

## Proximate Composition and Allocation of Energy to Body Components in *Acanthaster planci* (Linnaeus) (Echinodermata: Asteroidea)

JOHN M. LAWRENCE<sup>1</sup> and PETER MORAN

*Australian Institute of Marine Science, Townsville,  
Queensland 4810, Australia*

**ABSTRACT**—Protein was the major constituent by weight in all body components. The concentration of lipid was twice as great in the pyloric caeca as in the cardiac stomach and cardiac pouches. The body wall of an arm contained more organic material and energy (in kJ) than the pyloric caeca within the arm. The body wall of the arms is the greatest portion of the entire body, but is less important in terms of wet weight than in kJ. The ventral body-wall of the disc is massive, containing ca. 17% as many kJ as the ventral body-wall of all 16 arms. The type and amount of organic constituents allocated to the body components of *Acanthaster planci* indicate the functional requirements of the components. The greater amount of energy allocated to the body wall of an arm than to the pyloric caeca suggests that an increase in arm number is not adaptive unless it results in an increased capacity to obtain energy.

### INTRODUCTION

The proximate composition of asteroids differs among the body components in a species and between the same components of different species [1–10]. The differences are particularly great for the body wall, associated with the great variation in the body-wall functional morphology [11]. The proximate composition indicates the requirements for organic classes in the body components in either gravimetric or energetic terms. The proximate composition is expressed most often in relative terms, but the absolute amounts of the proximate constituents are of interest in considering production and allocation of material to body components. Production is best expressed in energy terms [12] and knowledge of the proportional representation of the organic classes can be of value [13]. The allocation of energy should be balanced among the body components according to the principle of economization in metabolic expenditure [14]. With optimal design (sym-

morphosis) the allocation of resources to structural elements should meet but not exceed the requirements of the functional system [15].

Studies of the allocation of proximate constituents to the body components of asteroids have concerned five-armed species except for the multiarmed *Pycnopodia helianthoides* [2, 5]. The relation between the relative amount of energy in the body components and body size has been established for the multiarmed *Acanthaster planci* [16]. The study of multiarmed species is important as a means of understanding the relationship between size in terms of dimensions and biomass of a body and its components [17]. These studies are of particular interest as the multiarmed condition is relatively rare in asteroids despite its long fossil record and widespread occurrence in different families. The present study addresses this question through consideration of the allocation of proximate constituents and its energy equivalents to the body components of *Acanthaster planci*.

### MATERIALS AND METHODS

*Acanthaster planci* were collected at Bowden Reef, Great Barrier Reef, Australia (147°56'E, 19°02'S) on 3 May 1989. At the date of collection

Accepted December 13, 1991

Received May 9, 1991

<sup>1</sup> Permanent address: Department of Biology, University of South Florida, Tampa 33620, U.S.A.

the perimeter of the reef had ca. 10–30% live coral cover and 1–10% dead coral cover [18]. The collected individuals were held in aquaria with running sea-water for 5–9 days before dissection.

The major (R) and minor (r) radii and the disc radius were measured immediately after the individual had been removed from the aquarium. The disc was defined as that portion of the body containing the cardiac stomach [19]. The individuals were dissected into their body components: dorsal and ventral body-walls of the arms and disc, cardiac stomach, cardiac pouches, and pyloric caeca. The cardiac pouches are extensions of the cardiac stomach in the proximal fused portion of the arms [20]. The arms were separated into the distal free portions and the proximal fused portions. Gonads were not analysed as the individuals were at the beginning of gonadal development [21]. Three arms were dissected from 6 individuals to ascertain variation in the wet weights of arm components. One arm was dissected from the remaining individuals. The entire disc was dissected from all individuals.

Portions of each body component were weighed, lyophilized, reweighed, and homogenized. The proximate composition of the components and their energy equivalents were measured by the methods used by Lawrence [3] and the insoluble protein calculated by subtraction. The amount of energy present in the components was calculated by multiplying (mg organic class/mg dry tissue) (mg dry tissue/mg wet tissue) (mg wet tissue of the body component) (kJ/mg organic class). The energy conversion factors for the organic classes

were those of Kleiber [22]. These values were used to calculate the amount of energy allocated to the body components of individuals of a standard size. The mean major radius was used to designate a standard-sized individual.

