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The spatial and size distribution of the rocky intertidal *Acanthopleura gemmata* (Blainville, 1825) (Mollusca : Polyplacophora) in the northern gulf of Aqaba

*Distribution spatiale et taille d'*Acanthopleura gemmata *(Blainville, 1825) (Mollusca : Polyplacophora) de la zone intertidale rocheuse, dans le nord du golfe d'Aqaba*

by Neil C. Hulings
Ranunkelgatan 7D, 431 32 Mölndal, Sweden

RÉSUMÉ

La distribution du chiton dans la zone médiolittorale des substrats à galets et en plaques est décrite. La répartition locale et régionale de la longueur moyenne est corrélée aux contraintes de l'exposition et de l'environnement. La distribution en rapport avec la patelle Cellana radiata *est aussi discutée.*

ABSTRACT

The distribution of the chiton in the midlittoral zone of slab and boulder substrata is described. The local and regional distribution of the mean length is related to exposure and environmental stresses. The distribution in relation to the limpet Cellana radiata (Born) *is discussed.*

MOTS CLÉS
CHITON, ÉCOLOGIE, CONTRAINTES, MER ROUGE

KEY-WORDS
CHITON, ECOLOGY, STRESSES, RED SEA

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INTRODUCTION

In a revision of the genus *Acanthopleura*, Ferreira (1986) put *Acanthozostera* Iredale and Hull, 1926 into synonymy with *Acanthopleura* Guilding, 1829. The species *Acanthopleura haddoni* Winckworth, 1927 and *A. spiniger* (Sowerby, 1840) were synonymized with *A. gemmata* (Blainville, 1825). Ferreira (1986) reports that *A. gemmata* has the widest geographic distribution of the intertidal chitons, from 32°E to 140°W and 29° 33'N to 6° 48'S.

Outside the Red Sea, investigations on *Acanthopleura gemmata* include those on ecology, feeding and activity patterns including homing by Thorne (1967, 1968 as *Acanthozostera gemmata*) at Heron Island, Australia ; that of Greenfield (1972) on the feeding and the physiology of the gut and Hartnoll (1976) on the ecology (both as *Acanthopleura spiniger*) in Tanzania ; and Chelazzi *et al.* (1983 a, 1983 b, 1987 as *Acanthopleura gemmata*), Chelazzi and Parpagnoli (1987) as *Acanthopleura gemmata* and Chelazzi and Vannini (1980 as *Acanthopleura spiniger*) on various aspects of the activity, homing and distribution in Somalia.

Reports on *Acanthopleura gemmata* as *A. haddoni* in the Red Sea, including the gulf of Aqaba, include those of Leloup (1937, 1960, 1980), Rees and Stuckey (1952), Safriel and Lipkin (1964), Eibschütz *et al.*(1967), Fishelson (1971), Mergner and Schuhlacher (1974), Pearse (1978, 1983), Mastaller (1978, 1979), Ayal and Safriel (1980), Hulings (1986, 1987 a) and Al-Hajj (1987) and as *A. spiniger* by Sykes (1907) and Soliman and Iskander (1982). Most of the above reports are on the occurrence in the rocky intertidal zone. Eibschütz *et al.* (1967) investigated the magnetic properties of the radula while Pearse (1978, 1983), Soliman and Iskander (1982), Hulings (1986) and Al-Hajj (1987) reported on various aspects of the reproduction. Hulings (1991) has described the homing and activity patterns of *A. gemmata* on the coast of Jordan.

This paper reports on the spatial and size distribution of *Acanthopleura gemmata* in the very northern gulf of Aqaba, the northernmost geographic occurrence of the species according to Ferreira (1986). In the northern gulf, *A. gemmata* is the only chiton occurring in the rocky intertidal and occupies the midlittoral zone. More specifically, it occurs in the mid midlittoral, the *Tetraclita* zone of Safriel and Lipkin (1964) and identifiable by the presence of the giant barnacle *Tetraclita squamosa rufotincta* Pilsbry, 1916, to the lower midlittoral-infralittoral fringe (of Safriel and Lipkin, 1964) contact.

