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FEEDING BIOLOGY OF THE SEA-STAR *ASTROPECTEN IRREGULARIS* PENNANT

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ABSTRACT

As other species of *Astropecten*, *A. irregularis* rests buried in the substrate between periods of feeding activity. These usually occur at twilight hours.

The sea-star can sense and localize prey buried underneath it with great precision.

Prey animals are quickly pushed through the mouth opening and into the stomach by the (sucker-less) tube feet surrounding the mouth.

Astropecten cannot dig deep enough to seize deep-sitting prey such as e. g. members of the Tellinidae and non-juvenile *Mya* spp. It feeds mainly on small animals, but may occasionally swallow very large prey.

Digestion of prey takes place in pockets of the stomach wall and requires that lobes of the stomach can be inserted and applied in direct contact with the digestible tissue.Protected prey organisms such as bivalves with tightly appended valves cannot be digested before they succumb and start to gape permanently due to a lack of oxygen. Since oxygen requirements differ, prey are retained in the stomach for varying periods of time. Whereas *Spisula subtruncata*, for example, is digested and the empty shells ejected well within 24 hours, specimens of (non-juvenile) *Venus gallina* and *Corbula gibba* may be retained for 2-3 weeks or more.

Certain prey as e.g. non-juvenile *Natica* spp., *V. gallina* of all sizes and *C. gibba* more than 2-3 mm long may often be ejected alive after a shorter or longer stay in the sea-star stomach.

Astropecten is a selective feeder, mainly engulfing bivalves, among which it exhibits a distinct preference for species with a low resistance to anaerobic conditions. This behaviour and a pronounced tendency to feed primarily on juvenile specimens ensure that the digestible matter of swallowed prey in most cases may be quickly assimilated.

Metabolic rate may seemingly be used as an index for attractiveness of bivalve prey, but the real stimulus is probably one or several metabolic end products.

Food uptake is significantly reduced in the absence of "first class" food species. If only highly undesirable food species are present, the sea-star may almost stop feeding and loose weight.

A medium sized *Astropecten* may pick up and digest more than 400 *S. subtruncata* spat within 24 hours and theoretically destroy some 30,000 spat annually. Among other bivalves taken in considerable numbers are *Mya truncata* and *Montacuta ferruginosa*. Newly settled *Echinocardium cordatum* are also heavily preyed upon, at least when attractive molluscan species are absent or scarse.

In Danish waters feeding practically stops below 4°C. Above this temperature the feeding rate depends highly on the density and types of potential prey spesies present. In the Øresund, for example, feeding rates are usually low at the most favourable temperature level because such attractive prey as 0-group *S. subtruncata* are exterminated while the tempereture still is low. This results in undernourishment and stops reproduction.

At 11-16°C, small specimens fed on attractive prey may daily consume an amount of food equal to about 18 % of their own living weight, whereas adult specimens consume considerably less, i. e. about 2 %.

Data from the literature indicates that the majority, if not all, of the *Astropecten* spp. probably are selective feeders which mainly feed on molluscs.

INTRODUCTION

During a field course at Frederikshavn, Northeast Jutland, in the summer of 1951 my attention was called to the feeding behaviour of the phanerozonian sea-star *Astropecten irregularis*, which occurs from Lofoten in Norway to Marocco in Africa (Mortensen, 1927). It was suggested that since this species – in contrast to for example the common European sea-star *Asterias rubens* – has intraoral digestion, it would be ideal for qualitative and quantitative studies on food uptake. Since practically all species of *Astropecten* are found on sandy bottoms in shallow water, it was further felt that any results obtained perhaps could be of value to other workers concerned with trophic relationships within communities inhabiting these bottoms (see Thorson, 1952).

A survey of the literature showed that up to that time (1951) comparatively little had been published on the feeding biology of sea-stars with intraoral digestion, except for information on stomach contents. Fortunately, a rising interest for these animals, including the genus *Astropecten*, has been noted in recent years.

As described for *Astropecten auranciacus* by Mangold (1908) and Seilacher (1953), for *A.marginatus* by Kenk (1944), and for *A.irregularis* by Sigalas (1922), Schäfer (1965), and Heddle (1967), these sea-stars are able to dig into the substrate with amazing speed, using their tube feet. It has, therefore, often been assumed that *Astropecten* does this when searching for food (Schiemenz, 1896; Ludwig, 1897; Gislén, 1924; Schäfer, op.cit.). On the other hand, Mangold (op. cit.) and Mori & Matutani (1952) clearly imply that *A.auranciacus* and *A.polyacanthus*, respectively, come out of the sand when hunting for food begins. On this background it seemed desirable to find out whether digging is initiated solely when a prey has been located or whether the sea-star digs, so to speak, in the hope of finding suitable prey. From the cited literature it was clear, however, that *Astropecten* lies burried in the substrate when resting.

Schiemenz (1896) states that *A.auranciacus* uses is extensible tube feet to push its food (bivalves and gastropods) through its highly dilatable mouth opening, but apart from this remark no information is available concerning the method used in handling prey.

Concerning the kind of food eaten, Forbes (1841) was apparently the first to mention *Astropecten* as a voracious predator, finding that *A.irregularis* mainly subsists on mulluscs. Scattered in the literature one may find additional information about the kind of food taken by this and other species of the genus. In many cases, only one or a few specimens were examined for food contents, but with a few notable exceptions one gets the impression that all *Astropecten* species feed mainly on molluscs, although all kinds of possible prey may be found in their stomachs.

Kisch (1958) and Wells, Wells & Gray (1961) emphasize that *Astropecten* is a good "bottom sampler" for the malacologists since it apparently picks up molluscan prey indiscriminately. Many species, including rare ones, may be found in the stomachs of *Astropecten* spp., but early observations in the Helsingør laboratory strongly suggested that *A.irregularis* exhibits a distinct selectivity in its feeding habits. This was confirmed in controlled experiments and a note on this appeared earlier (A. M. Christensen, 1962), but the supporting evidence together with additional information are given in the present paper.

Except for a rather loose estimation by Hunt (1925), no authors have attempted to determine the daily food uptake of any *Astropecten* species or any other sea-stars with intraoral digestion, let alone any changes in this due to seasonal temperature variations. Hulings & Hemlay (1963) noted a distinct difference in food uptake by *A.articulatus* between two successive years due to a change in the composition of the prey fauna. Massé (1966) mentions that the food of *A.aurantiacus* differs according to the type of bottom on which it is collected. In the present paper, regional, seasonal, and annual variations in food uptake will be considered. Apart from physical factors, it is also shown that the density of certain "key" species preferred by the sea-star plays a decisive role on feeding rate.

It was also hoped that an autecological study of the present scope would yield results of a more general nature of value for our understanding of certain prey-predator relationships, the influence of these on the structure of level-bottom communities and the numerical balance between their inhabitants. As earlier reported (A. M. Christensen, 1962), it has in fact been shown that predation by *A.irregularis* is primarily directed against fast-growing, quickly reproducing bivalves such as *Spisula subtruncata.*

The present work is based on an idea originally suggested to me by professor, Dr. G. Thorson, who also helped with the identification of a number of gastropods and gastropod eggs, and with whom I have had many fruitful discussions. Dr. H. Lemche kindly identified some of the tectibranchs. Many problems were discussed with Dr. K. W. Ockelmann, who also helped on many occasions with the identification of newly settled bivalves. Dr. T. Fenchel and Miss H. Hansen kindly helped me with experiments on the resistance of bivalves to anaerobic conditions. Dr. G. M. Christensen did much of the work involved in the same experiments and supplied me with algal cultures. Dr. E. Ursin, Dr. G. Gustafson, Dr. B. Swedmark, and Dr. J. Lützen supplied me with material from the North Sea and the Swedish west coast. Drs. W. Austin, B. Bayne, H. Feder and K. Muus kindly permitted me to use some of their unpublished data. Mrs. H. Andreasson and Miss B. Therkildsen gave me juch technical assistance. The photos used were taken by Mr. Holger Knudsen, and the drawings were made by the late Poul H. Winther and by Mr. Kai Olsen.

To all these persons, and to Danish and foreign colleagues with whom I have discussed various aspects of the present work, I wish to express my sincere thanks.

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MATERIAL

The material which forms the basis for the investigations of stomach content derived from a number of sources.