## RESULTS

The individuals varied little in size, with mean values (and SD) of  $182 \pm 11$ ,  $93 \pm 13$ , and  $45 \pm 8$  mm for R, r, and disc radius, respectively. The mean arm number was  $16 \pm 2$  ( $\bar{x} \pm \text{SD}$ ; range, 12 to 20). The wet weights of the arm components differed among individuals and varied irregularly for different components within an individual (Table 1). The amount of variation was small. The mean weights of the components of three arms of an individual varied as much as the means of components from one arm from each of 26 individuals.

The proximate composition of the body wall of all parts of the body was similar (Table 2). The composition of the pyloric caeca differed from that of the cardiac stomach and pouches. The gravimetric concentration of ash was higher in the body wall than in the viscera. Protein was the major organic constituent in all body components, and was present in highest concentration in the viscera. The concentration of lipid was twice as great in the pyloric caeca as in the cardiac stomach and pouches.

The kJ per g dry weight of the body wall was less than half that of the viscera (Table 3). The kJ per g ash-free dry weight for the body wall and cardiac

TABLE 1. Variation in g wet wt of arm components in individual *Acanthaster planci* (n=3 arms for each individual) and in 26 *A. planci* (one arm for each individual) from Bowden Reef in May 1989. Means  $\pm$  1 SD are given.

Individual	1	2	3	4	5	6	1–26
Free arm							
dorsal	14.9 $\pm$ 0.5	15.0 $\pm$ 2.8	15.2 $\pm$ 1.3	12.0 $\pm$ 1.3	6.9 $\pm$ 0.3	7.8 $\pm$ 1.2	13.5 $\pm$ 3.6
ventral	9.5 $\pm$ 1.3	8.0 $\pm$ 2.8	13.2 $\pm$ 1.2	7.6 $\pm$ 0.3	4.2 $\pm$ 1.0	4.0 $\pm$ 0.3	11.3 $\pm$ 3.1
Fused arm							
dorsal	8.2 $\pm$ 1.7	10.9 $\pm$ 4.0	8.2 $\pm$ 2.9	10.4 $\pm$ 0.5	4.2 $\pm$ 0.9	5.1 $\pm$ 0.2	9.2 $\pm$ 2.7
ventral	6.6 $\pm$ 1.1	12.2 $\pm$ 2.1	9.4 $\pm$ 0.9	9.5 $\pm$ 2.2	3.5 $\pm$ 0.4	4.8 $\pm$ 1.6	10.5 $\pm$ 3.0
Pyloric caeca	9.2 $\pm$ 1.6	19.6 $\pm$ 1.0	14.5 $\pm$ 1.3	16.2 $\pm$ 0.7	4.6 $\pm$ 0.8	5.0 $\pm$ 0.5	13.5 $\pm$ 5.3
Cardiac pouches	3.0 $\pm$ 1.0	2.0 $\pm$ 0.4	3.4 $\pm$ 0.8	2.3 $\pm$ 0.6	2.0 $\pm$ 0.3	2.3 $\pm$ 0.6	2.3 $\pm$ 0.5

stomach and pouches were similar and less than that for the pyloric caeca as a result of the difference in lipid level.

Protein was the major constituent of *Acanthaster planci* in either gravimetric or energetic units, but was less important in terms of the latter (76 vs 69% of the organic matter) (Table 4). The protein was equally distributed between soluble and insoluble

protein. Lipid constituted 28% of the 3491 kJ in the body of a standard-sized individual, with 32% of this in the pyloric caeca.

The wet or dry weights of the ventral and dorsal portions of the free and fused parts of the arm did not differ greatly (Table 4). The g organic material and kJ were slightly greater in the dorsal portion of the arm. The wet weight of the ventral body-wall

TABLE 2. Per cent dry weight (in % total weight) and proximate composition (in % g dry weight and % kJ) of body components of *Acanthaster planci* from Bowden Reef in May 1989. A: ash, C: carbohydrate, L: lipid, SP: soluble protein, IP: insoluble protein. Means  $\pm$  1 S.D. (n=10) are given for the % dry wt. The % kJ was calculated from the mean % dry wt values.