DESCRIPTION OF THE ROCKY INTERTIDAL ZONE

The rocky intertidal zone along the coast of Jordan has been described in detail by Hulings (1986, 1987 a). Briefly, the tides are of the mixed type, having a spring range averaging about 1 m and a neap range of around 50 cm and usually out of phase with the moon. The diurnal inequality of the highs averages 4,2 cm, that of the lows 4,7 cm. Annual fluctuations of sea level of up to 1 m occur, being higher during the period December through May and lower from July through October.

The fluctuations are related to the monsoon seasons in the Indian Ocean area. The sea level fluctuations result in tide levels being higher during the period December-May and lower during July-October. Additional fluctuations in tide levels occur in relation to atmospheric pressure (Uziel, 1968 ; Hulings, 1989).

The prevailing land to gulf winds are northerly (93 %) with Beauforts 3 and 4 occurring 63 % of the time. The extremes in air temperature are reflected in the monthly means, ranging from 16°C in January to 32°C in July-August ; the daily minimum-maximum during January averages around 12° and 20°C, respectively and that during July-August 26° and 37°C, respectively (Jordan Meterological Department). The evaporation rate is high, estimated to be 4,2 m/yr by Anati (1976, 1980) and there is strong solar insolation (Assaf and Kessler, 1976 ; Levanon-Spanier *et al.* 1979). These and other parameters reflect the very significant effect of the surrounding terrestrial area on the environmental conditions in the rocky intertidal zone of the very northern gulf over that of the marine realm which has a limited areal extent, 5 to 15 km wide by 20 km long.

Five localities in the northern gulf of Aqaba were investigated to determine the distribution of *Acanthopleura gemmata*. Three of the localities were near horizontal slab, being back reef areas of fringing reefs, on the windward or downwind sectors of the coast of Jordan. The other two localities included a boulder habitat, one being a man-made breakwater on the coast of Jordan and the other on the coast of Sinai.

Locality 1, composed of slab substratum, is at the Marine Science Station and is approximately 10 km south of the northern limit of the Jordanian gulf. The locality is relatively protected due to the elevated topography adjacent to and immediately north. The *Tetraclita* zone (= mid midlittoral) averages 5 m (range 2 to 8 m) wide and consists of discontinuous strips of beachrock (averaging 0,8 m wide, ranging from 0,25 to 1,5 m.) parallel to the shore. Depressions and tide pools averaging 14 cm deep (range 6 to 23 cm) occur between the strips ; numerous overhangs, crevices and small caves also occur.
The surface configuration of the fossil reef substratum upon wich the beachrock rests is very irregular. Below the *Tetraclita* zone and to the lower limit of the midlittoral, the substratum consists of near horizontal calcareous (fossil reef matrix) platform having a mostly even and uniform surface topography. The platform averages 15 m wide, varying from 10 to 18 m. Beyond the lower limit of the midlittoral is a back reef lagoon of the fringing reef which is 35 to 85 m wide, terminating at the outer edge of the reef.

Locality 2, approximately 14 km south, is on a point and the surrounding terrestrial topography offers little protection from the prevailing winds. The near horizontal *Tetraclita* zone averages 5 m wide, varying from 2 to 8 m wide. The surface topography is highly irregular, consisting mostly of numerous pinnacles of fossil reef topped with *Tetraclita* and some beachrock. The lower midlittoral is narrow, averaging 4 m (range 2 to 6 m) wide and is highly dissected, near horizontal fossil reef matrix. Apart from the dissected areas, the surface topography of the lower midlittoral is relatively smooth. The adjoining back reef lagoon to reef edge distance is about 50 m.

