

# THE NATURAL HISTORY, LIFE HISTORY AND ECOLOGY OF THE TWO BRITISH SPECIES OF *ASTERINA*

By R. G. CRUMP

*Orielton Field Centre, Pembroke, Dyfed SA71 5EZ*

and R. H. EMSON

*Department of Zoology, Kings College, London WC2R 2LS*

## ABSTRACT

The gibbous starlets or cushion stars (Echinodermata: Asterinidae) found on rocky sea shores in South-west Britain used to be ascribed to a single species, *Asterina gibbosa* (Pennant). However, Emson and Crump (1978) realised that British *Asterina* exhibit two discrete types of reproductive behaviour and this led, in 1979, to the recognition that two species were present—*A. gibbosa* (Pennant) and *A. phylactica*, Emson and Crump. Subsequent papers have clarified the degree of overlap and separation between the two species to such an extent that it is now possible to review their biology.

These two starfish provide an excellent example of the way in which small differences in anatomy and biology can together result in a high degree of ecological separation between two closely-related and rather similar species. The crucial differences between them, in terms of habitat partitioning where they are sympatric, seem to result from differences in behaviour, and especially from their responses to light. But in fact the whole life strategies of *A. gibbosa* and *A. phylactica* are different. In addition to the fact that *A. phylactica* broods the eggs and developing juveniles whereas *A. gibbosa* does not, *A. phylactica* matures earlier and has a shorter life span. Although the species appear to be morphologically similar and may be found together exploiting a similar food supply, it is shown in this paper that their ecological niches are quite different.

## INTRODUCTION

IN South-west Britain gibbous starlets or cushion stars are common animals on the low shore and in tide pools. Until recently there was thought to be only a single species, *Asterina gibbosa*, described by Pennant in 1897.

In 1978, we drew attention to the fact that part of a population in rock pools at West Angle Bay, Dyfed, Wales, was exhibiting a different reproductive behaviour pattern (Emson and Crump, 1978). Small dark-coloured individuals were found to brood the developing embryos under the oral (ventral) surface until the juveniles were mobile and crawled out from beneath the parent (Fig. 9A). At the time, we regarded these animals as a form of *Asterina gibbosa*, since examination revealed no major structural differences between the dark-coloured brooding form and *A. gibbosa* of the same size. Subsequently, large, virtually pure populations of this dark brooding form were found, and further study in Britain and the Mediterranean led us to describe this animal as a separate species, *Asterina phylactica* Emson and Crump (1979).

Biochemical evidence tending to confirm the specific status of *A. phylactica* has recently been obtained by Bullimore and Crump (1982) using starch gel electrophoresis. These authors showed that *A. gibbosa* and *A. phylactica* were genetically dissimilar and had probably been isolated for a considerable time. Other studies carried out since 1979 have clarified the degree of overlap and separation between the two species in terms of reproductive strategy (Marthy, 1980; Strathmann, Strathmann and Emson, in prep), behaviour and physiology (Emson,

1979; Emson and Foote, 1980) and ecology (Emson and Crump, in press).

Much information was, of course, published prior to 1979 on the two un-separated species as *A. gibbosa*. Most of this literature describes responses to light, gravity, etc. (Loeb, 1900; Mangold, 1921; Russell, 1919; Kalmus, 1929) or embryological studies and hermaphroditism (Cuenot, 1898; Ludwig, 1897; Bacci, 1949, 1951; Delavault, 1966; Brusle, 1968, 1969), and regeneration, e.g. Huet (1975). Our state of knowledge is now such that a brief paper reviewing the biology of the two species is possible.

#### MORPHOLOGY AND APPEARANCE

##### *Asterina gibbosa* (Pennant)

*A. gibbosa* is a small cushion star (spinulosan asterinid) not more than 5 cm diameter (arm tip to arm tip). It is subpentagonal ( $R = 1.2-2r$ )\* with five bluntly rounded arms (four- and six-armed individuals are rare) (Fig. 1). The colour in life ranges from olive green through muddy brown to bright orange, and mottled individuals are present in some populations. Lower-shore and sublittoral populations are invariably pale orange or pale grey, while those from high tide pools are usually dark olive. Colour varies with locality: e.g. Exmouth, Devon, *A. gibbosa* are predominantly dark grey/green, those from pools near Start Point, Devon, mottled in colour and near Angle, Dyfed, pool populations are dark olive.



FIG. 1.

Photograph taken in March showing a mature female *A. gibbosa*, a mature *A. phylactica* and a juvenile *A. gibbosa* approaching one year old. Note size difference between adults and colour pattern differences.

\*  $R$  is greatest radius: i.e. armtips to centre of mouth.  
 $r$  is least radius: i.e. between arms to centre of mouth.

*Asterina phylactica* (Emson and Crump)

*A. phylactica* may readily be recognised in the field by the distinctive colour pattern and small size (see Fig. 1, 9A). The general background colour of the animal is a dark green with distinctive chocolate brown substar on the aboral (dorsal) surface. The body shape is a regular pentagon, the arms having bluntly rounded tips and the r/R ratio is high (1–1.5/2). Specimens do not exceed 15 mm diameter (arm tip to arm tip) (R = 7 mm).

Morphologically, *A. phylactica* is very similar to *A. gibbosa*, but the ventral mouth plates do not bear the two spines found in *A. gibbosa*. The gonopores may be visible in *A. phylactica* over 6 mm (Fig. 2), whereas they are never obvious in *A. gibbosa* smaller than 16 mm in diameter.

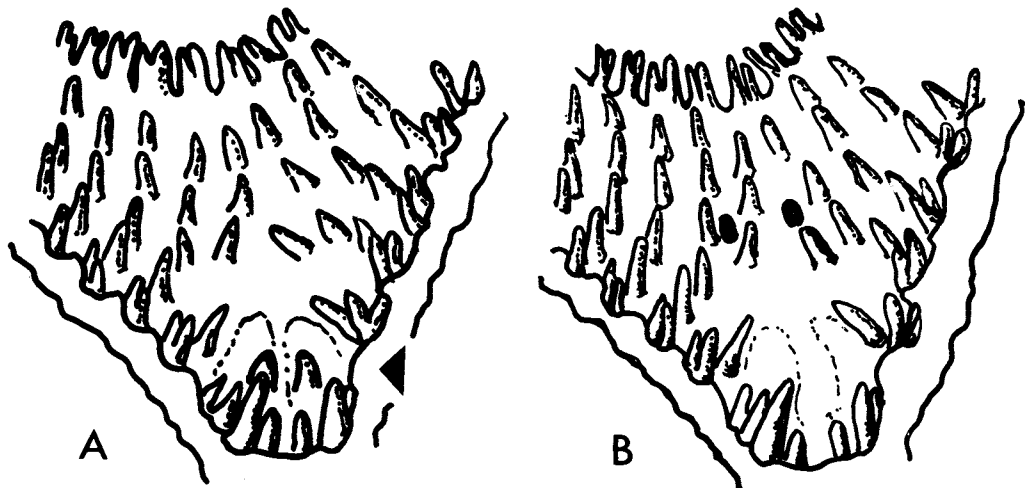


FIG. 2.