Body Component	dry wt	A	C	L	SP	IP
% dry wt						
Body wall						
Ventral disc	27 $\pm$ 2	64 $\pm$ 5	1.3 $\pm$ 0.2	3.3 $\pm$ 0.5	14 $\pm$ 2	16 $\pm$ 8
Dorsal disc	25 $\pm$ 1	49 $\pm$ 6	1.9 $\pm$ 0.2	5.1 $\pm$ 0.6	20 $\pm$ 3	25 $\pm$ 6
Ventral free-arm	23 $\pm$ 2	57 $\pm$ 6	1.6 $\pm$ 0.3	3.6 $\pm$ 0.4	19 $\pm$ 3	19 $\pm$ 6
Dorsal free-arm	25 $\pm$ 3	62 $\pm$ 5	1.6 $\pm$ 0.7	3.3 $\pm$ 0.4	15 $\pm$ 3	18 $\pm$ 3
Ventral fused-arm	21 $\pm$ 2	58 $\pm$ 6	1.6 $\pm$ 0.3	3.4 $\pm$ 0.5	17 $\pm$ 2	18 $\pm$ 8
Dorsal fused-arm	23 $\pm$ 2	54 $\pm$ 4	1.6 $\pm$ 0.3	4.1 $\pm$ 0.5	17 $\pm$ 3	24 $\pm$ 4
Pyloric caeca	24 $\pm$ 4	7.5 $\pm$ 2.1	7.0 $\pm$ 1.0	30 $\pm$ 11	34 $\pm$ 5	25 $\pm$ 10
Cardiac stomach	20 $\pm$ 3	9.8 $\pm$ 1.8	5.9 $\pm$ 1.7	15 $\pm$ 4	38 $\pm$ 5	30 $\pm$ 4
Cardiac pouches	21 $\pm$ 1	8.7 $\pm$ 1.4	6.1 $\pm$ 1.2	16 $\pm$ 1	32 $\pm$ 9	34 $\pm$ 4
% kJ						
Body wall						
Ventral disc			2.6	15	38	44
Dorsal disc			2.5	15	36	45
Ventral free-arm			2.5	13	42	42
Dorsal free-arm			2.7	14	38	46
Ventral fused-arm			3.0	13	40	44
Dorsal fused-arm			2.1	15	34	39
Pyloric caeca			4.9	50	34	12
Cardiac stomach			4.5	28	41	27
Cardiac pouches			4.4	28	33	35

TABLE 3. kJ per g dry weight and ash-free dry weight in body components of *Acanthaster planci* from Bowden Reef in May 1989. DBW: dorsal body wall, VBW: ventral body wall.

Body Component	Free arm		Fused arm		Disc		Cardiac stomach	Cardiac pouches	Pyloric caeca
	DBW	VBW	DBW	VBW	DBW	VBW			
kJ per g dry wt	9.3	11	11	10	13	8.6	23	23	27
kJ per g ash-free dry wt	25	25	25	24	26	24	26	25	31

TABLE 4. Calculated amounts (g and kJ) of total material and of proximate constituents in the body components of *Acanthaster planci* with 16 arms and a major radius of 182 mm. The values for dry weight and proximate constituents were calculated from the values for the % proximate composition given in Table 2. C: carbohydrate, L: lipid, SP: soluble protein, IP: insoluble protein, TOM: total organic material.