Locality 3, on the downwind shore of an embayment 25 km to the south, is characterized by fossil reef slab with the *Tetraclita* zone having a slope of about 10°. Only scattered and isolated *Tetraclita* pinnacles occur within the 2 to 3 m wide mid midlittoral ; refuges are few and restricted mostly to depressions in fossil coral heads and isolated crevices. The 12 m wide outer midlittoral is as at the other localities, calcareous fossil reef matrix having a smooth surface and considerably dissected. Beyond the outer limit of the lower midlittoral is a 25 m wide back reef lagoon.

Based on wind data (Hulings, 1979), the fetch, the surrounding terrestrial topography and the topography of the intertidal and adjacent subtidal zones, locality 1 is the least exposed to wind and the impact of wind-generated waves is minimal, locality 2 is intermediate and locality 3 is the most exposed to wind and wave action.

The boulder locality 20 km south on the Jordanian coast is directly exposed to heavy wave action. The bottom seaward of the boulders drops steeply so that wind-generated waves break with full force on the boulders. The other boulder locality investigated was the mid midlittoral of Faroun Island (named Geziret Fara'ûn on British Admirality Chart 3595) on the coast of Sinai, about 20 km south of Eilat (Reiss and Hottinger, 1984). The seaward (eastern) and south sides of the Island consists of numerous small boulders and are relatively protected from direct wind and wind-generated wave action.

METHODS AND MATERIALS

The data on vertical, density and size distribution of *Acanthopleura gemmata* were obtained from the three slab and two boulder localities during September and October 1988. Preliminary and additional data were obtained during October 1986 and March 1989. At the slab localities (1, 2 and 3), data on the distribution of *Acanthopleura gemmata* were obtained from within the mid midlittoral to the lower midlittoral-infralittoral fringe border, the portion of the midlittoral that *A. gemmata* occurs. At locality 1, an area of 100 m length parallel to the beach and averaging 20 m wide was surveyed ; at locality 2, a 65 m by 9 m area ; and at locality 3, an area of 120 m by 15 m.

The density of *Acanthopleura gemmata* was determined by recording the number of specimens per m^2 or a unit thereof and adjusting to a m^2. Measurements of length were made on specimens *in situ* in the field to the nearest mm. Statistical tests used include students t-test for comparison of means and the Pearson correlation coefficient for presence-absence of taxa. The following terminology and abbreviations are used in considering the distribution of *Acanthopleura gemmata* in the northern gulf of Aqaba. The mid midlittoral and the *Tetraclita* zone are used interchangebly and abbreviated MML. The upper portion of the lower midlittoral, abbreviated ULML, is just seaward of the MML. The lower portion of the lower midlittoral, LLML, includes the area bordering the infralittoral fringe.

RESULTS

The vertical distribution of *Acanthopleura gemmata* is from the mid midlittoral (MML) to the lower portion of the outer midlittoral (LLML). Along any given transect, however, the distribution is discontinuous between the upper portion of the lower midlittoral and the lower portion of the lower midlittoral. Thus, within the midlittoral, the chiton is restricted to the mid midlittoral (MML), the upper portion of the lower midlittoral (ULML) and the lower portion of the lower midlittoral (LLML).

Table 1 summarizes the mean density of *Acanthopleura gemmata* in the MML, ULML, and LLML, in all three slab localities (1,2 and 3). The mean density for all slab localities and subzones is 4,3 individuals/m^2 (SD = ± 2,9). The difference in the density between the various subzones of the midlittoral is statistically significant at P = .01 between MML and ULML (n-2 = 192) and between MML and LLML (n-2 = 181) and P = .001 between ULML and LLML (n-2 = 145). The statistical difference between localities is as follows : between locality 1 and 2 (n-2 = 185), P = .5 ; that between locality 2 and 3 (n-2 = 180) and locality 1 and 3 (n-2 = 153), P = .01.

