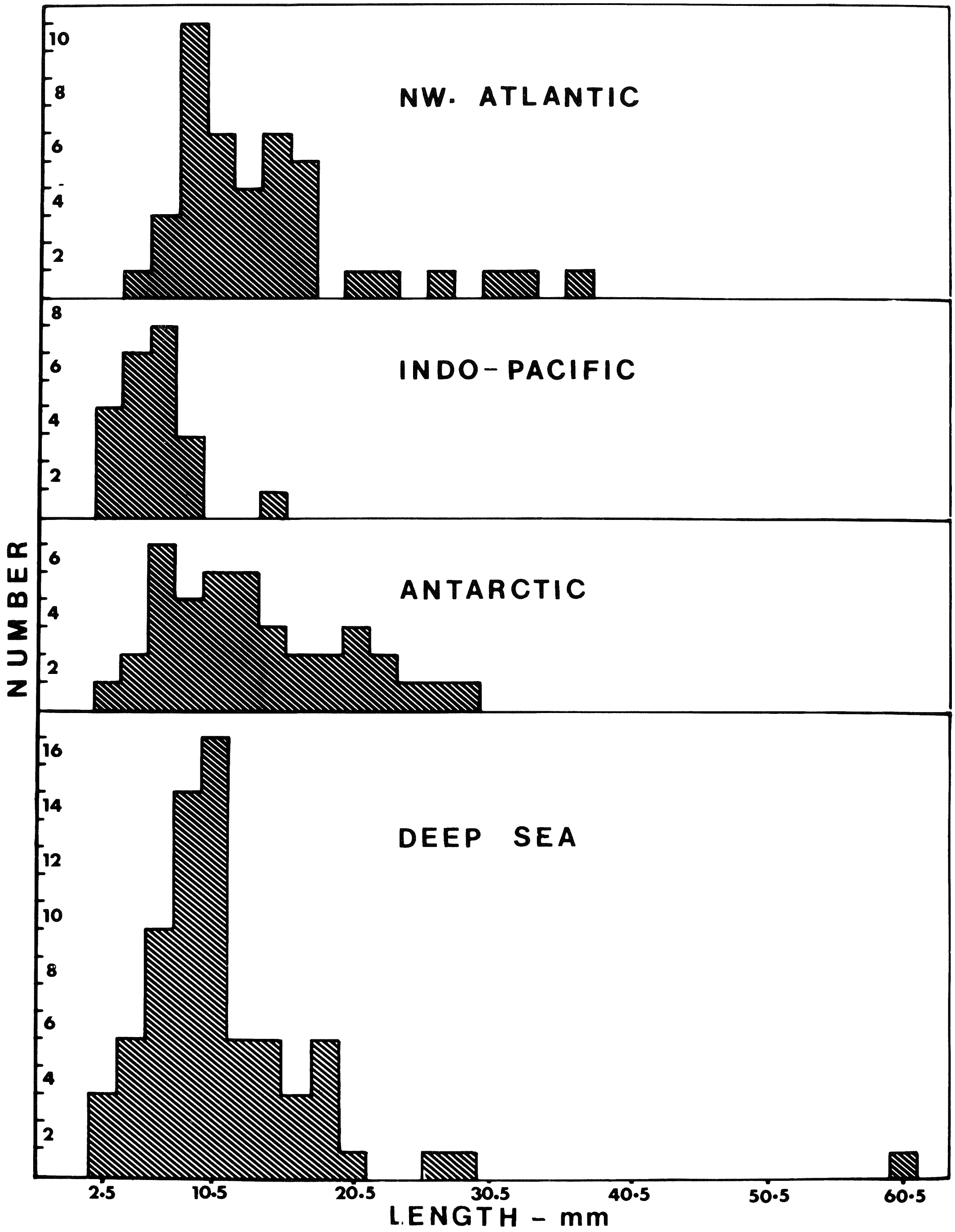

Fig. 1. Size compositions of mature female lysianassid amphipods.

Table 1. Body lengths of lysianassid amphipods

Area	N	Number <10 mm	%	Number >10 mm	%
N.W. Atlantic	42	14	33	28	67
Indo-Pacific	22	21	95	1	5
Antarctic	39	13	33	26	67
Deep Sea	69	31	45	38	55

Steele, 1969)) embryos taken from the brood pouch of ovigerous females. These measurements were also made with an eyepiece micrometer.

Measurements of specimens from the northwestern Atlantic (between the Bay of Fundy and the Alaskan border and including the Canadian Arctic Archipelago) were made by the author on specimens in the author's collections. Those from the Indo-Pacific, as delineated by Abbott (1959) are based on specimens of species collected at Nosy-Bé, Madagascar, by the author plus data extracted from a review of the literature on Indo-Pacific lysianassids. Data from the Antarctic are for species listed by Lowry and Bullock (1976) and were obtained in the literature. Those from the deep sea are for both bathypelagic and benthic species and are also from the literature. The literature consulted is not listed here but is available from the author. The species for which there is information on the sizes of mature females represent only a portion of the species known from each habitat but are considered to be a random selection and hence to be representative.