	wet wt	dry wt	ash	C	L	SP	IP	TOM
Grams								
Body wall								
Free arms								
Dorsal	216	55	34	0.8	1.8	8.2	9.8	21
Ventral	181	42	24	0.6	1.4	7.8	7.8	18
Fused arms								
Dorsal	147	34	18	0.5	1.4	5.6	8.0	16
Ventral	168	35	20	0.6	1.1	5.9	6.4	14
Disc								
Dorsal	27	6.7	3.3	0.1	0.3	1.3	1.7	3.4
Ventral	57	15	9.8	0.2	0.5	2.1	2.4	5.2
Total body-wall	796	188	109	2.8	6.5	31	36	78
Viscera								
Cardiac stomach	41	8.5	1.0	0.5	1.4	3.4	2.2	7.5
Cardiac pouches	36	7.6	0.6	0.5	1.2	2.6	2.7	7.0
Total	77	16	1.6	1.0	2.6	6.0	4.9	14.5
Pyloric caeca	216	52	3.8	3.5	15	17	13	49
Total viscera	293	68	5.4	4.5	18	23	18	64
Grand total	1089	256	114	7.3	25	54	54	142
kJ								
Body wall								
Free arms								
Dorsal				14	70	193	230	506
Ventral				11	57	185	185	437
Fused arms								
Dorsal				8.2	57	132	189	386
Ventral				11	44	140	151	346
Disc								
Dorsal				2.2	13	32	49	87
Ventral				3.4	20	51	58	131
Total body-wall				50	261	733	862	1893
Viscera								
Cardiac stomach				8.9	55	79	53	195
Cardiac pouches				8.1	51	60	64	183
Total				17	106	139	117	378
Pyloric caeca				60	606	411	142	1220
Total viscera				77	712	550	259	1598
Grand total				127	973	1283	1121	3491

of the disc was twice that of the dorsal body-wall, and contained 131 kJ (17% of the 783 kJ of the entire ventral body-wall of all 16 arms of a standard individual. The body wall was always the largest component of the arms regardless of the mode of measurement, but was more important when calculated in terms of dry weight (73% of the total) than in kJ (54% of the total). The viscera contained 1598 kJ (84% of the 1893 kJ of the entire body-wall). Almost 73% of the lipid was in the viscera. The pyloric caeca contained 85% of the viscera lipid. Protein comprised 84% of the kJ in the body wall, with slightly more insoluble than soluble protein. Protein comprised 51% of the kJ in the viscera, with more soluble than insoluble protein. The body wall contained only 66% of the total kJ due to protein as the total organic material in the viscera was so great.

### DISCUSSION

The body wall and pyloric caeca of the arms of individual *Acanthaster planci* vary in size, and the amount of variation differs among individuals. Despite this, the amount of variation found is small and no greater than found with complete dissection of other asteroid species [3, 7, 9, 10].

The proximate composition of the body components of *Acanthaster planci* is in the range reported for other species [1–10]. The concentration of energy in the body wall and pyloric caeca in terms of kJ/dry wt is similar to those reported for other asteroid species [5–8, 10, 23, 24], and shows the great influence of the amount of ash on the concentration. The differences in the concentration of energy in terms of kJ/ash-free dry weight reflect better the difference in proximate organic composition. Thus in these terms, the energy concentration of the body wall and stomach of *A. planci* are similar but less than that of the pyloric caeca.

The allocation of material and energy to the components of an organism must be interpreted in terms of its biology. *Acanthaster planci* is disc-shaped, multiarmed, pliable, and prehensile, with a large central disc and stomach [21, 26, 27]. These features are associated with its predation on coral by extraoral feeding. Lucas [28] noted the massive development of the stomach of *A. planci* which is

extruded over the coral in feeding. This development is so great that the disc does not contain the entire stomach, and extensions (the cardiac pouches) are found in the proximal portions of the fused arms. This may be a better solution to accommodating a large stomach than increasing the width of the disc. The great development of the ventral portion of the disc (the oral frame) supports the retraction of the massive stomach. The slightly higher concentration of ash in the ventral body-wall is probably associated with requirements for the supporting structures. Blake and Guensburg [29] listed a robust oral frame as one of a suite of characters for the "pyncopodaform" shape of multiarmed asteroids. They did not relate it to the mass of the stomach or include a massive stomach as one of the characters. The stomach has been ignored in studies of component parts of asteroids, but this may be a major error in the study of pyncopodaform species.

Blake and Guensburg [29] also listed a robust, strongly articulated ambulacral column as a character of pyncopodaform asteroids, although this is also true for other asteroid forms (Lawrence, unpub. obs.). However, the amount of material and energy allocated by *Acanthaster planci* to the ventral body-wall of the arms is similar to that allocated to the dorsal body-wall except for the disc. The dorsal body-wall is fragile, as pointed out by Kettle and Lucas [16], in keeping with the flexibility of the body noted above. Flexibility seems more important than having an armor to protect against predation as is more usual in tropical asteroids [30]. The toxic dorsal spines of *A. planci* are few and represent a minor allocation of energy (Lawrence, unpub.). The high incidence of regenerating arms [31] indicates the susceptibility of *A. planci* to breakage or predation. This moderate allocation to protection would be predicted for a species with a competitive life-history strategy [32].