Comparison of the oral between arm areas of *A. gibbosa* (A) and *A. phylactica* (B) of identical size (diameter 8 mm). Note the presence of two extra spines on the mouth plates of *A. gibbosa* (arrowed) and the presence of gonopores on *A. phylactica* (black ovals).

## GEOGRAPHICAL DISTRIBUTION

*A. gibbosa* has a centre of distribution south of the British Isles and reaches its northernmost limits in this country. Like many Lusitanian species (Lewis, 1964) it is confined to the west coast of Britain and is most abundant in the south-west, its eastern limit in the Channel being Poole, Dorset. It is found abundantly in Devon and Cornwall and throughout Wales, in the Isle of Man, and is also widely distributed in Eire. North of the Isle of Man, however, there are only isolated records of the species. It is also found on the Atlantic coasts of France and Spain, and throughout the Mediterranean, in habitats very similar to those in which it is found in the British Isles.

*A. phylactica* is also a western species. It is at present known only from rock pools at a small number of sites in South Wales (West Angle Bay, type locality), Anglesey (Rhoscolyn), Cornwall (Rosemullion Head), South Devon (Langerstone Point), North Devon (Hartland Quay), the Isle of Man (Port Erin and Port St. Mary Bays), South-west Scotland (Dunure) and County Cork, Ireland (Carrigathorna). It is also found under stones in the shallow sublittoral of Lough Ine, Co. Cork.

In the Mediterranean, it is common in the very shallow sublittoral at Banyuls-sur-Mer and has also been found in intertidal rock pools (Marthy, *personal communica-*

tion). At Rovinj, Yugoslavia (Adriatic) and the surrounding area. *A. phylactica* is also very common in the shallow sublittoral and it appears likely that the species is found throughout the Adriatic and Mediterranean Seas.

#### HABITAT

*A. gibbosa* is most commonly found by turning over boulders and stones on the low shore at low tide. A typical location in Pembrokeshire is Sawdern Point (grade 6 on the scale of Ballantine, 1961), a sheltered shore on Angle Bay. The shore is a gently shelving platform with bedrock ridges and dense furoid algal cover in the intervening gullies. On the lower shore, bedrock covered in *Fucus serratus*. L. gives way to a sandy region below MLWS with large numbers of boulders ranging in size from 250 cm<sup>2</sup> to 1,000 cm<sup>2</sup>. Tidal currents, and thus water movement, are considerable, but the maximum exposure to air does not exceed three hours on low spring tides. *A. gibbosa* are found closely adpressed to the undersides of the boulders. Those easily seen range in size from 3 to 44 mm diameter (see Fig. 3), and in March 1982 the density of animals was 0.5 m<sup>-2</sup>.

Wherever similar conditions exist around the south and west of Britain, *A. gibbosa* may be expected. It is not, however, confined to sheltered shores and in Pembrokeshire has been found on a range of shores from sheltered (grade 6) to semi-exposed

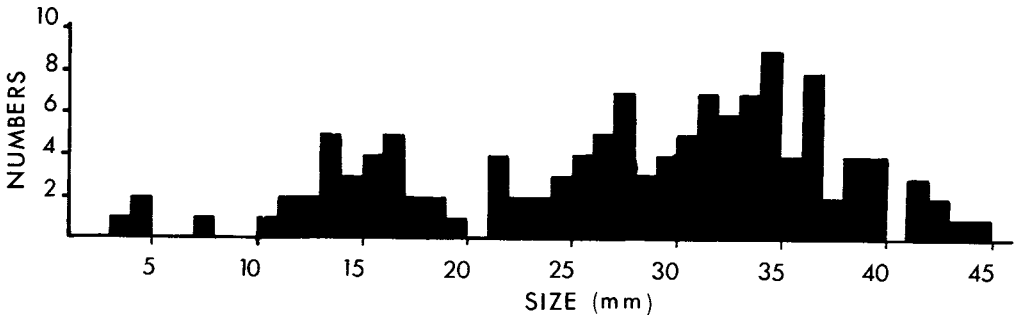


FIG. 3.

Size frequency distribution of a pure population of *Asterina gibbosa* from the undersides of boulders on the lower shore at Sawdern Point, Dyfed.

(grade 3) (Ballantine, 1961) wherever boulder scree dominates the lower part of the shore.

*A. gibbosa* is susceptible to desiccation and is rarely found in the open except on low shore gully walls, overhangs and in caves. Careful examination of these habitats at low water on spring tides often reveals numbers of starfish wedged into crevices between the encrusting organisms characteristic of such habitats (sponges, tunicates, etc.). The seaward-running gullies of Langerstone Point, South Devon, are an example of such a habitat.

The third main habitat for *A. gibbosa* is intertidal rock pools. Pools below MHWN on exposed, semi-exposed and sheltered shores may contain occasional individuals. Pools with stable boulders are more likely to contain *A. gibbosa* than those without and large pools are more likely to contain large populations.

Some tide pools contain an abundance of *A. gibbosa* (up to 10 m<sup>-2</sup>). Such pools lie near MHWN on moderately-exposed shores with broken contours protected from heavy wave action but receiving considerable water exchange daily. The pools at West Angle Bay, Dyfed, are a good example (Fig. 4). They are sheltered from direct

wave action by a rock rampart on the seaward side, but gaps in this permit water exchange with every tide. The pools contain large numbers of boulders and stones lying on a relatively silt-free bottom and the sides of the boulders and the pool fringes support and abundant algal flora among which *Cystoseira* sp., *Enteromorpha* and *Ulva lactuca* (L.) predominate. There is also a diverse macrofauna present. In these pools, most *A. gibbosa* are found by day under the stones.