The fishermen from Frederikshavn often catch significant numbers of *Astropecten* when seining for the plaice, *Pleuronectes platessa,* in the northern Kattegat. Through one of these fishermen 322 adult specimens from June-July were secured (Table 1). The reason why smaller specimens were absent must be that the large mesh size of the seine allows them to be washed out. The sea-star has a long life span (p. 00) so that it would require several years' failure in recruitment and upgrowth to arrive at a situation where only adult specimens were present. During autumn and early winter fishing takes place on other grounds and very few *Astropecten* are caught. However, even in late January or early February when the fishermen return to the "summer" grounds they only catch few specimens. However, in February 1952 (exact date unknown) more than 400 specimens were caught when the seine by accident sheared into the bottom. Of these, 105 were used for stomach analysis. Another 8 specimens were taken in February-March 1957 and sent to me.

Except for the first mentioned winter material, all *Astropecten* were preserved in alcohol on board the fishing vessel. Since this winter material was taken on a very cole day, and the delay in preservation was no more than 4-5 hours, it is not believed that this affected the stomach contents to a significant extent, although *Astropecten* does display a tendency to empty its stomach when caught (cf. Table 6).

The fishermen took the material from depths between 12 and 30 metres. More than one-fourth of the sea-stars contained egg capsules of the shallow-water prosobranch *Hydrobia ulvae* which indicates that these were caught in the more shallow depths. On the other hand, the presence of a significant number of *Amphiura* remains shows that others came from muddy bottoms in the deeper parts. On the whole, however, the prey organisms found indicate that the material was taken mainly on a sandy bottom inhabited by a *Venus gallina* community.

After the erection of the laboratory in Helsingør in 1958, it became possible to collect *Astropecten* on a year round basis. Throughout the year of 1960 collections were made in a rather restricted area in the Hornbæk Bay in the northwestern part of the Øresund one to three times every month and, to secure an overlap, sampling was continued in the first few months of 1961 (Table 10). Smaller samples were also taken in the summer or autumn during the years 1962-1964. Of these samples, one from August 1964 was the most important since Dr. Kirsten Muus was at the same time taking quantitative samples of the meiofauna, which by far constitutes the main bulk of the food taken by *Astropecten* in the Øresund. I was thus given an opportunity to compare stomach contents with the available prey.

TABLE 1. Size distribution of all *Astropecten irregularis* collected and examined in detail for stomach contents.

Locality and time of collection	<10	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	>55	Total number
North Sea:												
1932-1955	17	8	5	14	16	6	1	.	.	.	.	67
May 1953	.	.	.	6	21	11	.	.	.	.	.	38
29.iv. 1957	.	.	.	.	2	1	4	2	.	.	.	9
Kattegat:												
Off Frederikshavn												
February 1952	.	.	.	.	.	1	2	17	35	39	11	105
4-7.vi, 1952 (46) 15-30.vi, 1952 (256) 15-31.vii, 1952 (20)	.	.	.	.	.	15	70	108	89	35	5	322
Off Læsø 17.v. 1960	.	.	.	9	10	15	9	2	.	.	.	45
Gullmarfjord:												
Near Bonden Island												
2.ix. 1957	.	.	.	.	.	4	3	5	2	.	.	14
South Midtskär												
10.ii. 1962	.	.	.	9	13	3	.	.	1	.	.	26
Øresund:												
Hornbæk Bay												
Jan. 1960 – June 1961	26	300	449	159	47	31	24	15	.	.	.	1051
19.ix, 1962	.	.	.	3	6	7	1	.	.	.	.	17
14.viii, 1964	.	.	1	.	5	12	4	.	.	.	.	22
GRAND TOTAL*												1716

* Eight adult specimens taken in February-March 1957 off Frederikshavn were not measured.

The sea-stars were collected with different types of gear, ranging from a small bottom trawl to a triangular, rather heavy dredge, but over half of them were taken with a Sigsbee trawl. In total over 1000 specimens were collected and used for stomach investigations. The size distribution was quite different from that encountered at Frederikshavn (Table 1), and although this in part must be due to the use of different collecting gears, it is well established that only few *Astropecten* in the Øresund reach the normal size found in other localities (Brattström, 1941).

Within the narrow strip sampled in the Hornbæk Bay there is in general a shift from a clean sand-bottom on the shoreward side to a somewhat muddy sand-bottom at greater depths, the shift being especially pronounced at about 19 metres depth (Hansen, 1965). This was not known when *Astropecten* was collected in 1960-61, but because Brattström (1941) states that *Astropecten* is most common at about 20 metres depth, all hauls were taken between 16 and 24 metres. There was no possibility afterwards to split the material according to collection depth, since no attempts were normally made to keep the trawl or dredge at a certain depth during a haul, and since all sea-stars taken on a collection trip were preserved in the same jar. The material taken on 14 August 1964 (Table 33), however, was taken with care exactly on the 18 metres ground sampled by Dr. K. Muus.

All sea-stars collected in the Øresund for stomach analysis were preserved in alcohol as soon as they were removed from the collecting gear.

A total of 114 *Astropecten* collected in the North Sea (Table 1) by the Danish Institute for Fisheries and Marine Research were placed at my disposal by Dr. E. Ursin. A few were taken before the last world war, but most of them were collected in the years 1951 to 1957. The material is not identical with that used by Ursin (1960), who based his studies on quantitative samples, but derives almost entirely from trawl and dredge hauls. His Fig. 16 shows, however, in which areas of the North Sea *Astropecten* occurs. There is a very notable lack of this species on the clean sand bottom covering the Dogger Bank, although Ursin's appended tables show that the species occurs on most types of bottoms, being most common on clayey sand. As far as known, all the animals were preserved shortly after being removed from the collecting gear, usually in formalin. This prevented the use of some additional material, since remains of bivalve soft tissue showed that swallowed shells had been dissolved by the preservative. The majority of the sea-stars were collected at depths ranging between 37 and 50 metres, with the remainder coming from deeper waters. All samples were taken during spring or summer, with more than half of the material deriving from May alone.

A small number of *Astropecten* were dredged at two localities at the mouth of the Gullmarfjord on the Swedish west coast in September 1957 (depth 18-22 metres) and in February 1962 (depth 28-32 metres). The first lot was placed in running sea-water and examined the day after, but all the material ejected in the meantime was carefully identified and measured. The winter material was taken by Dr. J. Lützen and placed in alcohol directly from the dredge.

Dr. K.W. Ockelmann secured 66 specimens from 18 to 27 metres depth near the island of Læsø in the Kattegat in May 1960. This was of special interest since the majority were collected on a typical "*Amphioxus*" bottom with a fauna quite different from that found in the other major collecting localities. As usual all animals were preserved in alcohol on board the research vessel.

In addition to the sea-stars collected for use in stomach investigations many were collected for use in various experiments. Thus, about 100 were collected at Frederikshavn in July 1952 and over 400 were collected in the Øresund in 1959-1969.

The animal is easy to keep in the laboratory, and the very few mortalities seen over the years were due to a fungus disease attacking the epidermis and, in the later stages, also other tissues of the animal.

For feeding experiments of various kinds, several thousand bottom invertebrates – mainly bivalves – were collected by dredging in the Øresund. Newly settled bottom stages were secured with the aid of the detritus-sledge described by Ockelmann (1964).

METHODS

Stomach investigations

Following the proceduce outlined by Conheim (1901), the stomach was as far as possible removed intact from each sea-star. The dorsal body wall of the disc was carefully cut around the area to which the pyloric stomach is attached, the connective strands and the oesophagus were cut and the stomach removed from the main body. Now and then a stomach pouch extended into an arm, and in these cases damage to the stomach was easily caused. The inside of such damaged specimens were examined for any stomach contents.

The detached stomach was examined in alcohol under a binocular dissecting microscope. A very careful examination proved necessary since the majority of the swallowed food items were of meiofauna size and very often completely enveloped by the stomach wall.

All important food items were identified to species, if possible, and measured to the nearest tenth of a mm. This could obviously not be done with soft tissue remains, broken polychaete tubes, or test remains of echinoids, for example. The measurements were usually done with the aid of an ocular micrometer; only larger specimens were measured with a pair of vernier callipers.