The high amount of insoluble protein allocated to the body wall indicates the primarily structural role of the body wall, although the large amount of soluble protein shows considerable numbers of cells are present. The lack of difference in the proximate composition of the dorsal and ventral body-walls show the basic similarity in construc-

tion of the two. An increase in strength and support seems to involve an increase in size and not difference in composition although this might occur at the histological level. McClintock [5] noted a decrease in concentration of inorganic material in the body wall of *Pycnopodia helianthoides* with an increase in body size, indicating a greater reliance on organic material for strength with an increase in size. Kettle and Lucas [16] reported a decrease in the relative amount of energy allocated to the body wall with an increase in body size in *A. planci*, but did not indicate the absolute amount of energy involved or separate the body wall into components.

Giese (2) pointed out that large amounts of organic material in the body wall of asteroids could constitute a nutrient reserve, and Lawrence and Lane [25] suggested that the material might be used during body-wall resorption during starvation. The concentration of organic material in the body wall of *Sclerasterias mollis* decreases with starvation [10]. The importance of body size in regard to a role of the body wall in nutrient reserve is seen with scaling (the proportion of body wall decreases with size in *Acanthaster planci* [16]) and composition (the concentration of organic material in the body wall increases with size in *Pycnopodia helianthoides* [5]).

The amount of material and energy allocated to the cardiac pouches is nearly as much as to the cardiac stomach within the disc. The greater amount of insoluble protein may be associated with the ligaments that retract the pouches. The absolute amount of lipid in the cardiac stomach and pouches is high. The gut of echinoids stores lipid [33], and the lipids in the cardiac stomach may function as reserves also. The amount of lipid allocated to the pyloric caeca is far greater. The nutrient-reserve function of the pyloric caeca is well known, but the caecum is a combination of digestive and reserve cells [34] that makes it difficult to know the exact allocation to either [25].

The multiple arms of *Acanthaster planci* result in a proportionally greater allocation of material and energy to the arm components than in five-armed species. The greater allocation of material has been noted for *Luidia senegalensis* [35] and *Pycnopodia helianthoides* [5]. This greater allocation is

probably associated with both an increased cost of development and maintenance. If so, a positive return should result for the multiarmed condition to be adaptive [17].

Blake and Guensburg [29] pointed out that it is uncertain whether or not multiple arms are adaptively neutral. Multiarmed asteroids can be separated into two groups: those with 6 to 12 arms that are constant in number, and those that have 8 or many more that are variable in number [36]. It is possible the functioning of genera in the first group (*Luidia*, *Asterina*, *Leptasterias*) is not affected sufficiently for arm number to be a selective factor. Blake and Guensburg suggested that the similar morphologies of pycnopodaform asteroids of disparate geological ages and ancestry strongly imply not only the benefit based on predatory feeding advantages, but that the benefit has endured. Genera in the second group (*Acanthaster*, *Crossaster*, *Heliaster*, *Pycnopodia*, *Solaster*) are all active, voracious carnivores in which the additional arms probably increase feeding capacity. Just as homeothermy is advantageous, but only if the return is worth the cost, the development of the multiarmed condition should increase the capacity to obtain energy that meets the energy requirement for the development and maintenance of the additional arms.

In this regard, Calder [37] pointed out that it is the body mass (how much tissue must be sustained and regulated) rather than the mass of the constituent parts, topographical layout, or history of use that determines basic support costs, opportunities, and homeostatic needs. Recognizing the role of body size in the functioning of an organism, he concluded that body mass is not only an expedient measure of size but the biologically appropriate one. The amount of energy rather than weight better represents biomass. This is clear in echinoderms where so much of the mass may be inorganic. *Acanthaster planci* has a much larger biomass in terms of kJ than the few other species for which values have been reported (3, 6, 38).