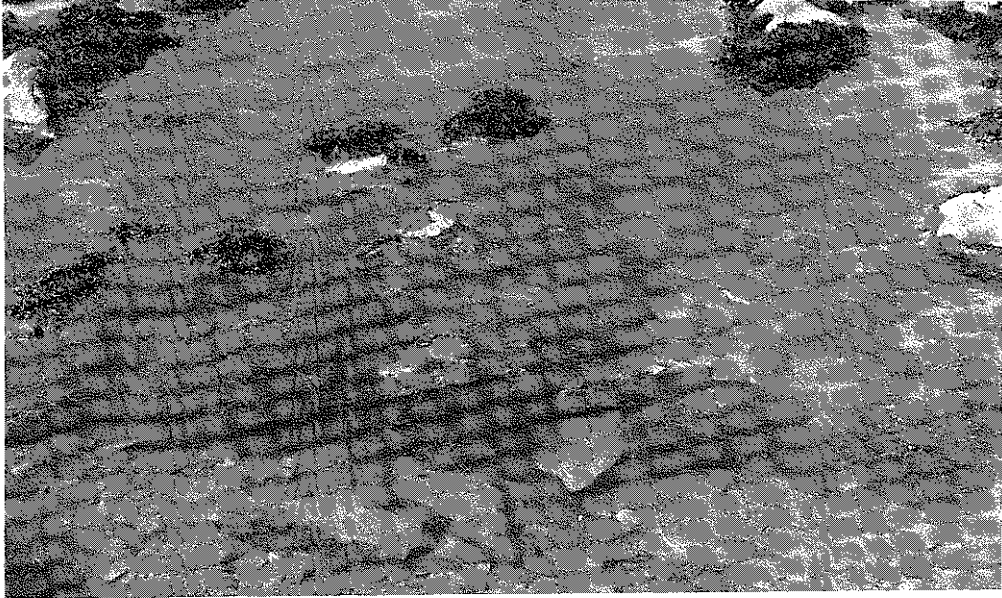


FIG. 4.

Tide pool at West Angle Bay, Dyfed, a typical *Asterina gibbosa* habitat. Shows the rock-strewn bottom and fringe of perennial algae.

Off Pembrokeshire, *A. gibbosa* has been found on bedrock and boulders in the kelp zone (*Laminaria hyperborea* (Gunn.) Fosl.) in areas of moderate exposure down to 10 m. Other workers have recorded it to depths of 20 m (K. Hiscock, *personal communication*) and c. 125 m (Mortensen, 1927).

In British waters *A. phylactica* is characteristically found in high shore tide pools with an extensive and persistent algal flora on moderately to completely exposed shores. It was first discovered co-existing with *A. gibbosa* in the extensive rock pool system at West Angle Bay and is here found principally on the sides of the boulders among the perennial algae.

It was present in comparatively small numbers in this situation. Although *A. gibbosa* was found in the lower shore rock scree adjacent to these tide pools and in the sub-littoral nearby, *A. phylactica* was not. It has not been found in tide pools in more sheltered locations in South Wales or South-West England. At Langerstone Point, South Devon, near Slapton Ley Field Centre, a series of large, deep rock pools extends from low water mark upwards on a grade 3 (Ballantine, 1961) exposed shore. From mid-shore level up, these pools were found to contain very large numbers of *A. phylactica* (100–500 m<sup>-2</sup>) but only very rarely *A. gibbosa*. These pools contain very few large boulders, but are covered with a carpet of both perennial and ephemeral algae. The most abundant perennial species here are

*Cystoseira tamariscifolia* (Huds) Papenf., *Corallina officinalis* L. and *Bifurcaria bifurcata* Ross.

In an adjacent, more sheltered area, are pools similar to those at West Angle which support mixed populations of *A. gibbosa* and smaller numbers of *A. phylactica*.

The other records of *A. phylactica* are all from very similar locations, that is, algal-dominated pools on exposed shores. Even very exposed shores may support populations if the rock conformation is such as to give sufficient shelter for a diverse algal flora to develop. Thus at Carrigathorna, Co. Cork (near Lough Ine) on a grade 1 (Ballantine, 1961) exposed shore, there is a series of large and spectacular pools. These pools, intensively surveyed by Goss-Custard *et al.* (1979) have walls carpeted by *Corallina* turfs and have been found (Emson and Crump, in press) to harbour considerable populations of *A. phylactica*.

The apparently exceptional record for the British Isles is that for the sublittoral of Lough Ine, Co. Cork. Lough Ine is a landlocked basin with a small tidal range, filled with clear oceanic water. The shores are composed of boulders covered with luxuriant algal growths. *A. phylactica* are found on these in areas near the entry channel where considerable water flow regularly occurs (Emson and Crump, in press). The conditions are thus highly similar to those in the tide pool situation elsewhere.

On the Mediterranean sites so far investigated, *A. phylactica* is common on the undersides of large and small boulders at the low water mark and below. It shares this habitat with *A. gibbosa*, but is found nearer the water surface and more abundantly in more exposed situations.

### Microdistribution

In the pool habitat, most *A. gibbosa* are, by day, found underneath boulders and in crevices on the sides (Fig. 5). Careful examination of rock surfaces beneath the algae (e.g. *Cystoseira* spp.) will reveal occasional specimens. On overcast days and on

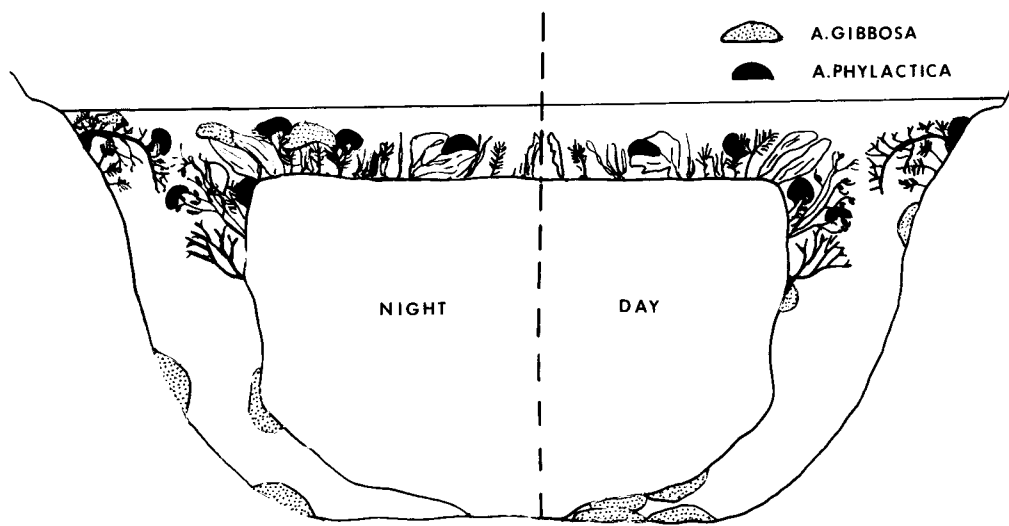


FIG. 5.

Diagrammatic representation of the distribution patterns of *Asterina gibbosa* and *Asterina phylactica* on a boulder in a tide pool by day and by night.

heavily overgrown boulders, a small number of *A. gibbosa* may be found on the upper surfaces.