For all bivalves and some of the prosobranchs found in the stomachs of sea-stars collected in the Øresund it was immediately noted whether the internal organs had been digested or not. The same is true for the material from Læsø and part of the North Sea material. All the bivalves from the Frederikshavn sea-stars were studied from this point of view after they had been removed from the sea-stars and stored in alcohol for several years.

Experiments

Experiments were carried out in the Helsingør laboratory from October 1959 through November 1962 and in 1967-1970. Most of the experiments were carried out in standard glass aquaria of various sizes, ranging between 300 and 1300 cm^2 in bottom area. Unless otherwise stated the bottom was covered with a 4 to 7 cm thick layer of clean, sifted sand, of which over 94 % by weight consisted of grains varying between 125 and 500 μ in "diameter". The aquaria were supplied with running sea-water from the recirculating system of the Helsingør laboratory.

Obviously, the substrate used was not identical with that found in nature with respect to grain size and other physical factors, nor with respect to chemical and biotic factors. It would have been unpractical, however, to use the natural substrate for practically all types of experiments carried out. For most experiments there are no reasons to doubt the validity of the results obtained due to this factor, but in a few, to which attention will be drawn in the proper context, the substrate factor may well have had a considerable influence.

The temperature generally ran between 10 and 15°C, but in the summer and autumn of 1962 and 1968 some experiments were carried out at temperatures running as high as 16-17°C.

When checking for the presence of remaining food animals and ejected shells, the sea-stars were first picked up and placed in a container with running sea-water, but without sand. Then the sand in the aquarium was run through a sieve to retain all animals and shells. Before the sea-stars were replaced in the aquarium, and at the start of each experiment, all bivalves and other burying prey specimens were allowed to dig into the sand. It happened a few times that a sea-star ejected swallowed prey specimens while placed in the "waiting" container; these were either fully alive or completely digested. In the former case the animals were simply returned to the experimental aquarium.

Stocks of food animals were kept in aquaria with sandy substrate. Except for the experiments carried out in 1968 and later, they were not fed, but may have been able to filter some food from the circulating water which always contains *Phaeodactylum tricornutum* and other algae. The point is important in so far as starving animals lower their metabolic rate whereby their attractiveness to *Astropecten* may be reduced. An attempt was made to minimize this effect by using recently caught prey animals whenever possible and by not using any bivalves which did not burrow into the substrate willingly when placed on the surface of the sand.

Experiments involving newly settled bivalves, often less than one millimetre long, were carried out in broad glass jars rather than aquaria. These had to be supplied with sand so fine that it would run through a sieve with a mesh size of 264 μ to enable one to retain the bivalves when checking the predation on them. In these jars the bottom layer of sand was usually only 1 to 2 cm thick.

Other details concerning the procedures used for various experiments are given in connection with the recording of the results obtained from them.

The survival of different bivalves under anaerobic conditions was investigated using sea-water deprived of oxygen by bubbling with nitrogen gas. The animals were placed in jars with a tightly closing stopper, which was furthermore sealed with silicone fat. The jars were placed in a constant temperature bath at 10-11°C, and to prevent any photosynthesis by algae present in the water, the jars were covered with aluminium foil. Checks on actual oxygen content were carried out, both at the start of an experiment and at appropriate intervals during the experiment, with the aid of a polarographic Clark electrode (see Kanwisher, 1959). Whenever a specimen was found dead in a jar, the water was exchanged with cool, deoxygenated water.

In some of the growth experiments it was necessary to weigh the sea-stars, which is difficult to do with reasonable accuracy. An adult, well fed animal may show a difference in weight of as much as 3 grams between two weighings done the same day if it is just picked out of the water and immediately weighed in another dish with water.

For this reason each animal was first placed on blotting paper and turned several times under light pressure until the water given off was negligible. This procedure had no discernable ill effect on the sea-stars, since they would feed at the same rate as specimens not subjected to weighing. In most experiments each sea-star was weighed at intervals of about 14 days.

INVESTIGATION OF STOMACH CONTENTS

Introductory remarks

Table 1 lists practically all the *A. irregularis* analyzed for stomach contents during the present study. More detailed data on the Øresund material (Hornbæk Bay) are given in Table 2 since this was the only locality where collections were made at all times of the year and at more or less regular intervals for a prolonged period of time. Tables 3 to 10 list the organisms found in the sea-star stomachs at the various localities.

In the following account the different food items are treated separately. Some organisms such as hydroids, kinorhynchs, halacarids, solenogastres (one *Chaetoderma nitidulum*), and bryozoans were so rare, however, that no further comments will be made on them. Finds of three hydroid colonies, two gastrotrichs, three halacarids, and one *Psolus phantapus* have, furthermore been omitted from Table 10.

TABLE 2. Size distribution for each sampling date of all *A. irregularis* collected in the Hornbæk Bay and examined in detail for stomach contents. Length of longest arm (R) in mm.

Date	Total number	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	Mean R
1960										
13.i	4	.	.	4	.	.	.	.	.	16.4
27.i	11	.	4	6	1	.	.	.	.	15.5
12.ii	75	4	29	18	4	4	5	5	6	20.0
19.ii	74	5	32	16	3	1	4	6	7	19.6
14.iii	53	2	28	16	1	.	3	2	1	16.3
30.iii	32	2	17	10	2	.	1	.	.	15.1
26.iv	59	3	19	29	4	1	2	1	.	16.4
10.v	42	1	15	24	2	.	.	.	.	15.5
27.v	52	.	12	34	6	.	.	.	.	16.9
9.vi	92	1	24	56	9	.	1	1	.	16.7
21-22.vi	70	.	18	44	6	.	2	.	.	17.1
20.vii	48	1	17	26	2	1	.	1	.	16.4
9.viii	11	.	3	6	1	.	.	1	.	18.6
15.viii	12	.	3	9	.	.	.	.	.	15.4
22.viii	14	.	1	11	2	.	.	.	.	19.3
9.ix	43	.	6	22	15	.	.	.	.	18.2
22.ix	52	1	5	31	15	.	.	.	.	18.4
5.x	23	.	4	6	10	1	2	.	.	20.2
20.x	19	.	11	3	5	.	.	.	.	15.8
27.x	31	1	7	12	9	2	.	.	.	18.3
4.xi	21	.	4	12	3	1	1	.	.	17.6
8.xi	15	1	4	6	3	1	.	.	.	16.5
18.xi	12	.	4	5	3	.	.	.	.	16.9
21.xiii	27	2	6	9	4	5	.	1	.	18.7
1961										
4.i	12	.	1	2	4	2	3	.	.	23.8
8.i	20	1	8	3	1	1	3	2	1	21.3
26.i	20	1	3	4	5	4	2	1	.	21.5
15.ii	8	.	1	1	4	1	.	1	.	22.9
1.iii	11	.	3	4	3	1	.	.	.	18.5
16.iii	17	.	4	1	5	5	1	1	.	22.7
29.iii	19	.	5	6	6	2	.	.	.	18.8
26.v	5	.	1	1	1	2	.	.	.	21.6
26.vi	47	.	1	12	20	12	1	1	.	23.0
1962										
19.ix	17	.	.	.	3	6	7	1	.	29.1
1964										
14.ix	22	.	.	1	.	5	12	4	.	30.7

TABLE 3. Numbers of food animals found in 67 *A. irregularis* collected in various localities in the North Sea in the months of April-August of the years 1932-34, 1938, 1948, and 1950-55, with some remarks on size and other factors.