RESULTS

Examination of the size frequencies (Fig. 1) shows that most lysianassids in the northwestern Atlantic, the Antarctic and the deep sea are relatively small (6–13 mm). Large species are present but their numbers are relatively few and while the size frequencies are skewed to the right, large species are probably not more frequent than one would expect in a group of organisms in a habitat. In contrast, the Indo-Pacific lysianassids are almost all small and with a lower modal size than those from the cold water regions. What is most striking, however, is an apparent complete lack of large species. The frequency curve is truncated and almost no species is more than 10 mm in length (Table I). It appears therefore that giants are not more frequent than might be expected in cold water habitats and that their size compositions are similar to the theoretical model developed by Hutchinson and MacArthur (1959). The questions to be answered concern tropical waters: (1) why is the modal size reduced there and (2) why are large species apparently absent?

DISCUSSION

Body size is probably the most easily varied species characteristic and varies both within a species and between closely related species, as for example in *Anonyx* spp. (Steele and Brunel, 1968). Thus there is no reason to expect that large species could not evolve in tropical water, expecially as some lysianassid genera have species in both warm and cold water habitats.

There are at least three possible explanations of the small sizes of species in the Indo-Pacific. They are not mutually exclusive.

1. *Predation Hypothesis*

Many recent studies, reviewed by Hall *et al.* (1976), have documented how selective predation by fish in fresh water lakes can result in zooplankton populations with small body sizes compared to those in fishless lakes where such predation is absent.

A similar phenomenon could be postulated to occur in the oceans since fish species diversity varies in different habitats. It is highest in warm tropical habitats (Table II) and there fish predation is considered a highly significant factor in organising the fish communities themselves (Johannes, 1978). The number of species is much less in the northwestern Atlantic and in the deep sea and declines with latitude and depth respectively. Thus it is possible that predation may be less in the cold water habitats where large

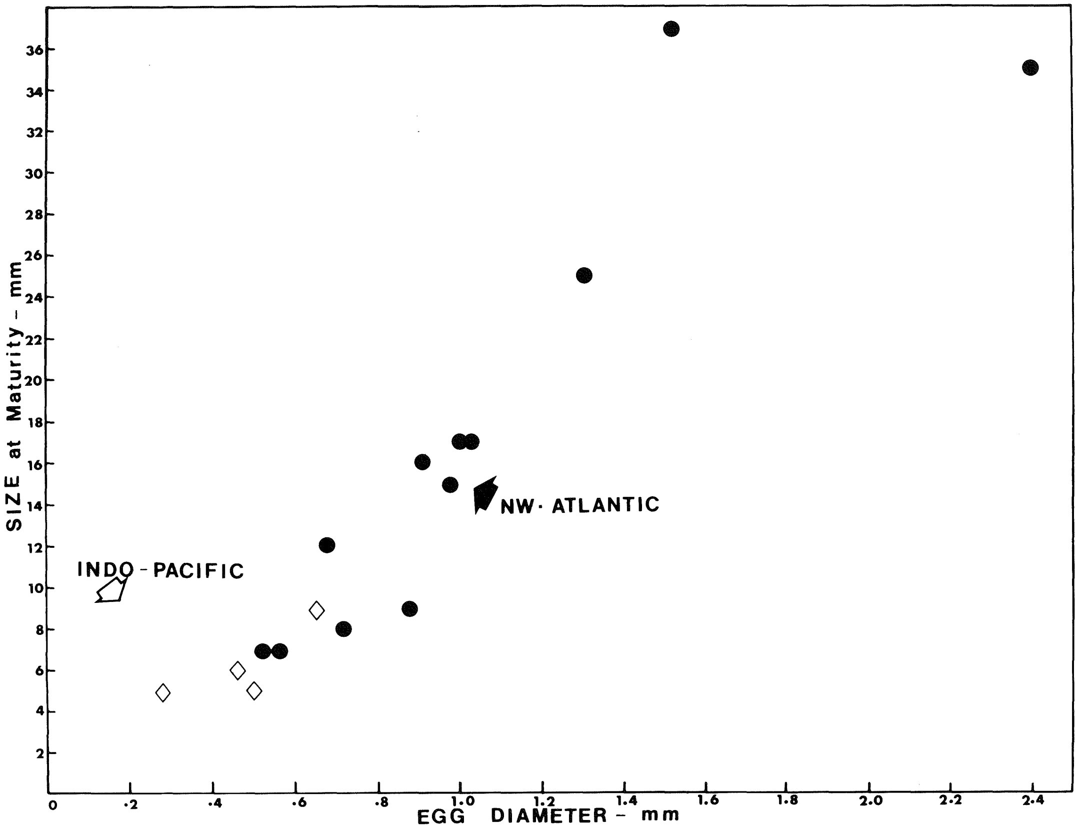

Fig. 2. Size at maturity of females related to egg diameters in lysianassid amphipods.