Table 1 - Mean density of Acanthopleura gemmata *in the mid midlittoral (MML), upper lower midlittoral (ULML) and lower lower midlittoral (LLML) at slab localities along the coast of Jordan.*

Subzone	n (frames)	$\bar{X}$ (no/m^2)	SD
MML	115	4,5	3
ULML	79	5	3,2
LLML	68	3,3	2,2

For the boulder habitats, *Acanthopleura gemmata* was absent at the locality on the coast of Jordan. At Faroun Island, the density in the MML was 3,1 individuals/m^2 (SD = ± 1,7).

Table 2 gives the mean length of *Acanthopleura gemmata* in the subzones of the slab localities. The mean length is consistently highest in the LLML, intermediate in ULML and lowest in MML. In addition, the differences are statistically significant between subzones at each locality at P = .001 in six of nine comparisons, P = .1 in one and P = .4 and .5 in the remaining two.

Table 2 - Mean length of Acanthopleura gemmata *locality and subzone in the northern gulf of Aqaba (MML = mid midlittoral ; ULML = upper lower midlittoral; LLML = lower lower midlittoral ; All = all subzones within a locality).*

Locality Subzone	n (individuals)	$\bar{X}$ (mm)	SD
Locality 1			
MML	60	47	7,6
ULML	50	53,3	6,2
LLML	50	59,8	9,8
All	160	53	8,6
Locality 2			
MML	75	47	9,1
ULML	52	50,4	7,7
LLML	36	53,7	8
All	163	49,5	8,2
Locality 3			
MML	116	42	5,7
ULML	40	48,2	6,3
LLML	57	49,3	7,6
All	213	45	7,3
Faroun Island			
MML	141	64,9	11,8

The mean length of all chitons in the MML of localities 1, 2 and 3 is 44,7 mm (SD = ± 7,4), that of ULML 50,8 mm (SD = ± 7,1) and LLML, 53,7 (SD = ± 8,6). The difference in statistical significance between all subzones of all localities is as follows : P = .001 for all MML vs all ULML (n-2 = 391) and all MML vs all LLML (n-2 = 392) and P = .01 for all ULML vs all LLML (n-2 = 283).

Table 2 also shows the overall mean length of the chitons of all subzones at each locality with locality 1 having the highest, locality 2 intermediate and locality 3 the lowest. The differences between the localities are statistically significant, being P = .001 for locality 1 vs locality 3 (n-2 = 371) and locality 2 vs locality 3 (n-2 = 374) and P = .01 for locality 1 vs locality 2 (n-2 = 321).

The mean length of *Acanthopleura gemmata* in the MML of Faroun Island is 64,9 mm (SD = ± 11,8). The difference between this mean length and that of LLML in the slab localities is significant at P = .001 (n-2 = 282).

DISCUSSION

The overall spatial distribution of *Acanthopleura gemmata* in the midlittoral in the northern gulf of Aqaba appears to be essentialy the same as that at Heron Island (Thorne, 1967), in Tanzania (Hartnoll, 1976), in Somalia (Chelazzi and Vannini, 1980) and in the Red Sea proper (Mastaller, 1978). Along the coast of Sinai (Gulfs of Aqaba and Suez), Ayal and Safriel (1980) note the occurrence of *A. gemmata* only in the upper midlittoral, a more restricted vertical distribution than found herein.

Within the Jordanian rocky intertidal, *Acanthopleura gemmata* is consistently absent in the area between the lower portion of the upper lower midlittoral (ULML) and the upper portion of the lower lower midlittoral (LLML) in the slab localities. However, the absence cannot be explained by available data. Within the total area, the nature and configuration of the substratum is essentially the same.

In terms of the general distribution of *Acanthopleura gemmata* in relation to exposure, that found in the northern gulf of Aqaba is similar to that reported by Chelazzi and Vannini (1980) on the coast of Somalia, namely from exposed, less rather than more, to sheltered and essentially the same as that given in Ayal and Safriel (1980) for the coast of Sinai and the gulf of Suez. Hartnoll (1976) found *A. gemmata* to prefer exposed and steep substrata at Dar es Salaam.