Prey species group	Number of specimens	Remarks
Foraminifera	10	
Nematoda	1	
Kinorhyncha	1	
Pectinaria koreni	71	All with larval tube. Also many remains.
Other Polychaeta	4	
Natica spp.	9	Distributed in 8 sea-stars.
Other Prosobranchia	6	(*Balcis devians, Eulima trifasciata,* a.o.)
Opisthobranchia	7	(*Chrysallida, Turbonilla, Retusa,* a.o.)
Montacuta sp.	15	
Cyprina islandica	32	Found in 17 sea-stars; 26 less than 2 mm long
Venus spp.	19	(Two *V. fasciata,* remainder *V. gallina)*
Ensis sp.	155	Found only in 14 sea-stars, 46 in one sea-star, 29 in another. All less than 1 mm long.
Spisula solida	67	All in one sea-star, all undigested, 1-3 mm long.
Other Bivalvia	34	All but one less than 2 mm long.
Harpacticoidea	7	
Ostracoda	21	
Cumacea	21	All less than 2 mm long.
Isopoda	3	All less than 1 mm long.
Amphipoda	3	All less than 2.3 mm long.
Other Crustacea	8	Mostly unidentifiable, but including one *Upogebia.*
Ophiuroidea	17	Including 13 undamaged *Ophiura* sp. with disc diameters from 0.3 to 4.5 mm, of which 10 were 1 mm or less.
Echinoidea	29	All less than 2.5 mm long.
Fish eggs	about 120	All in one sea-star. Diameter about 650 μ.
Total number of animals	540	

The food items

Diatoms: One specimen collected in the North Sea in May 1953 was full of *Coscinodiscus* sp., many of which still contained chromatophores. Six other specimens had swallowed lesser numbers. Eichelbaum (1909) also found diatoms – although not many – in his North Sea material. Generally, however, such finds are rare and very few were found in specimens collected in inner Danish waters. In one specimen taken in the Hornbæk Bay in March 1960, a small piece of a *Chaetoceras* chain was found.

Foraminifera: Although Hansen (1965) found from 5 to 25 foraminiferans per cm^2 in the Hornbæk Bay they were only found in 31 out of 1064 *Astropecten* (Table

TABLE 4. Data on stomach contents of 38 medium-sized *A. irregularis* taken at three close stations (Dana Sts. 8458, 8517 & 8519) in the south-eastern North Sea in May 1953. The bottom in the area consists of clay with a small amount of sand (E. Ursin, personal communication.)

Prey species or group	Total number of specimens	Number of sea-stars containing prey	Remarks
Foraminifera	?	7	
Nematoda	1	1	
Pectinaria koreni	59	16	Also many tube fragments. Not found at St. 8517.
Other polychaetes	3	3	
Turritella terebra	9	6	All juveniles
Balcis devians	1	1	
Natica pulchella	5	3	
Other prosobranchs	5	4	
Odostomia eulimoides	3	2	
Retusa umbilicata	8	6	
Philine denticulata	1	1	
Nucula nitida	6	4	
Modiolaria nigra	2	2	
Montacuta ferruginosa	1	1	
Cyprina islandica	111	33	All but four less than 3 mm long.
Venus gallina	7	6	
Syndosmya sp.	1	1	
Spisula subtruncata	1	1	
Mya truncata	3	3	
Corbula gibba	6	4	
Harpacticoidea	63	17	Also many fragments. Not found in the 10 sea-stars at St. 8517.
Copepoda	1	1	
Ostracoda	16	7	
Cumacea	11	9	
Ophiura albida	18	8	Disc diameter less than 3 mm. only at St. 8517.
Echinocardium sp.	4	4	
Total number of prey specimens	346 + foraminiferans		

10). Earlier Blegvad (1914) had found some in specimens from the Kattegat. Data from French waters (Bouchet & Le Campion, 1962) also show that even when abundant, foraminiferans are only swallowed in insignificant numbers.

Since many foraminiferans are as large as newly settled bivalves, which often dominate the stomach contents, size is not the reason why so few foraminiferans are taken.

TABLE 5. Stomach contents of 9 *Astropecten irregularis* collected in the North Sea (Dana St. 10277(95); 52°20′N, 3°00′E) on 29 April 1957.

Prey group	Total number found of each prey group	Number of *Astropecten* in which the prey	Size range of prey in mm
Pectinaria koreni	7	2	2.0-2.4
Cingula alderi	2	1	0.66-0.77
Turritella terebra	4	1	5.5-7.6
Natica pulchella	31	6	0.9-5.2
Ensis sp.	8	2	0.34-0.96
Spisula solida	99	6	0.50-1.68
Cumacea	15	5	0.52-1.44
Unident. Crustacea	1	1	?
Ophiura sp.	1	1	0.72 (disc. diameter)
Echinocyamus pusillus	1	1	0.80
Total number of prey	168		

TABLE 6. Stomach contents of 14 *A. irregularis* collected near the island of Bonden on the Swedish Skagerak coast on 2 September 1957 and examined the following day (for further details see text).

Prey species or group	Number ejected before stomach removal	Number found in stomach on final examination	Total number present when sea-stars were caught
Gibbula tumida	1	1	2
Cingula sp.	1	1	2
Eulima stenostoma	1	0	1
Natica pulchella	6	9	15
Other prosobranchs	3	2	5
Laevicardium norvegicum	21	32	53
Spisula elliptica	0	1	1
Pagurus sp.*	4	18	22
Portunus sp.	0	5	5
Other crustaceans	1	2	3
Ophiura albida	1	0	1
Echinocyamus pusillus	2	5	7
Total numbers	41	76	117

* The majority of the hermit crabs were found in shells of *Bittium reticulatum;* the remainder in shells of *Natica pulchella*, *Nassa* sp. and *Littorina* sp.

TABLE 7. Data on bivalve prey found in the stomachs of 322 *A. irregularis* collected off Frederikshavn, Kattegat, in June-July 1952.

Species or genus	Total number of specimens found	Number of sea-stars containing the prey	Remarks
Nucula nitida	112	71	Only 49 of meio-fauna size.
Nucula tenuis	1	1	
Modiola modiolus	2	2	Juveniles.
Thyasira spp.	23	20	All less than 3 mm long.
Mysella bidentata	774	215	Nearly all worn and full of sand. About 20 *Montacuta ferruginosa* included.
Cardium echinatum	31	9	
Cyprina islandica	1	1	
Venus gallina	858	205	
Tellina spp.	8	8	
Syndosmya alba?	29	26	All empty, and majority worn.
Cultellus pellucidus	12	12	
Spisula subtruncata	1360	227	
Mya truncata	100	69	May include a few *M. arenaria.*
Corbula gibba	262	138	
Total number of bivalves	3573		
Total number of prey organisms	3573 + 1555 (Table 8) = 5128, or 15.9 per sea-star.		

Nematoda: Nematodes play a dominating role among the meiofauna animals on most level bottoms, including Hornbæk Bay (Ockelmann, 1964; K. Muus, unpublished), yet only 43 specimens occurred in more than 1000 sea-stars collected in the latter locality in 1960-62 (Table 10). Usually only one or two specimens were found in the same sea-star, but one of the *Astropecten* collected in May 1960 contained 20 specimens, i. e. nearly half of all the nematodes found. Even if some specimens may have been overlooked, which may well be the case, nematodes obviously play a very insignificant role as food for *Astropecten.*

The majority of nematodes found seemed intact but since some were found partly digested they cannot be stomach parasites. The tough cuticle may no doubt prevent digestion for many hours or even days. Smith (1951) states that they may pass unharmed through the alimentary canal of the plaice, but they may also be digested (Bregnballe, 1961). Since level bottom nematodes may withstand anaerobic conditions for many days (Moore, 1931), they may possibly creep around in the sea-star stomach for days before they become weak enough to be held tight in a stomach pocket – a prerequisite for digestion (p. 57). At any rate,

TABLE 8. Data on prey animals, other than bivalves, found in the stomachs of 322 *A. irregularis* collected off Frederikshavn, Kattegat, in June-July 1952.

Prey species or prey groups	Total number of specimens found	Number of sea-stars containing prey	Remarks
Foraminifera	>21	21	Rarily more than one per stomach.
Nematoda	3	3	
Nemertini	2	2	
Pectinaria koreni	17	16	
Pomatoceros triqueter	3	2	
Other polychaetes	58	53	Mostly undeterminable remains.
Gibbula cineraria	1	1	
Turritella terebra	8	8	All juveniles.
Cingula vitrea	14	13	
Aclis minor	2	2	
Aporrhais pespelicani	1	1	Juvenile.
Natica pulchella	1	1	
Buccinum undatum	1	1	Juvenile.
Nassa pygmaea	5	5	
Nassa incrassata	10	9	
Lora turricola	15	14	
Mangelia attenuata	5	5	
Mangelia brachystoma	7	4	
Mangelia costata	1	1	
Retusa umbilicata	695	174	Nearly all undigested.
Philine aperta	36	29	Finds of gizzard plates incl.
Philine denticulata	23	20	
Philine scabra	4	4	
Cylichna cylindracea	24	21	
Diaphana minuta	3	3	
Ostracoda	4	3	
Balanus improvisus?	250	63	Swallowed along with substrate.
Cumacea	90	70	Mostly *Diastylis rathkei.*
Caprella sp.	13	10	
Other amphipods	14	11	Not identified.
Decapoda	15	15	In most cases probably not swallowed as whole animals.
Ophiura albida	56	48	Only 23 whole specimens.
Amphiura sp.	69	67	Nearly only arm remains.
Echinocardium cordatum	82	82	Correct figure probably only 54 (cf. text).
Total number	1555		

Table 9. Data on stomach contents of 45 *A. irregularis* collected on an *Amphioxus* bottom near Læsø, Kattegat, on 17 May 1960. Depth: 18-27 metres. Temperature: 7.5°C at 20 metres depth.