Table II. Numbers of fish species

Area		N	Source
N.W. Atlantic	>60°N	90	Leim & Scott, 1966
	Total	325	
Indo-Pacific		3000+	Briggs, 1974
Deep Sea	>2000m	100 pelagic 260 benthic	Marshall, 1963
	Total	2000	

amphipods are found. Nelson (1980) has made a similar suggestion to explain the decrease in size with latitude of epifaunal amphipods in eelgrass beds.

However, this simple correlation between amphipod size and number of fish species is confounded by differences in fish density in the different habitats, and it is not clear for example, how predation by large populations of certain species, such as cod (*Gadus morhua*) which passes through several growth stanzas, compares to the predation by the many species of fish in the Indo-Pacific. In addition, predation on lysianassids is limited by the fact that most species spend most of their time burrowed in the substrate and hence are unavailable to predators. Also the predation hypothesis is difficult to reconcile with the

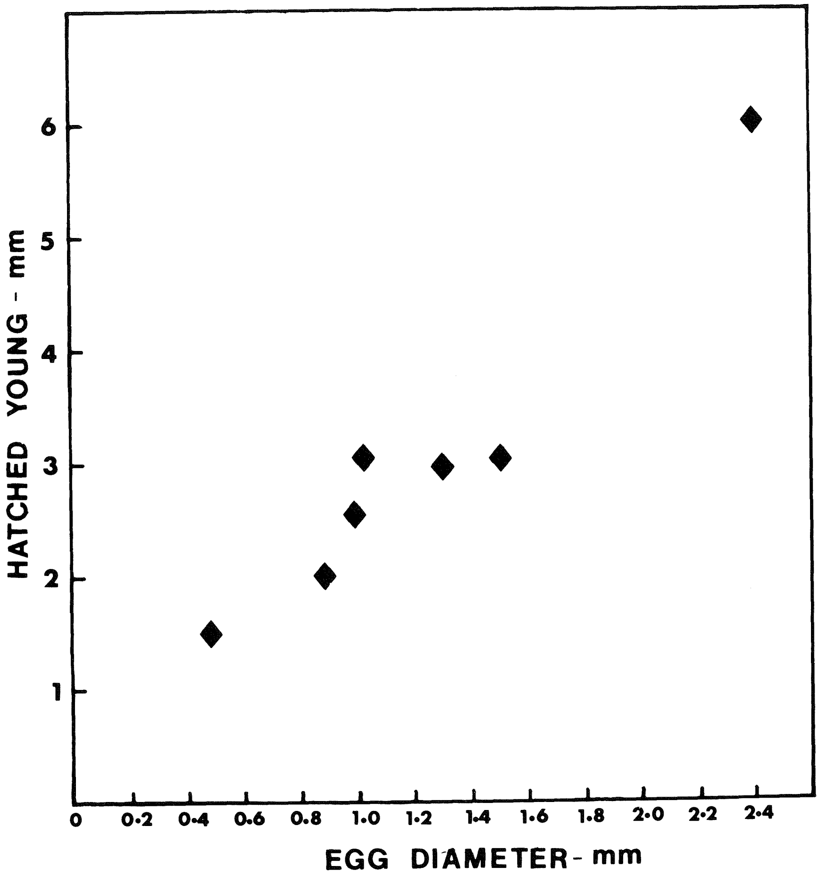

Fig. 3. Sizes of hatched young in the brood pouch related to egg diameters of lysianassid amphipods.

distribution of the decapod Crustacea which are also preyed on by fish. These are most numerous and also small in size in warm tropical waters where fish predation should be most intense (personal observation).

2. *Competition Hypothesis*

The scavenging habits of lysianassids in the Arctic, Antarctic and deep sea are legendary and one of the easiest methods to catch them in large numbers in these areas is with baited traps. However, in warm water habitats such as the Indo-Pacific, competition from fish and decapod Crustacea must increase considerably for this type of food. Both fish and decapods are probably better competitors than the lysianassids since they are more mobile, have better visions and are typically larger and they are what is usually attracted to bait in the warm water habitats.