The results of the data on the density of *Acanthopleura gemmata* in the northern gulf must be interpreted with care. In any given locale, *A. gemmata* occupies refuges such as under overhangs, crevices, caves depressions., etc., if available rather than exposed surfaces. Though the density surveys were conducted during ebbing and low tides when *A. gemmata* forages, not all individuals leave the refuges during consecutive tide cycles and days (Hulings, 1991).

Thus, the density reported herein is considered to be conservative. The significant differences between subzones and slab localities as well as differences between subzones within localities may reflect subzone microhabitat complexity but more detailed data are needed.

A factor influencing the spatial distribution of *Acanthopleura gemmata* is its occurrence with the patellid limpet *Cellana radiata* (Born, 1778). The limpet occurs from the mid midlittoral to the lower lower midlittoral as does *A. gemmata*. Based on quantified density data, when one of the two species is present, the other is likely to be absent.

For the slab localities, the correlation coefficient is negative and significant at P =.01 (n-2 = 222). Another example is seen on the boulders on the Jordanian coast that are fully exposed to heavy wave action. As note above, *A. gemmata* is completely absent at this locality and the density of *C. radiata* is high ($24/m^2$, SD = ± 19,2, n = 38) compared to that on slab ($7/m^2$, SD = ± 8, n = 124).

The nature of the exclusive distribution between the chiton and the limpet is not known. *Cellana radiata* is a temporary homer and migrates vertically with changes in sea level (Hulings, 1985) while *Acanthopleura gemmata* is a permanent homer and, contrary to Hulings (1987 a), does not migrate vertically with changes in sea level (Hulings, 1991).

Possible explanations include the maintenance of territorality by *A. gemmata*. In fact, many individuals have a recognizable grazing area (Hulings, 1991). On the other hand, in no case has physical or aggressive exclusion of another individual in the grazing area or home scar, whether another *A. gemmata* or species, been observed. And in the case of the distribution of *A. gemmata* and the pulmonate limpet *Siphonaria laciniosa* Linnaeus, 1758, a mid midlittoral permanently homing non-migrant, Hulings, 1985), both occur together (correlation coeffecient positive and not significant, n = 89 m^2). Perhaps the relationship between *A. gemmata* and *C. radiata* is indicative of space and/or resource partitioning between the two species.

The statistically significant differences in the mean length of *Acanthopleura gemmata* between the subzones within a slab locality and between all the subzones of all slab localities are consistent as seen in the results.

The significant differences in mean length can be explained in terms of the continuous and periodic exposure and environmental stresses. Exposure is longer and environmental stresses greater and more varied during the period July through October. It is during this period that a combination of mixed tides having diurnal inequality that may fluctuate in leval with variations in atmospheric pressure, lowered sea level, higher air temperatures (mean daily maximum-minimum 37° and 26°C, respectively), long day length and high solar insolation and dry winds results in greater stresses that include high substrate temperatures and desiccating conditions.

Of the subzones in which *Acanthopleura gemmata* occurs, the mid midlittoral (MML) is exposed to atmospheric conditions more frequently on a daily basis and for a longer period of time each day than the subzones of the lower midlittoral. In the latter, however, the upper portion of the lower midlittoral is more exposed in terms of frequency and temporally than the lower portion of the midlittoral but less so than the mid midlittoral and more so than the lower lower midlittoral (LLML).

During neap tides, the latter subzone may not be exposed to atmospheric conditions at all ; the same applies to the upper lower midlittoral (ULML) under certain conditions. Though more benign conditions prevail from December through May including higher sea level thus reducing prolonged exposure, lower air temperatures (mean daily maximum-minimum 20° and 12°C, respectively), shorter day length and reduced solar insolation and more humid winds, the relative degree of exposure of the subzones described above remains approximately the same.