Prey species or group	Total number of specimens	Number of sea-stars containing prey	Remarks
Foraminifera	16	10	Rather large specimens
Pectinaria sp.	10	7	
Pomatoceros triqueter	2	2	
Other polychaetes	8	8	Unidentifiable remains
Cingula alderi	36	7	All of meio-fauna size.
Rissoa sp.	23	2	22 in one stomach, all worn, probably not swallowed alive.
Turritella terebra	1	1	
Balcis devians	3	3	
Natica pulchella	25	17	21 of meio-fauna size.
Buccinum undatum	2	2	Both of meio-fauna size
Lora turricola	1	1	
Other prosobranchs	9	4	
Odostomia turrita	8	8	
Retusa sp.	2	2	
Diaphana sp.	28	12	11 of meio-fauna size
Philine sp.	5	4	
Pecten sp.	1	1	
Astarte montagui	2	1	Both undigested
Mysella bidentata	3	1	
Montacuta ferruginosa	2	1	
Cardium minimum	1	1	
Cyprina islandica	2	1	
Dosinia lincta	1	1	
Venus gallina	8	3	All less than 3 mm long
Venus ovata	2	2	
Syndosmya prismatica	1	1	
Psammobia ferroensis	1	1	
Spisula elliptica	85	15	All of meio-fauna size
Mya truncata	1	1	
Corbula gibba	1	1	
Thracia sp.	7	7	
Polyplacophora	1	1	
Cladocera	1	1	
Harpacticoidea	1	1	
Ostracoda	6	4	
Cumacea	7	5	
Cypris larvae	28	5	
Balanus sp.	1	1	
Arcturella dilatata	2	1	
Lepidepecrum longicorne	1	1	
Other amphipods	7	4	
Insecta	3	3	
Ophiura sp.	6	6	
Echinocyamus pusillus	11	7	
Gastropod eggs	?	4	
Total number of specimens	372, or 8.2 specimens per sea-star stomach.		

[illegible] Numbers of prey animals found in 1051 *A. irregularis* collected in Hornbæk Bay, Øresund, from January 1960 through June 1961 and in 17 specimens collected in the same locality on 19 September 1962.

Months	Jan. 1960	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan. 1961	Feb.	Mar.	May	June	Total	Sept. 1962
No. of *Astropecten*	15	149	85	59	94	162	48	37	95	73	48	27	52	8	47	5	47	1051	17
Foraminifera	.	1	.	.	2	9	3	.	2	4	.	.	4	.	.	.	6	31	.
Nematoda	.	.	2	2	20	13	2	.	.	1	1	.	.	.	.	.	2	43	.
Kinorhyncha	.	.	1	1	1	4	1	.	1	7	.	.	.	.	1	.	1	18	.
Pectinaria spp.	.	.	.	2	1	19	5	5	3	2	.	.	1	.	.	.	3	41	2
Other polychaetes	.	1	1	.	3	22	3	3	2	6	1	.	1	.	1	2	8	54	1
Rissoa spp.	2	2	4	.	.	7	153	97	14	.	.	.	.	.	.	.	1	280	25
Other prosobranchs.....	3	10	11	6	6	11	.	3	43	19	4	3	7	.	2	.	7	135	1
Opisthobranchs	.	1	2	.	.	15	1	2	.	1	1	.	1	.	.	.	6	30	.
Nucula spp.	.	.	.	1	1	1	.	1	1	.	.	.	1	.	.	.	.	6	1
Mytilidae.............	.	.	1	1	3	3	41	33	13	4	.	1	.	.	1	.	8	109	14
Mysella bidentata	.	12	9	3	.	7	4	6	13	10	.	2	5	.	8	2	5	86	.
Montacuta ferruginosa...	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	320
Cardium spp.	.	3	5	1	.	4	2	4	7	2	.	1	.	.	.	.	3	32	7
Cyprina islandica	.	1	7	11	9	54	11	3	5	3	.	.	.	1	7	1	85	198	.
Venus gallina	.	.	1	.	3	2	2	.	8	5	1	.	.	.	7	.	3	26	21
Tellina spp.	.	.	.	1	1	2	.	.	1	.	.	.	.	.	.	.	1	6	2
Syndosmya alba	.	.	.	5	2	23	2	7	9	3	3	.	.	.	.	.	6	60	1
Cultellus pellucidus......	.	5	20	7	8	11	1	1	.	4	.	1	.	.	1	.	.	59	.
Spisula subtruncata	4	35	138	29	22	807	4209	2880	618	19	2	.	.	.	.	.	.	8763	12
Hiatella rugosa	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	5	.
Mya truncata?	.	107	217	48	54	172	52	48	22	1	.	.	1	.	4	2	103	831	.
Corbula gibba	.	1	19	11	8	24	1	4	13	24	5	2	.	.	.	.	5	117	18
Other bivalves	.	2	23	8	6	14	11	.	4	5	5	3	4	.	3	1	8	97	.
Cladocera	.	.	.	.	6	54	1	.	.	.	.	.	.	.	.	.	2	63	.
Harpacticoidea	.	1	5	2	8	20	1	1	8	15	1	3	.	.	.	.	3	68	.
Ostracoda	.	3	24	5	8	33	3	1	5	8	1	2	2	.	5	.	8	108	.
Cumacea	.	2	27	6	3	13	5	.	3	3	.	.	2	.	1	.	3	68	.
Isopoda	.	.	.	1	.	.	1	.	1	.	.	.	.	.	1	.	.	4	.
Amphipoda...........	.	.	.	2	1	1	1	.	4	5	.	.	1	.	.	.	2	17	.
Decapoda	.	.	.	.	.	3	1	1	9	4	.	.	.	1	.	.	2	21	3
Other crustaceans	.	.	.	2	3	16	.	.	5	2	1	.	.	.	1	.	1	31	.
Crustacean larvae	.	.	.	1	1	9	1	1	.	1	.	.	.	.	.	.	2	16	2
Insecta	.	.	.	3	.	6	1	.	1	1	.	.	.	.	.	.	.	12	.
Asterias rubens	.	.	.	.	.	.	.	.	1	2	.	1	1	1	.	.	.	6	.
Ophiuroidea	1	28	18	.	4	11	5	5	19	24	16	5	16	1	17	.	9	179	29
Echinoidea	.	1	.	.	.	3	24	36	10	9	.	.	.	.	.	.	4	87	261
Total for each month ...	13	216	535	159	184	1393	4549	3142	845	194	42	24	47	4	54	8	298	11707	720
Number per sea-star	0.9	1.6	6.3	2.7	2.0	8.6	94.8	85.0	8.9	2.7	0.9	0.9	0.9	0.5	1.2	1.6	6.3		42.4

the low number of nematodes found is certainly not due to a quick digestion of them.

Part of the reason why so few are taken by the sea-star could be that the smooth cuticle and very quick movements of the worms make it difficult for the sea-star to pick them up with their sucker-less tube feet. It is also possible that the sea-star "dislikes" nematodes and only swallows them when little else is available. Some may conceivably be swallowed by accident since they are known to enter newly settled bivalves (G. M. Christensen, in Thorson, 1966).

Polychaeta: With the exception of *Pectinaria*, only few polychaetes were found in an identifiable condition. Fragments of tubes, empty cuticles, and bristles were often the only remains present. General observations, feeding experiments, and the fact that barnacles or molluscan egg capsules were not found on them indicate that such finds represent the remains of swallowed, living animals. A worm may break into pieces while being swallowed, but since all the specimens and remains found indicate that only sedentary, tube-building forms are taken, this factor is not likely to play any major role. All the same, it is often difficult or impossible to estimate either the sizes or numbers of swallowed specimens from present remains. The large majority of the specimens found were only a few millimetres long, but larger tube-pieces (up to 4 cm long) occurred in a few sea-stars.