#### ACKNOWLEDGMENTS

We thank D. B. Blake and J. B. McClintock for their helpful comments on the manuscript.

## REFERENCES

- 1 Giese, A. C. (1966) On the biochemical constitution of some echinoderms. In "Physiology of Echinodermata". Ed. by R. A. Booloottian, Interscience Publ., New York, pp. 757-796.
- 2 Giese, A. C. (1976) Physiology of the echinoderm body wall. *Thalassia Jugoslav.*, **12**: 153-163.
- 3 Lawrence, J. M. (1973) Level, content, and caloric equivalents of the lipid, carbohydrate, and protein in the body components of *Luidia clathrata* (Echinodermata: Asteroidea: Platyasterida) in Tampa Bay. *J. Exp. Mar. Biol. Ecol.*, **11**: 263-274.
- 4 Lawrence, J. M. and Guille, A. (1982) Organic composition of tropical, polar and temperate-water echinoderms. *Comp. Biochem. Physiol.*, **72B**, 283-287.
- 5 McClintock, J. B. (1989) The biochemical and energetic composition of somatic tissues during growth in the sea star, *Pycnopodia helianthoides* (Echinodermata: Asteroidea). *Comp. Biochem. Physiol.*, **93A**: 695-698.
- 6 McClintock, J. B. (1989) Energetic composition, reproductive output, and resource allocation of antarctic asteroids. *Polar Biol.*, **9**: 147-153.
- 7 McClintock, J. B., Pearse, J. S. and Bosch, I. (1988) Population structure and energetics of the shallow-water antarctic sea star *Odontaster validus* in contrasting habitats. *Mar. Biol.*, **99**: 235-246.
- 8 McClintock, J. B., Hopkins, T., Watts, S. A. and Marion, K. (1990) The biochemical and energetic composition of somatic body components of echinoderms from the northern Gulf of Mexico. *Comp. Biochem. Physiol.*, **95A**: 529-532.
- 9 Scheibling, R. E. and Lawrence, J. M. (1982) Differences in reproductive strategies of morphs of the genus *Echinaster* (Echinodermata: Asteroidea) from the eastern Gulf of Mexico. *Mar. Biol.*, **70**: 51-62.
- 10 Xu, R. A. and Barker, M. F. (1989) Laboratory experiments on the effects of diet on the gonad and pyloric caecum indices and biochemical composition of tissues of the New Zealand starfish *Sclerasterias mollis* (Hutton 1872) (Echinodermata: Asteroidea). *J. Exp. Mar. Biol. Ecol.*, **136**: 23-45.
- 11 Blake, D. B. (1989) Asteroidea: Functional morphology, classification and phylogeny. *Echinoderm Studies*, **3**: 179-223.
- 12 Brody, S. (1945) Bioenergetics and growth. Hafner Publishing Company Inc., New York.
- 13 Paine, R. T. (1971) The measurement and application of the calorie to ecological problems. *Ann. Rev. Ecol. Syst.*, **2**: 145-164.
- 14 Calow, P. (1984) Economics of ontogeny—adaptational aspects. In "Evolutionary Ecology". Ed. by B. Shorrocks, Blackwell Scientific Publications, Oxford, pp. 81-104.
- 15 Taylor, C. R. and Weibel, E. R. (1981) Design of the mammalian respiratory system. I. Problem and strategy. *Respir. Physiol.*, **44**: 1-10.
- 16 Kettle, B. T. and Lucas, J. S. (1987) Biometric relationships between organ indices, fecundity, oxygen consumption and body size in *Acanthaster planci* (L.) (Echinodermata: Asteroidea). *Bull. Mar. Sci.*, **41**: 541-551.
- 17 Lawrence, J. (1988) Functional consequences of the multiarmed condition in asteroids. In "Echinoderm Biology". Ed. by R. D. Burke, P. V. Mladenov, P. Lambert and R. L. Parsley, A. A. Balkema, Rotterdam, pp. 597-602.
- 18 Bass, D. K., Davidson, J., Johnson, D. B., Miller-Smith, B. A. and Mundy, C. N. (1989) Broadscale surveys of crown-of-thorns starfish on the Great Barrier Reef 1987 to 1988. The Crown-of-thorns Study. Australian Institute of Marine Science: Townsville.
- 19 Lawrence, J. (1990) The relationship between the major and minor radii and the internal anatomy of asteroids. *Northeast Gulf Sci.*, **11**: 90.
- 20 Jangoux, M. (1982) Digestive systems: Asteroidea. In "Echinoderm Nutrition". Ed. by M. Jangoux and J. M. Lawrence, A. A. Balkema, Rotterdam, pp. 235-272.
- 21 Moran, P. J. (1986) The *Acanthaster phenomenon*. *Ocean. Mar. Biol. Ann. Rev.*, **24**: 379-480.
- 22 Kleiber, M. (1975) "The Fire of Life". Robert E. Krieger Publishing Company, Huntington.
- 23 Dayton, P. K., Robilliard, G. A., Paine, R. T. and Dayton, L. B. (1974) Biological accommodation in the benthic community of McMurdo Sound, Antarctica. *Ecol. Monogr.*, **44**: 105-128.
- 24 Lawrence, J. M. (1987) Echinodermata. In "Animal Energetics". Ed. by T. J. Pandian and F. J. Vernberg, Academic Press, San Diego, pp. 229-321.
- 25 Lawrence, J. M. and Lane, J. M. (1982) The utilization of nutrients by postmetamorphic echinoderms. In "Echinoderm Nutrition". Ed. by M. Jangoux and J. M. Lawrence, A. A. Balkema, Rotterdam, pp. 331-371.
- 26 Birkeland, C. (1989) The Faustian traits of the crown-of-thorns starfish. *Am. Sci.*, **77**: 154-163.
- 27 Birkeland, C. and Lucas, J. S. (1990) *Acanthaster planci*: major management problems of coral reefs. CRC Press, Boca Raton.
- 28 Lucas, J. S. (1984) Growth, maturation and effects of diet in *Acanthaster planci* (L.) (Asteroidea) and hybrids reared in the laboratory. *J. Exp. Mar. Biol. Ecol.*, **79**: 129-147.
- 29 Blake, D. B. and Guensburg, T. E. (1989) Two new multiarmed Paleozoic (Mississippian) asteroids (Echinodermata) and some paleobiologic implications. *J. Paleont.*, **63**: 331-340.
- 30 Blake, D. B. (1983) Some biological controls on the