Examination of the same areas at night reveals that a substantial proportion of individuals have moved out and up on top of the boulders and onto the algae of pool bottom and sides (Fig. 5), where the animals can use a different food supply. *A. phylactica*, however, when on the same boulder, is found predominantly on the tops and sides and on the algae covering the boulders, both by day and at night (Fig. 5).

Such patterns have been observed at West Angle Bay, Langerstone Point and Lough Ine. Quantitative daytime estimates at Langerstone Point showed that 80% of *A. phylactica* were on the upper half of boulders (*A. gibbosa*, 14%) and similar results (84% *A. phylactica*, 7% *A. gibbosa*) were obtained at Lough Ine.

In pools with few rocks, *A. phylactica* are found on the algae from the edges to the deepest extent of the algal forest; at Langerstone they have been found in only 5 cm water, in the open, on the upper surfaces of algae during daylight. The distribution changes at the breeding season, when a high proportion of adults will be found clustered in crevices in the rock and where these are not available, in and adjacent to the holdfasts of the algae. Their distribution at this time suggests that they are showing temporary rugophilia and temporary sensitivity to high light levels. At other times of the year, they show apparent disregard for light and in early autumn may be seen in large numbers near the edges of pools with their guts extended over the surfaces of the algae. No difference in distribution between night and day is detectable.

#### Factors controlling activity and distribution

Clearly the position of an individual *Asterina* in a pool is a result of the animal's response to various stimuli. The stimuli inducing or inhibiting activity include light and gravity, oxygen concentration and various chemical stimuli, including food "odours".

*Asterina* is known (Kalmus, 1929; Crozier, 1935, a) to have a negative response to gravity; thus they tend to climb up vertical surfaces in subdued light or darkness. Such a response would tend to keep populations in the shallow water in which they are usually found and would account for their presence in pools high in the intertidal. However, it has been demonstrated that animals climbing upwards in dim light can be caused to reverse by shining light at them, and a highly important difference between the species is in the light level which causes this reversal. *A. phylactica* shows a greater tolerance of high light intensity, and both species are more tolerant of light in summer than in winter.

Thus, in winter, *A. gibbosa* shows reversal of negative geotaxis at 1,400 Lux and *A. phylactica* at 3,700 Lux, while in summer 5,000 Lux induces reversal in *A. gibbosa*, and *A. phylactica* requires light intensities in excess of 10,000 Lux (Emson, 1979).

Evidently responses to light and gravity can account for the pattern of distribution of *A. gibbosa* and the differences in microdistribution between day and night. The high tolerance of light shown by *A. phylactica* results in the different distribution of that species.

The abundance of *A. gibbosa* in high shore rock pools suggests that they can tolerate fluctuating environmental conditions. The factors liable to considerable fluctuations are oxygen tension, pH, salinity and temperature (Daniel and Boyden,

1975). *A. gibbosa* is capable of surviving near-anoxia for as long as five hours at 25°C. The animal responds to lower oxygen tension by increased activity and climbs to the top of the experimental vessel. It will also remain active and feed at all temperatures between 2 and 30°C. It dies, however, if kept at 35°C for more than a short period. *A. gibbosa* becomes immobilised in salinities below 18‰ but it recovers completely from immersion in a salt concentration of 14‰ for 24 hours at 17°C and retains the ability to feed down to 27‰. (Emson, 1979).

*A. phylactica* is not found in very sheltered areas which could imply a tolerance of silt, or a vulnerability to low oxygen conditions, or less overall tolerance of environmental extremes than *A. gibbosa*, yet it lives in those parts of pools subject to the greatest changes in oxygen, salinity and temperature. *A. phylactica* has been shown to be at least as tolerant as *A. gibbosa*. Thus, for example, 24 hours in oxygen concentrations of 1 ppm is without any discernible harmful effects and *A. phylactica* is capable of tolerating immersion in water of 14‰ and 44‰ salt content (normal seawater = 35‰) for at least 24 hours at 25°C (Emson and Foote, 1980). Conditions likely to occur in tide pools seem unlikely to pose problems to such a tolerant animal.

#### FEEDING

Several authors have suggested that *Asterina gibbosa* is primarily carnivorous. Mortensen (1927) stated that *A. gibbosa* includes live worms, molluscs and ophiuroids in the diet, and Vasserot (1961) remarked that *A. gibbosa* attacked sponges and other sedentary animals, notably ascidians as well as damaged bivalves.

These observations, however, are completely at variance with our records over the past decade. In high shore pools, *A. gibbosa* appears to feed primarily on surface films of diatoms, detritus and bacteria and to some extent on decaying plant or animal material. We have never seen *A. gibbosa* capture or eat living prey.

*A. gibbosa* feeds by everting the cardiac stomach through the mouth, and spreading the stomach lobes over the rock surface. Digestive enzymes are poured over the lining of the stomach along ciliated tracts and digestion is external. Between 1972 and 1975 several thousand living *A. gibbosa* were examined. Animals were scored as feeding if the cardiac stomach was everted (even if no recognisable food resource was obvious). Food items were identified and recorded. Over 95% of all feeding animals showed no macroscopic food in the folds of the stomach and were almost certainly feeding on detritus and bacterial/diatom film on the rocks. In many cases, on close inspection, a patch different in colour from the surrounding area could be clearly seen. Macroscopic food identified included dead *Carcinus maenas* L., *Littorina littorea* L., *Gibbula umbilicalis*, *Asterina phylactica* (alive), unidentified hydroids, *Ulva lactuca* L., decaying *Laminaria* fronds and other unidentifiable drift algae. These observations, our laboratory observations and those of Pye (1970) who observed that *A. gibbosa* fed on decaying algae (e.g. *Fucus serratus* L., *Littorina* faeces and corpses of *Mytilus edulis* (L.), *Ostrea edulis* L. and *Littorina littorea* L., all suggest that *A. gibbosa*, like several other asterinids studied, e.g. *Patiria miniata* (Araki, 1964), *Patiriella regularis* (Crump, 1969) and *Patiriella calcar* (Martin, *personal communication*), is an opportunist, omnivorous scavenger which normally subsists on a predominantly microphagous diet.

While a proportion of the animals will be found feeding by day, there are always more feeding at night when they come out from beneath the boulders on to upper



surfaces (Fig. 5). The majority of feeding must take place at night.

*A. phylactica* also appears to be an omnivorous scavenger which may also feed by accident or design on small epiphytic animals and microorganisms living on perennial algae. Where it co-exists with *A. gibbosa* under stones on pool bottoms, both have the same food resources, and no difference in feeding has been observed. Field observations of *A. phylactica* show that those on weed have the gut everted over the alga itself or over epiphytic animals even in daylight.