It is concluded, therefore, that the lower mean length of *Acanthopleura gemmata* in the mid midlittoral (MML) in the northern gulf of Aqaba is a function of more exposure and greater environmental stresses and the higher mean length in the lower lower midlittoral (LLML) can be attributed to less exposure and fewer stresses. The conditions in the upper lower midlittoral (ULML) are intermediate between the two extremes and so is the mean length. Support for the mean length-stress relationship is seen in the much greater length of *A. gemmata* occurring on boulders at Faroun Island. The chitons occur on boulders, resulting in many more refuges and moderated environmental conditions, especially reduced desiccating conditions and substrate temperature compared to slab. In comparing the mean length of *A. gemmata* in the lower lower midlittoral (LLML), the most benign of the slab subzones, with that in the mid midlittoral at Faroun (the only subzone investigated), the difference is significant at P = .001 (n-2 = 282). Hulings (1987 a, b) reported a similar relationship in the size distribution of *Nodolittorina millegrana* (Philippi, 1848) between boulders (benign) and slab (exposed).

In comparing the mean length of *Acanthopleura gemmata* by locality in the northern gulf, there is a significant decrease from the northern slab locality 1 to the southern slab locality 3 *(table 2)*. As noted in the description of the localities, locality 1 is considered to be the least exposed, locality 2 intermediate and locality 3 the most exposed thus a north to south increase in environmental stresses. This stress gradient is, in turn, reflected in the decrease in mean length of *A. gemmata* along the north-south gradient. This is in agreement with the inferred relationship between stress and mean length within the subzones at each locality discussed above.

The stress-mean length relationship is also seen in comparing the mean lengths of the chiton between locality 1 and Faroun Island. The difference between the least stressed of the slab localities and the most benign of all localities (slab and boulder) investigated is significant at P = .001 (n-2 = 299). In comparing three boulder habitats, Faroun Island, one fully exposed to wind but moderately exposed to wave action and one fully exposed to heavy wind and wave action, the mean length of the chitons on the moderately exposed boulders was found to be 37,1 mm (SD = ± 7,3; n = 116). In the latter case, *A. gemmata* is completely absent ; however, as discussed above, the absence may be due to the high density of the limpet *Cellana radiata*.

Regionally, there is a similar stress-mean length relationship in *Acanthopleura gemmata* between the northern gulf of Aqaba, based on data reported herein, and inferred from the data of Pearse (1978, 1983). The mean length of all *A. gemmata* occurring in all of the subzones of all slab localities in the northern gulf is 48,7 mm (SD = ± 8,6). Pearse found the mean length of *A. gemmata* on platforms in the northwestern gulf of Suez to be 57 mm (SD = ± 2) and that of shore specimens in the northwestern Red Sea proper to be 69 mm (SD = ± 2).

The rocky intertidal of the northern gulf of Aqaba investigated herein is considered to be subjected to more severe stresses than the area of the gulf of Suez investigated by Pearse (1978, 1983). The inference is based on the much greater areal expanse of the surrounding land in relation to the limited marine area of the northern gulf. On the other hand, the area of the gulf of Suez is larger in relation to the surrounding land area, the result being a possible moderation of environmental extremes when compared to the northern gulf of Aqaba. An indication of this is seen in the data given in Morcos (1970) including the prevailing winds and the lower air temperatures at Suez than at Aqaba. Pearse (1978, 1983) pointed to the influence of the surrounding terrestrial area at the locality in the gulf of Suez resulting in greater extremes in environmental parameters than in the Red Sea where the extremes are less.

Thus, regionally, and locally as discussed above, there is a direct relationship between mean length and environmental stress in *Acanthopleura gemmata*, the relationship being increased length with decreased stress. It is interesting to note that the 64,6 mm mean length of *A. gemmata* in the most benign habitat in the most environmentally severe northern gulf of Aqaba, the relatively protected boulders at Faroun Island, compares favorably with the 69 mm mean length in the less environmentally extreme northwestern Red Sea of Pearse (1978).

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