- distribution of shallow water sea stars (Asteroidea; Echinodermata). *Bull. Mar. Sci.*, **33**: 703–712.
- 31 McCallum, H. I., Endean, R. and Cameron, A. M. (1989) Sublethal damage to *Acanthaster planci* as an index of predation pressure. *Mar. Ecol. Prog. Ser.*, **56**: 29–36.
- 32 Lawrence, J. M. (1990) The effect of stress and disturbance on echinoderms. *Zool. Sci.*, **7**: 17–28.
- 33 Lawrence, J. M., Lawrence, A. L. and Giese, A. C. (1966) Role of the gut as a nutrient-storage organ in the purple sea urchin (*Strongylocentrotus purpuratus*). *Physiol. Zool.*, **39**: 281–290.
- 34 Nimitz, Sister M. A. (1971) Histochemical study of gut nutrient reserves in relation to reproduction and nutrition in the sea stars, *Pisaster ochraceus* and *Patiria miniata*. *Biol. Bull.*, **140**: 461–481.
- 35 Lawrence, J. (1987) Une histoire de deux étoiles: l'effet du nombre des bras sur la biologie. *Bull. Soc. Sc. Nat. Ouest France. Suppl. H. S.*, 59–61.
- 36 Lawrence, J. M. and Komatsu, M. (1990) Mode of arm development in multiarmed species of asteroids. In "Echinoderm Research", Ed. by C. De Ridder, P. Dubois, M.-C. Lahaye and M. Jangoux, A. A. Balkema, Rotterdam, pp. 269–275.
- 37 Calder, W. A. (1984) Size, Function, and Life History. Harvard Univ. Press, Cambridge.
- 38 Lawrence, J. M. (1985) The energetic echinoderm. In "Echinodermata". Ed. by B. F. Keegan and B. D. S. O'Connor, A. A. Balkema, Rotterdam, pp. 47–67.