### Seasonality in feeding intensity

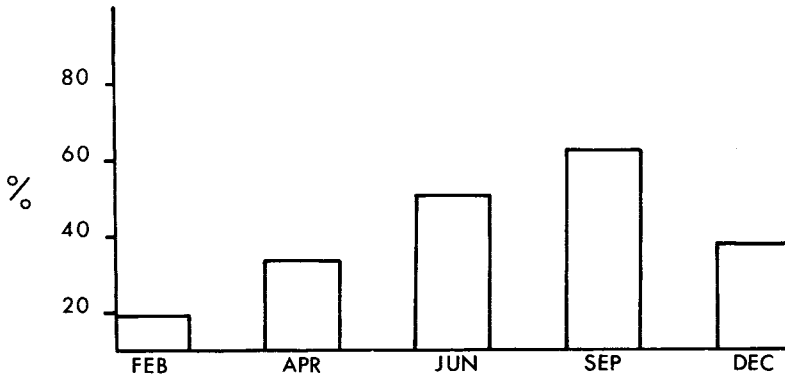


FIG. 6.

Through the year variation in percentage of *Asterina gibbosa* found feeding by day.

The percentage of *A. gibbosa* with the gut everted, in tide pool populations, in daylight, is lowest in late winter and highest in the early autumn (Fig. 6). This may be related to water temperature, but the high incidence of feeding in the autumn also reflects an apparent peak in attractiveness of the food material.

In *A. phylactica*, a high proportion are found to have the gut everted when examined at all times of the year. In summer, however, when the outer parts of the algae and epifauna such as hydroids and bryozoans are regressing, all the animals examined are found to be feeding. Clearly this is a very important time of the year for both *Asterina* species.

### POPULATION DYNAMICS

Size frequency distributions are often used by workers to deduce age structure, growth and mortality in populations of echinoderms (Ebert, 1973). Such a technique was used for juveniles of *A. gibbosa* and gave good information on growth in the first year of life. Although it is also possible to collect size frequency data for adult *A. gibbosa* populations, it is rare for these to show clear-cut size classes. The data for Sawdern Point (Fig. 3) (for example, show no reliable pattern despite the large number of animals collected. There is, unfortunately, no easy method of ageing starfish and analysis of the population dynamics depends upon indirect methods.

In Fig. 7, diameters of *A. gibbosa* populations from rock pools at West Angle Bay, Dyfed, are plotted as size-frequency histograms for samples taken in June and December 1975. Analysis of the data using probability paper (Harding, 1949) and a

modification of this technique devised by Cassie (1954) reveals that at least five adult year classes are present in both samples. Using the means and the standard deviations derived from the analysis (Table 1/ Fig. 7), it is possible to superimpose a series of normal curves on histograms drawn of the same data and show the apparent year classes.

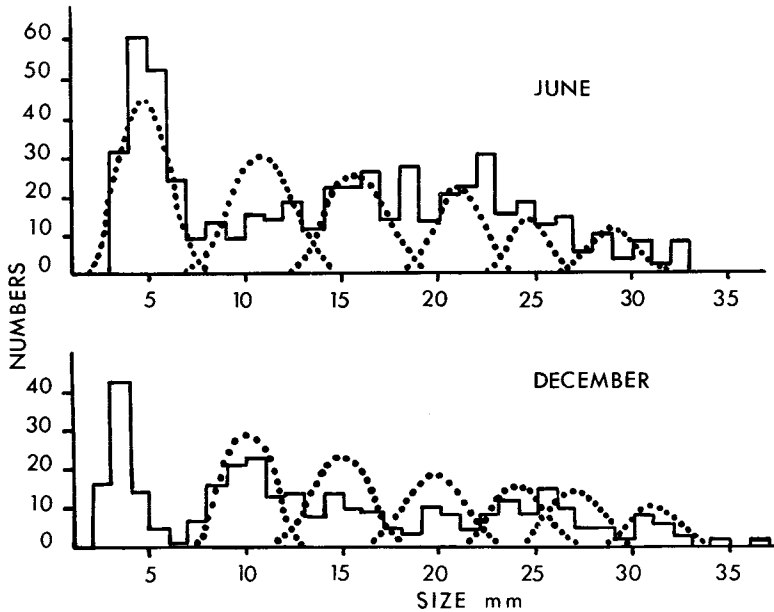


FIG. 7.

Size frequency data for West Angle Bay *A. gibbosa* for June and December 1975 with superimposed, normal curves derived from Cassie analysis of the data and the year when the group of animals was spawned (after Crump and Emson, 1978, with permission).

Table 1. *The apparent mean sizes of year classes within a population of A. gibbosa from West Angle as shown up by Cassie analysis of size-frequency data (cf. Cassie, 1954)*

| Year class | June       |    | December   |    |
|------------|------------|----|------------|----|
|            | Mean size  | SD | Mean size  | SD |
| 0+         | 4.5 ± 1.4  |    | 2.7 ± 0.8  |    |
| 1+         | 10.5 ± 1.4 |    | 9.3 ± 1.5  |    |
| 2+         | 15.6 ± 1.8 |    | 14.3 ± 1.3 |    |
| 3+         | 20.6 ± 1.4 |    | 19.1 ± 0.9 |    |
| 4+         | 24.5 ± 1.4 |    | 23.4 ± 1.5 |    |
| 5+         | —          |    | 26.4 ± 1.3 |    |
| 6+         | —          |    | 30.1 ± 1.0 |    |

This data coupled with marking experiments using Nile Blue sulphate dye to follow the growth of individual animals in the field (Crump and Emson, 1978) showed that *A. gibbosa* in this situation lives to five or six years old and very large specimens (40+ mm diameter) may be older.

Establishment of age, growth rates and mortality are easier for *A. phylactica* than for *A. gibbosa*. Samples of *A. phylactica* were measured at Langerstone Point (South

Devon) and West Angle (Dyfed) at intervals from 1974 onwards. Since the juveniles of *A. phylactica* and *A. gibbosa* cannot be reliably distinguished until the colour patterns and spination differences develop at approximately one year of age, it is assumed that the growth pattern established for all juveniles of *Asterina* at West Angle Bay is characteristic of *A. phylactica* and results in animals of mean size 4.5 mm at one year old. This supposition is strengthened by samples collected in February 1976 and October 1977 at Langerstone Point, where *A. phylactica* occurs in virtual isolation; they show exactly the same peaks in size frequency distribution, corresponding to 0 group animals, as the West Angle Bay samples.