Newly settled *Pectinaria koreni* were found in significant numbers in the North Sea material (Tables 3 & 4). As many as 47 whole specimens and a number of tube fragments occurred in a single sea-star (Table 11). The large majority were still in the characteristic hyaline, larval tube, which in some cases had the first grains of the sandy tube attached. A few considerably larger specimens were found in the Hornbæk Bay material.

Sessile polychaetes such as *Pomatoceros triqueter* may occasionally be swallowed along with the substrate to which they are attached (see also Hunt, 1925).

Since polychaetes may constitute the most numerous group among the animals found in the Hornbæk Bay *Venus*-community (Ockelmann, 1964) it is quite evident that *Astropecten* only utilizes this food resource to a very small extent (Table 10). Size cannot be a limiting factor in this respect since over 70 % of the polychaetes belong to the meio-fauna just after settling (see Thorson (1966) for references). Most of the errant species are probably so vivacious that *Astropecten* is unable to seize them.

Prosobranchia: Kisch (1958) found at least 33 prosobranch species in his very large material of *A. irregularis* collected off the French west coast. In my material from Frederikshavn 13 species were present, but none in any significant numbers (Table 8). In the larger Øresund material even fewer species were represented. In some instances, however, a notable number of specimens was found.

TABLE 11. Maximum numbers of certain prey animals found in a single stomach of *Astropecten irregularis* in the present investigation.

Date	Locality	Name of prey	Number	Remarks
25. v. 1960	Øresund	Nematoda	20	Only very rarily found in stomachs.
20. v. 1954	North Sea	*Pectinaria koreni*	47	All newly settled; also remains.
17. v. 1960	Læsø	*Cingula alderi*	17	Normally very rare in stomachs.
June 1952	Frederikshavn	*Retusa umbilicata*	28	Only abundant in Frederikshavn material
3. i. 1964	Øresund	*Rissoa inconspicua?*	25	All juveniles and undigested.
29. iv. 1957	North Sea	*Natica pulchella*	7	Rare except on gravel grounds.
19. ix. 1962	Øresund	*Montacuta ferruginosa*	97	Another specimen contained 95 specimens.
1. viii. 1952	Frederikshavn	*Cardium echinatum*	12	All of meio-fauna size.
26. vi. 1961	Øresund	*Cyprina islandica*	17	All of meio-fauna size.
June 1952	Frederikshavn	*Venus gallina*	25	Size range: 1.7-4.8 mm.
3. v. 1952	North Sea	*Ensis* sp.	46	All newly settled.
17. v. 1960	Læsø	*Spisula elliptica*	39	All of meio-fauna size.
17. vi. 1934	North Sea	*Spisula solida*	67	Size Range: 1-3 mm, all undigested.
9. viii. 1960	Øresund	*Spisula subtruncata*	422	16 other *Astropecten* from same area contained over 200 specimens.
30. iii. 1960	Øresund	*Mya truncata*	16	All newly settled.
14. iii. 1960	Øresund	Cumacea	11	Not uncommon in most materials, but rarily more than one or two specimens in a stomach.
17. v. 1960	Læsø	Cypris larvae	21	Normally very rare in stomachs.
June 1952	Frederikshavn	*Balanus improvisus?*	36	Only found in Frederikshavn material.
19. ix. 1962	Øresund	*Ophiura albida*	13	All juveniles.
14. viii. 1964	Øresund	*Echinocardium cordatum*	160	All juveniles.

As many as 22 *Rissoa* sp. occurred in one of the sea-stars collected near Læsø in May 1960, but they were all worn to such an extent that irregular holes were common in the shells. Hence they were almost certainly not swallowed alive. Practically all *Rissoa* found in the Hornbæk Bay material the same year (Table 10) were also eroded and full of sand. However, in some small samples taken in the Hornbæk Bay in the winter of 1963-64 (not listed in Table 10 since they were not completely analyzed) a fair number of undigested *Rissoa inconspicua?* were found. Thus, one sea-star collected on 3 February contained 25 completely undigested juvenile specimens. The fact that this occurred at a time of the year when few juvenile specimens of the preferred bivalve species are present is probably significant.

Natica spp. were occasionally found in significant numbers, but only in sea-stars taken in localities inhabited by what Thorson (1957) calls a *Venus fasciatum-Spisula elliptica-Branchiostoma* community. In these communities practically none of the species belongs to what one may term as first-class *Astropecten* food, except perhaps for newly settled *S. elliptica* and juvenile *Laevicardium norvegicum.* The latter occurred abundantly in the material taken off the Gullmarfjord (Table 6). It was also present in noticable numbers in the *Astropecten* investigated by Bouchet & Le Campion (1962) whose specimens probably also originated from a gravel or shell bottom (p. 85). *N. poliana* was the most abundant prosobranch in the material investigated by Kisch (1958), but he gives no exact figures on number of prey organisms found, nor on the nature of the bottom where the sea-stars were taken. It cannot be a coincidence, however, that very few *Natica* were found in more than 1500 *Astropecten* collected off Frederikshavn and in the Øresund (Tables 8 & 10) on sandy bottoms inhabited mainly by animals belonging to the *Venus* community as defined by Thorson (1957). This indicates that they are only swallowed in the absence or scarsity of more suitable prey, and experimental evidence supporting this view is given elsewhere (p. 67). It is also possible, however, that *Natica* may escape more easily in sand and muddy sand than in a gravelly substrate.

Practically all *Natica* found in the stomachs had their operculum tightly closed and were in a completely "fresh" condition, suggesting that they were still alive when the sea-stars were caught.

Although Kisch (op. cit.) found many prosobranch specimens in his material, bivalves were more abundant. In the *Venus* community sampled in the Øresund small prosobranchs are present in very large numbers (Ockelmann, 1964). They are, nevertheless, taken by the sea-stars in very small numbers (Table 10), especially when it is recalled that the majority of the *Rissoa* listed probably were swallowed as empty shells. It is also striking that although egg capsules of *Hydrobia ulvae* occurred abundantly in the Frederikshavn material (Table 12), not a single mother animal was found.

Opisthobranchia: These were seldom found in large numbers, but notable exceptions occurred. The small *Retusa umbilicata* was present in over half of the *Astropecten* collected off Frederikshavn in June-July 1952, and only three bivalves, of which one (*Mysella bidentata*) probably should be discounted, occurred in larger numbers (Tables 7 & 8). Nearly all the 695 *Retusa* looked very "fresh". More or less empty shells as well as gizzard plates revealed that at least 90 specimens of other opisthobranchs belonging to the genera *Philine*, *Cylichna* and *Diaphana* had been swallowed, but this is a small number compared with a total of 5128 ingested prey specimens. Even if it is taken into consideration that at least *Philine* seems to be digested rather quickly and contains a large percentage of organic matter compared with most other prey types they play a minor role in the food budget of *Astropecten*.

Very few opisthobranchs occurred in the large Hornbæk Bay material (Table 10) although *Philine* spp. is very common in the area (B. Muus, 1964). They were also rare in the sea-stars from other localities, although it is worth noting that 12 out of 45 specimens taken near Læsø (Table 9) had swallowed one or a few *Diaphana* sp.

Bivalvia: This prey group dominated the stomach contents in all major localities (Fig. 1). Among the species encountered in the largest materials, *Spisula subtruncata* was clearly the most abundant (Tables 7 & 10), and the remaining materials were not collected on grounds where this species commonly occurs. Off Frederikshavn, *Venus gallina* ranked next in abundance, whereas it was much rarer in the Hornbæk Bay material. As for the abundance of other bivalves reference is made to Tables 3-10. As is the case for many non-bivalve species, it is to be noted that a number of species are not as abundant in the stomachs as one would expect from known densities of them in the collecting localities (cf. Table 33). This poses a number of questions which will be considered later. Hence, to avoid unnecessary repetitions, specific cases will not be pointed out here.