3. *Reproductive Strategy Hypothesis*

Studies of *Gammarus* spp. (Steele and Steele, 1975) and haustoriid amphipods (unpublished) indicate that small size is an advantage in warm habitats with a long period of food availability, since reducing generation time, which can be accomplished simply by reducing size at maturity and egg size, produces more offspring than increasing clutch size by growing larger. This seems to have been at least part of the reason why the introduced *Gammarus tigrinus* has displaced the native *Gammarus* spp. in parts of Holland (Pinkster, Dieleman and Platvoet 1980). On the other hand, large size and a resulting high

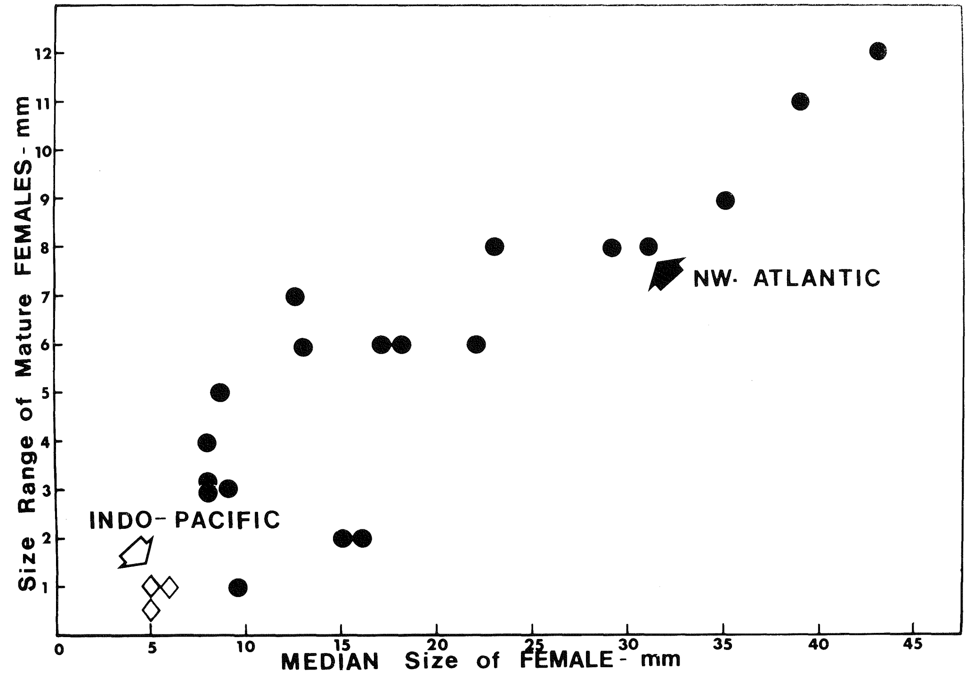

Fig. 4. Size ranges of mature females related to their median sizes in lysianassid amphipods.

fecundity will be an advantage in a cold habitat where there is a short period of food availability. If a species can produce only a single brood per year but can survive to produce later broods then larger broods are advantageous.

Data for the Indo-Pacific lysianassids are incomplete and the life cycle of no species is known, but is it possible to extrapolate from known species in other areas in order to determine if they follow this scheme.

The small Indo-Pacific lysianassids (Fig. 1) obviously mature at a small size and age. Egg sizes which are correlated with size at maturity in lysianassids (Fig. 2), as they are in *Gammarus* spp. (Steele and Steele 1975), are also small, which indicates that development time will be short at the high tropical temperatures. Both of these factors will result in a short generation time in this region as has been found in other amphipod species (Steele 1973). Clutch sizes are small (4–22 eggs in females 4–8.5 mm long) and the young when they hatch will also be small (Fig. 3).

Survival rates are unknown for any of the amphipods but an indication can be obtained by determining the size ranges of the mature animals since they will be greater if the animals survive to breed more than once rather than producing only a single brood. Figure 4 shows that the size ranges of the mature females are correlated with their sizes. In part this will be due to the cumulative effects of differences in growth rates and measurement errors for large individuals but the ranges of the large species are too great to be accounted for by these factors alone and suggest that the large species, with some exceptions, apparently do survive to produce more than one brood whereas the small species do not. The Indo-Pacific species with their small size ranges are at the low end of the scale and probably do not survive long after they mature. Unlike the decapods, the lysianassids seem to lack specific reproductive adaptations for life in warm water such as pelagic larvae and their small sizes are therefore explicable in the advantages they obtain from having short generation times in the warm water of this region. This agrees with what has been suggested for other amphipod groups elsewhere (Steele and Steele 1975). On the other hand, the relatively small size of many lysianassids in the northwestern Atlantic and other cold water areas is unlike the situation in *Gammarus* spp. or the haustoriids where the body size increases with latitude. The only explanation that can be offered for this difference is that the lysianassids as benthic scavengers may have suitable food available for a longer period during the year then is the case for the *Gammarus* or haustoriid species that are more dependent on ephemeral algae for food.

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