The largest sample collected from Langerstone Point, that of October 1977, shows the age classes of the whole population. At least three are apparent (Fig. 8). The 0+ (less than 1 year old) year class, although small because of sampling difficulty, is clear, with a mean size of about 2.5 mm, as is 1+ year class (1976) with a mean size of about 6 mm, and the 2+ year class (1975) with a mean size of 9–10 mm. Some of the few 12–14 mm animals may represent the 3+ age group.

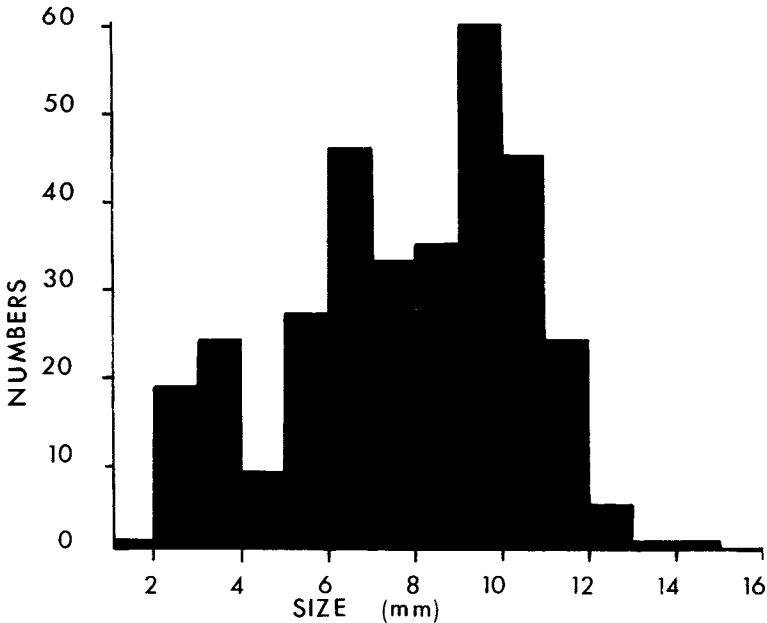


FIG. 8.

Size frequency data for *A. phylactica*. Data for Langerstone Point, South Devon, showing the presence of three apparent year classes (October) (from Emson and Crump, 1979, with permission).

It is suggested that in British waters *A. phylactica* has a life expectancy of up to four years, but most individuals live only two or three years and die before, during, or shortly after the first or second spawning. Annual growth increments in terms of mean diameter are approximately:

|          |                    |
|----------|--------------------|
| 1st year | 0.75–4.5 mm (500%) |
| 2nd year | 4.5–6.5 mm (44%)   |
| 3rd year | 6.5–9.5 mm (46%)   |

The greatest reduction in growth rate between first and subsequent years may be due to the diversion of energy from somatic growth to the developing gonads in two- and three-year-old animals.

#### REPRODUCTION

*A. gibbosa* is a protandrous hermaphrodite (that is, individuals are first male and then female) which in British waters becomes mature as a male at two years old and enters the female phase when four years old and 18–22 mm in diameter (Crump and Emson, 1978). It is not uncommon to find large animals with both ripe spermatozoa and ova present in the gonads and self-fertilisation is a distinct possibility (Cognetti and Delavault, 1962). External fertilisation, however, is normally the rule.

In late May, females lay masses of up to 1,000 large (0.55 mm diam.) directly-developing, sticky, bright orange eggs on the underside of rocks and in crevices (Fig. 9B). The animals tend to aggregate together and to enter crevices at this time. They adopt a slightly humped posture while laying the eggs, but once laid (usually after 24 hours) the eggs are abandoned. If not consumed by predators such as prawns (*Palaemon elegans* Rathke, *Palaemon serratus* (Pennant)), they develop to the stage where they become mobile juveniles in about 16–21 days (Marthy, 1980). In all populations studied, recruitment has been regular and a considerable percentage survive (Crump and Emson, 1978).

The juveniles (0.75 mm diam.) disperse and may be found on the underside of rocks in the lower shore and in high shore rock pools in early June and grow quite rapidly, attaining a size of 2–3 mm diameter by October. Growth during the winter is minimal, but a further burst in growth in April and May enables the animals to achieve an average diameter of 5 mm in the first year of growth (see Fig. 7).

In reproductive biology *A. phylactica* and *A. gibbosa* are clearly distinct. *A. phylactica* matures at a much lower size (and age), laying eggs when a diameter of only 5–6 mm is reached. In the Mediterranean it is possible that animals reach this size within a year (Emson and Crump, 1979; Marthy, 1980). At 5–6 mm *A. phylactica* is, at maturity, amongst the smallest starfish known. *A. phylactica* is a simultaneous hermaphrodite, both male (white) and female (orange) gonads being present in spring, and histological examination demonstrates the presence of ripe sperm and ova at the same time. Material from the West Angle, Banyuls and Rovinj populations appears identical. From early spring onwards, bright orange eggs can be seen inside the animal through the oral body wall, and in late May individuals seek out crevices in boulders and weed holdfasts to lay the eggs. *A. phylactica* form highly characteristic compact aggregations of five to ten individuals up to two weeks before spawning and remain in the aggregation until the development of the juveniles is complete. The most distinctive feature of the reproductive biology is the protection given to developing eggs by the adults which, either alone or in aggregation, adopt a humped-up posture over the egg mass and remain so until the juveniles crawl away (Fig. 9A). The development from fertilised egg to competent juvenile takes up to three weeks depending on temperature. A proportion of animals fails to brood the eggs and may digest them. Some eggs are lost during the brooding process, with smaller individuals brooding a larger proportion of eggs laid than larger individuals (Strathmann, Strathmann and Emson, in prep). Although *A. phylactica* forms aggregations with other members of its own species (presumably to