The presence of empty shell pairs, not to mention single valves, does not prove that living bivalves were swallowed. Thus, none of the Mytilidae (including specimens of *Mytilus edulis*) found in the Hornbæk Bay material (Table 10) contained remains of soft tissues, and many of them were heavily eroded. However, after storms it is not uncommon to find that large amounts of detached algal material have been carried into deeper water, and attached to the algal fragments may be juvenile *Mytilus* as well as empty shells. Furthermore, in September 1968 a group of graduate students opened up a small number of *Astropecten* from the mentioned bay and actually found a few completely undigested *Mytilus*. I have, therefore, placed all empty, but otherwise intact valve pairs, in the table. Quantitatively, a possible error does not make much of a difference since the Mytilidae account for less than one per cent of all the bivalves found. In the laboratory, even juvenile *Mytilus* never seem to be taken.

All the *Syndosmya* found in the Frederikshavn and the Øresund materials were likewise worn and often full of sand grains. Furthermore, there were almost just as many single valves (not listed in the tables), and this strongly suggests that most of them, if not all, were picked up as empty shells.

The majority of the many *Mysella bidentata* found in the Frederikshavn material (Table 7) and those taken in the Øresund material lacked a periostracum

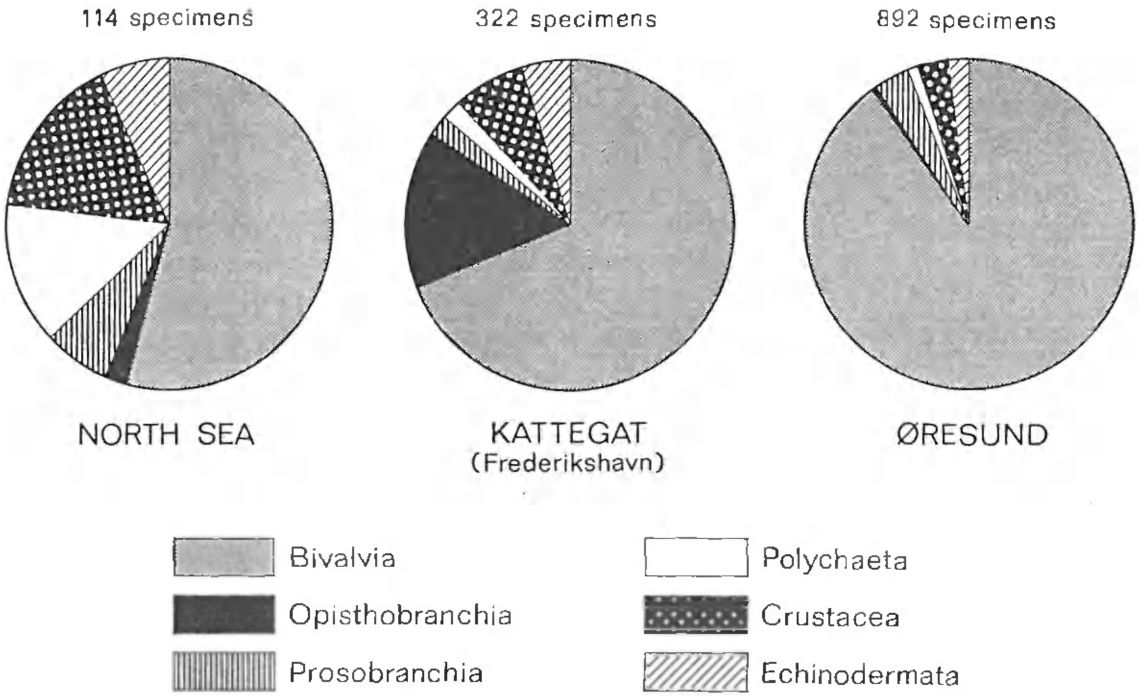


FIG. 1. Quantitative distribution of prey groups found in *Astropecten irregularis* from three different localities. Number of specimens analyzed for stomach contents is given at top.

and were full of sand grains. It is possible that a closer check of the Frederikshavn material, which was worked up in 1952-53, would have made it possible to state with more certainty whether an animal had been swallowed alive or not. When rechecking the material later for other purposes, it was found that some of them had egg capsules of *Hydrobia* attached without any periostracum underneath. However, since a few were undigested, and since three out of fifteen specimens found in 26 *Astropecten* collected off the Swedish west coast (Midtskär, Table 1) also were undigested, all appended shell pairs have been included in Table 7.

Evidence presented later (p. 78) shows that *M.bidentata* is either able to escape or is disliked by *Astropecten.* Many of the empty shells and single valves of Mytilidae, *Syndosmya* and *M.bidentata* were probably picked up because something edible, such as gastropod egg capsules (Fig. 3) were attached to them.

Crustacea: Although all the major groups of *Crustacea* are represented in the food taken by *Astropecten,* they never occur in large numbers, except under special circumstances. As could be expected, the smaller forms are most commonly found.

Some Cladocera occurred in the *Astropecten* collected in the Hornbæk Bay in the early summer of 1960 (Table 10). There were a few *Podon* present, but the majority were *Evadne;* all of them were parthenogenetic females carrying a few young in their brood sack.

In the Hornbæk Bay material, ostracods were the most abundant crustaceans

(Table 10), and in the North Sea material taken at three near-by stations in May 1953 they were found in 7 out of 38 sea-stars (Table 4).

Seventeen out of 28 sea-stars collected at two of the three stations mentioned contained 63 whole harpacticoid copepods in addition to numerous remains, and in this particular case these crustaceans constituted a significant part of the food during the collecting period. They must contain a rather high percentage of organic matter, and one gets the impression that they soon "deteriorate", i. e. that they are quickly digested. However, when it is considered that more than 5000 harpacticid copepods may be found per m² on *Venus gallina* bottoms in the Øresund (B. Muus, 1964) where *Astropecten* is most common, and compare this with the findings listed in Table 10, one realizes how insiginificant a role this group plays as food under normal circumstances. They are probably difficult to seize, and may possibly be taken only when dead or in a weak condition.

Table 8 shows that a surprisingly large number (250) of *Balanus*, probably all *B. improvisus*, were found in the *Astropecten* taken off Frederikshavn in the summer of 1952. They were practically all found attached to small test fragments of the irregular sea-urchin *Echinocardium cordatum*.

As could be expected under the circumstances, all the specimens were juveniles, the largest having a base diameter of less than 6 mm. The fact that barnacles were only found in the Frederikshavn material, shows that they play a very minor role as food for *Astropecten*.

Cypris larvae are also sometimes encountered, and as many as 21 have been found in a single stomach (Table 11).

Although never numerous, cumaceans, mostly *Diastylis rathkei*, may in rare cases be found in more than 20 % of the *Astropecten* collected on a sandy bottom (Table 8).

It is no wonder that such fast-moving animals as isopods and amphipods only rarely occur in the stomachs, and it is most likely that those found were dead or somehow immobilized when swallowed.

The decapods listed in the different tables mainly refer to remains of hermit crabs or true crabs in the form of chelipeds or other appendages, but whole specimens may also be found. In early September 1957, several intact *Portunus* sp. measuring up to 5.6 mm in carapace width were found in *Astropecten* from Swedish waters (Table 6), and in the fall of 1960 several juvenile *P. pusillus* were found in specimens collected in the Hornbæk Bay. One may wonder how the sea-star is able to cope with these crabs, but as in the case of isopods and amphipods, it is likely that only weakened or dead specimens are taken. The occurrence of two mysids and one euphausian in a material taken in the Hornbæk Bay in September 1962 can certainly only be explained in this way. Bouchet & Le Campion (1962) also state that *Astropecten* may feed on crabs and other crustaceans thrown or washed overboard from fishing boats when the crew cleans the deck after sorting the fish caught by trawls or seines. Such animals will usually be dead, or at least be in a very poor condition, before they are back in the sea. Both at Frederikshavn and in the Hornbæk Bay such fishing takes place.

In the Swedish material mentioned above a fairly large number of juvenile hermit crabs were present (Table 6), mostly inhabiting shells of *Bittium reticulatum*. Pagurids were also found in *A. irregularis* by Hunt (1925). It is perhaps possible for the sea-star to "trap" hermit crabs in the hollows found on shell-gravel bottoms where, moreover, these animals may be very common. There is also the possibility that the pagurids may be caught while trying to obtain food from the substrate stirred up by the sea-star (cf. Weber, 1968).