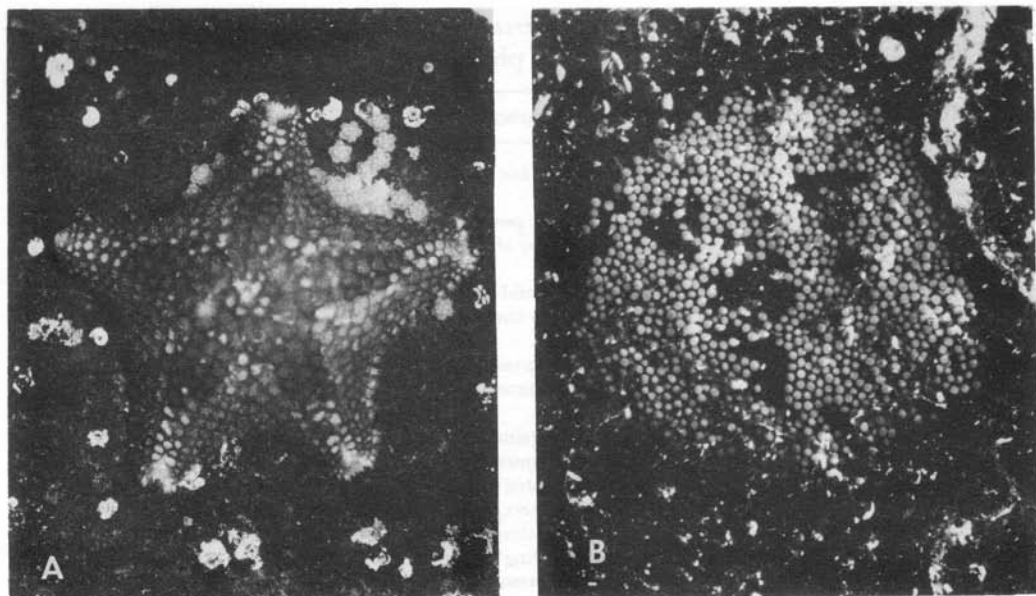


FIG. 9.

A. Individual brooding *A. phylactica* with young emerging from beneath it.

B. Egg mass of *A. gibbosa*.

allow cross-fertilisation), self-fertilisation is also possible and successful. Strathmann, Strathmann and Emson (in press) kept individuals separate from each other and induced spawning. The eggs developed normally and the number of juveniles successfully brooded was closely similar to comparable individuals in the field.

#### DISCUSSION

The two starfish species whose way of life has just been outlined are representatives of a group which flourish worldwide in similar environments. They are successful because they are efficient, tolerant and undemanding omnivorous scavengers. In addition, they are apparently subject to very little predation pressure.

They are efficient because they can spread the gut out over a large area and externally digest whatever material is available. This must be a particular advantage on rough detritus-covered surfaces or algae and means that choice items of carrion can be completely engulfed. They are undemanding in that, like many echinoderms, they can survive long periods on minimal food, utilising body reserves, and are not particular as to the kind of food they eat. Their feeding efficiency allows them to make maximum use of the food available and to convert food very rapidly when conditions are favourable. Their high degree of tolerance allows them to exist and be successful on the low shore or in tide pools where physical conditions may be highly variable, and thus to take advantage of the rich food resources which may be available in these areas.

These two starfish also provide an excellent example of the way in which small differences in anatomy and biology can together result in a high degree of ecological separation in two closely-related and rather similar species which have overlapping distributions and thus may exist sympatrically (summary in Table 2).

Table 2. *Summary of significant differences between Asterina gibbosa and Asterina phylactica*

| FEATURE OF COMPARISON                                | <i>A. phylactica</i>  | <i>A. gibbosa</i>                                 |
|--|---|---|
| 1. Horizontal distribution with respect to exposure  | Very exposed (grade 1) to exposed (grades 3-4)                  | Exposed (grade 3) to sheltered (grade 6)          |
| 2. Vertical distribution with regard to tides        | Restricted to tide pools concentrated near MHWN                 | MHWN down to 100 m below ELWST, mostly around LWM |
| 3. Distribution on boulders in sympatric populations | Principally tops and sides                                      | Principally sides and undersides                  |
| 4. Association with <i>Corallina</i>                 | Adults often very abundant in <i>Corallina</i>                  | Adults very rarely in <i>Corallina</i>            |
| 5. Reaction to light (sensitivity)                   | Low sensitivity (greater than 10,000 lux in summer)             | High sensitivity (5,000 lux in summer)            |
| 6. Movement/activity                                 | Diurnally active  | Principally nocturnal                             |
| 7. Colour pattern                                    | Consistent dark pattern   | Variable  |
| 8. Size  | Up to 15 mm diameter  | Up to 50 mm diameter                              |
| 9. Reproductive method                               | Large eggs brooded to mobile juvenile state, direct development | Large eggs, direct development                    |
| 10. Aggregative behaviour                            | Lengthy aggregation (three weeks) for brooding                  | Brief aggregation for egg laying                  |
| 11. Reproductive pattern                             | Simultaneous hermaphrodite                                      | Protandrous hermaphrodite                         |
| 12. Age at first egg production                      | Two years (in Britain)  | Four years (in Britain)                           |
| 13. Number of broods                                 | One to three  | Three to seven                                    |
| 14. Life span  | Up to four years  | Up to seven years or more                         |

The crucial difference between the species in terms of habitat partitioning where they are sympatric seem to result from differences in behaviour. There is clear evidence that the distribution patterns of *A. gibbosa* and *A. phylactica* on boulders are so different that only limited utilisation of the same space (and hence food) occurs, and that this part of niche separation between the species results from their different behaviour in response to light. This may also explain their differing vertical distribution patterns. Size is, however, also important in separating the species ecologically. *A. gibbosa* is not found in exposed tide pools among coralline turf nor to any extent upon algae in pools where the two species are sympatric. This appears to be due to size difference as well as light sensitivity, since the small size of *A. phylactica* allows it to find shelter in coralline turf where adult *A. gibbosa* cannot, and to climb easily on fronds of algae such as *Cystoseira*. Evidence to support such a hypothesis is that small *A. gibbosa* are sometimes found on weeds in deep shade. Whether the dark colour of *A. phylactica* is the cause or effect of lower light sensitivity in that species is difficult to determine. It would seem likely that a dark variant arose within the ancestral stock, which was tolerant of light and thus able to exploit areas not accessible to the rest of the parent stock. This trend was favoured by evolution, as was the trend towards earlier maturity.

In fact, the whole life strategies of *A. gibbosa* and *A. phylactica* are significantly different. In addition to the fact that *A. phylactica* broods the eggs and developing juveniles whereas *A. gibbosa* does not, *A. phylactica* matures earlier, laying eggs when only two years old and 6 mm in diameter against four years and 20 mm in *A. gibbosa*. A greater proportion of assimilated energy is devoted to reproductive products in *A. phylactica* which also has a shorter life span (usually two to three years) whereas *A. gibbosa* may live to seven years or more. With the exception of the brooding habit, *A. phylactica* has, compared with *A. gibbosa*, the characteristics of an r. selected species

(Stearns, 1976). Thus, although the species appear morphologically similar and may be found together exploiting a similar food supply, when all the differences just discussed are summed, it can be seen that their ecological niches are quite dissimilar.

## ACKNOWLEDGEMENTS

We are grateful to the Editor of the *Journal of the Marine Biological Association of the United Kingdom* for permission to reproduce Figs. 4 and 5. We also thank all those friends and students who have at one time or another helped us with data collection.

## REFERENCES

- ARAKI, G. S. (1964). *Physiology of Feeding and Digestion in the Sea Star, Patiria miniata*. Unpublished Doctoral Dissertation, Stanford University.
- BACCI, G. (1949). Recherche su *Asterina gibbosa* (Penn) II. L'hermaphroditismo in una popolazione di Plymouth. *Archivio Zoologico Italiano* 33-4, 49-73.
- BACCI, G. (1951). On two sexual races of *Asterina gibbosa* (Penn). *Experientia* 7, 31-33.
- BALLANTINE, W. J. (1961). A biologically defined exposure scale for the comparative description of rocky shores. *Field Studies* 1(3), 1-19.
- BOOLOOTIAN, R. (Ed.) (1966). *Physiology of Echinodermata*. Interscience, London.
- BRUSLÉ, J. (1968). Nouvelles recherches sur l'hermaphroditisme d'*Asterina gibbosa* de Roscoff. *Cahiers de Biologie Marines* 9, 121-132.
- BRUSLÉ, J. (1969). Les cycles genitaux d'*Asterina gibbosa*. *Cahiers de Biologie Marines* 10, 271-287.
- BULLIMORE, R. and CRUMP, R. G. (1982). Enzyme electrophoresis and taxonomy of two species of *Asterina* (Asteroidea). In: *Proceedings of International Echinoderms Symposium*. Tampa. (Ed. J. M. Lawrence), pp. 185-188.
- CASSIE, R. M. (1954). Some uses of probability paper in the analysis of size-frequency distributions. *Australian Journal of Marine and Freshwater Research* 5, 513-522.
- COGNETTI, G. and DELAVAUULT, R. (1962). La sexualite de Asterides. *Cahiers de Biologie Marines* 3, 157-182.
- CROZIER, W. J. (1935). The geotropic response in *Asterina*. *Journal of General Physiology* 18, 729-737.
- CRUMP, R. G. (1969). *Feeding, Growth and Reproduction in the Asteroids Patiriella regularis (Verrill, 1867) and Coscinasterias calamaria (Gray, 1840)*. Unpublished Doctoral Dissertation, Otago University, New Zealand.
- CRUMP, R. G. and EMSON, R. H. (1978). Some aspects of the population dynamics of *Asterina gibbosa* (Asteroidea). *Journal of the Marine Biological Association of the United Kingdom* 58, 451-466.
- CUENOT, L. (1898). Notes sur les echinodermes. III. L'hermaphroditisme protandrique d'*Asterina gibbosa* Penn et ses variations suivant les localities. *Zoologischer Anzeiger* 21, 273-279.
- DANIEL, M. J. and BOYDEN, C. R. (1975). Diurnal variations in physico-chemical conditions within intertidal rockpools. *Field Studies* 4, 161-176.
- DELAVAUULT, R. (1966). Determination of sex. In *Physiology of Echinodermata*. (Ed. R. Boolootian). Interscience, London, pp. 615-638.
- EBERT, T. A. (1973). Estimating growth and mortality rates from size data. *Oecologia* 11, 281-298.
- EMSON, R. H. (1979). The importance of tidal and day and night cycles in the distribution of British Asterinids. In: *Cyclic Phenomena in Marine Plants and Animals*. (Ed. E. Naylor and R. Hartnoll). Pergamon Press, Oxford, pp. 347-353.
- EMSON, R. H. and CRUMP, R. G. (1978). Brooding in *Asterina gibbosa* Pennant. *Thalassia Jugoslavia* 12(1), 99-108.
- EMSON, R. H. and CRUMP, R. G. (1979). Description of a new species of *Asterina* (Asteroidea), with an account of its ecology. *Journal of the Marine Biological Association of the United Kingdom* 59, 77-94.
- EMSON, R. H. and CRUMP, R. G. (in press). Comparative studies on the ecology of the *Asterina gibbosa* Pennant and *Asterina phylactica* Emson and Crump at Lough Ine. *Journal of the Marine Biological Association of the United Kingdom*.
- EMSON, R. H. and FOOTE, J. (1980). Environmental tolerances and other adaptive features of two intertidal rock pool echinoderms. In: *Echinoderms Present and Past*. (Ed. M. Jangoux). Balkema, Rotterdam, pp. 163-169.
- GOSS-CUSTARD, S., JONES, J., KITCHING, J. A. and NORTON, T. A. (1979). Tide pools of Carrigathorna and Barloge Creek. *Philosophical Transactions of the Royal Society B* 287, 1-44.

- HARDING, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journal of the Marine Biological Association of the United Kingdom* 28, 141–153.
- HUET, M. (1975). The rôle du système nerveux au cours de la regeneration du bras chez une Etoile de Mer: *Asterina gibbosa* Penn (Echinoderme, Astéride). *Journal of Embryology and Experimental Morphology* 33, 535–552.
- KALMUS, H. (1929). Versuche über die Bewegungen der Seesterne, besonders von *Asterina gibbosa*. *Zeitschrift für Vergleichende Physiologie* 9, 703–733.
- LEWIS, J. (1964). *The Ecology of Rocky Shores*. English University Press, London. 323 pp.
- LOEB, J. (1900). *Comparative Physiology of the Brain and Comparative Psychology*. Putnam, New York. 309 pp.
- LUDWIG, H. (1897). Seesterne. *Fauna und Flora des Golfes von Neapol* 24. 491 pp.
- MANGOLD, E. (1921). Der Undrehreflex bei Seesternen und Schlangensterne. *Pflügers Archiv für gesamte Physiologie des Menschen und der Tiere*. 189, 73–98.
- MARTHY, H. J. (1980). Étude descriptive du développement de l'oeuf d'*Asterina* (Échinoderme, Astéride) son intérêt en embryologie expérimentale. *Vie et Milieu* 30(1), 75–80.
- MORTENSEN, J. (1927). *Echinoderms of the British Isles*. Oxford. 471 pp.
- PYE, A. V. (1970). *The Functional Anatomy of the Gut of the Sea Star Asterina gibbosa (Pennant)*. Ph.D. Thesis, University of London.
- RUSSELL, E. S. (1919). Note on the righting reaction of *Asterina gibbosa*. In: *Proceedings of the Zoological Society of London*, 86, 423–432.
- STEARNS, S. C. (1976). Life history tactics: a review of the ideas. *Quarterly Review of Biology* 51, 3–47.
- STRATHMANN, R., STRATHMANN, M. and EMSON, R. H. (in prep). Does limited brood capacity link adult size, brooding and simultaneous hermaphroditism? A test with the starfish *Asterina phylactica*.
- VASSEROT, J. (1961). Caractère hautement spécialisés du régime alimentaire chez les Asterides *Echinaster repositus* et *Henricia sanguinolenta* prédateurs de spongiaires. *Bulletin de la Société Zoologique de France* 86, 796–809.