Crustacean larvae were also found (Table 10), although only in very small numbers. The majority were the cyprids mentioned earlier, but a few zoas's and megalopa's were also encountered.

Echinodermata: Apart from a find of a juvenile *Psolus phantapus* in an *Astropecten* taken in the Hornbæk Bay in November 1960 no holothurians were encountered, nor are there any records in the literature.

Very rarely one may find other sea-stars, notably *Asterias rubens,* in the stomachs (see e. g. Table 10). A specimen taken at Knähaken south of Helsingborg contained another juvenile *Astropecten.*

Although *Echinocardium cordatum* is listed as occurring in 82 out of the 322 *Astropecten* collected off Frederikshavn (Table 8), only two whole specimens were actually present, but the nature and number of fragments in 52 of the other sea-stars indicate that each sea-star had swallowed a single 1-2 cm long *Echinocardium.* All these specimens were no doubt crushed during the rather rough treatment of the sea-stars in the cod end of the seine.

In the remaining 28 sea-stars, however, only a single or very few test fragtments were found. Many of these were completely devoid of spines, and judging from their slight curvature, thickness and the diameter of the spine sockets, it is almost certain that they could not have been part of a sea-urchin small enough to be swallowed by the sea-star. Furthermore, some of them bore marks indicating that something had been attached to them.

In any case, only about 1 % of all the prey specimens taken by the sea-stars at Frederikshavn were *E. cordatum.* In more than 1000 *Astropecten* collected in the Hornbæk Bay from January 1960 to June 1961 only 79 *Echinocardium* were present. However, three later samples yielded quite different data. The 17 sea-stars taken on 19 September 1962 contained a total of 261 newly settled *Echinocardium* (Table 10). On 18 October 1963, 19 sea-stars were collected in Hornbæk Bay, and 16 of these contained remains of 2-4 mm long *Echinocardium.* Although exact countings were impossible due to too much fragmentation of the material, it is safe to state that the average content was at least 15 *Echinocardium* per sea-star. Finally, on 14 August 1964 no less than 921 newly settled *Echinocardium* were found in 22 sea-stars (Table 33).

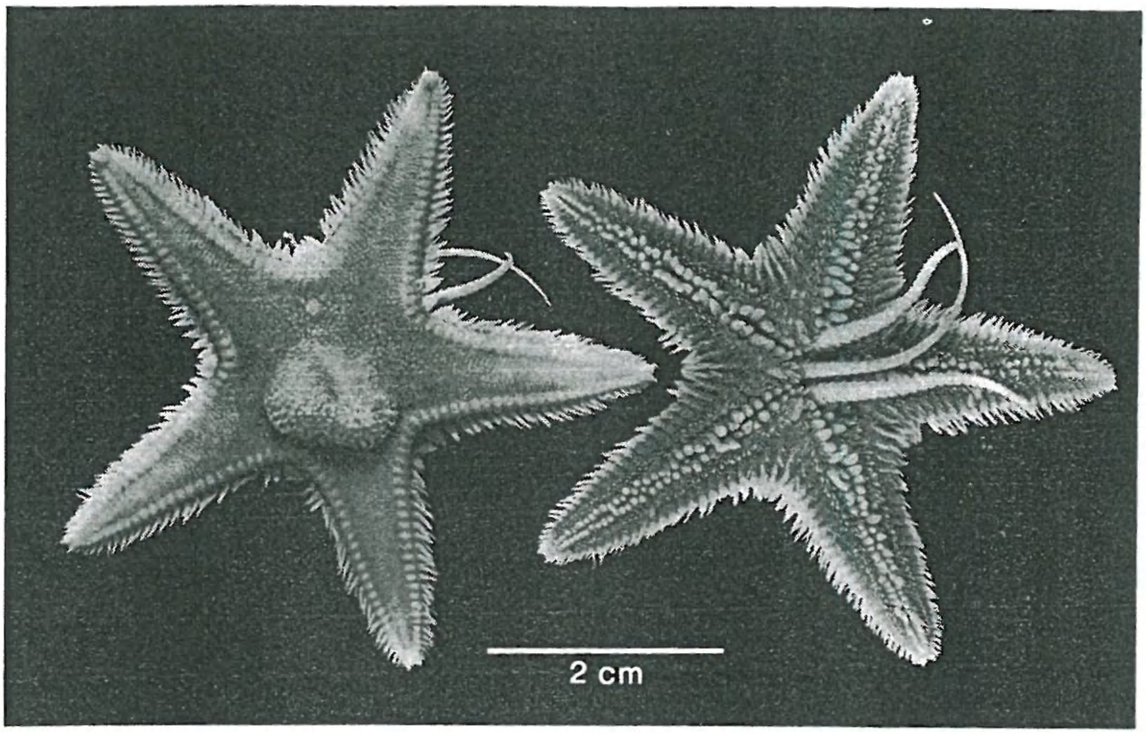


FIG. 2. Specimen of *A. irregularis* with partially engulfed *Ophiura albida*. The whole disc was present in the stomach, whereas only few remains could be found of the two "missing" arms, i.e. the ophiuroid may not have been complete when swallowed.

The only other sea-urchin encountered was *Echinocyamus pusillus*, which mainly occurred in small numbers in sea-stars collected on shell or gravel bottoms (Table 9). This species was found, however, in more than half of the *Astropecten* taken by Hunt (1925).

When examining the tests of *Echinocyamus* ejected by *Astropecten* in the laboratory it was observed that a certain amount of tissue had been left undigested. The reason for this is probably that the complicated system of supporting walls inside the test makes it very difficult for the sea-star to reach all digestible matter with a stomach lobe inserted through the small mouth opening.

Ophiuroids or their remains were found in *Astropecten* from all localities investigated, but the composition of these finds showed some notable differences.

Practically all the ophiuroids found in the North Sea material were rather complete juvenile specimens of *Ophiura albida* (Tables 3 & 4).

In contrast to this, only 25 specimens with the disk and parts of one or more arms present were found in the Frederikshavn summer material, although 83 of the sea-stars contained fragments of brittle-stars. The size of the arm fragments often showed that only an arm or part of an arm had actually been picked up. Both at Frederikshavn and in the Hornbæk Bay *Astropecten* with large *Ophiura* arms protruding far out of the mouth opening were found. Thus, one specimen with an R of 12.7 mm had seized a 29.5 mm long arm of *O. albida*, but almost

$^2/_3$ was still outside the mouth. The arm looked quite fresh and there were no other ophiuroid remains inside the stomach. In one case an *Astropecten* had attempted to swallow a very large *Ophiura albida* (Fig. 2). It is possible that *Astropecten* in such cases may continue to push the protruding arm or arms inside in step with the digestion and subsequent disintegration of the swallowed part.

Most brittle-stars are apt to autotomize one or more arms when being attacked by a predator (see e. g. H. Christensen, 1967, p. 270). This is not least true for *Amphiura* spp. which accounted for at least half of the arm remains found in the Frederikshavn material, whereas *Ophiura* spp. made up almost 100 % of the specimens and remains found in the material from other localities.

Only rarely may one find more than one or a few ophiuroids in the same *Astropecten,* but in one specimen collected in the Hornbæk Bay, 13 juvenile *O. albida* were found (Table 11). Ophiuroids were present in more than 25 % of the sea-stars taken off Frederikshavn (Table 8), and at one locality in the North Sea, ten *Astropecten* contained together 18 *O.albida* (Table 4). Table 10 shows that during the constant period of sampling in 1960-61 in the Hornbæk Bay, only two bivalves and one gastropod were found in higher numbers than brittle-stars (nearly all *O.albida*). Nevertheless, in the last mentioned locality, for example, the ophiuroids still only accounted for about 1.5 % of all the food specimens.

Carrion: Kisch (1958) found insects in the stomach of *Astropecten* taken off the French west coast. Some specimens, mostly beetles, were also present in the material from Frederikshavn (not noted in Table 8) and other near-shore localities (Tables 9 & 10). Since most of them contained internal tissue, these finds show that *Astropecten* may act also as a scavenger. This was also observed in the laboratory where they willingly feed on dead shrimps (*Crangon*) and fish (juvenile *Gobius* sp.).

This supports the view that the many specimens of vivacious or planktonic crustaceans probably were swallowed in a weak or dead condition.

Eggs of gastropods and fishes: In one of 29 *Astropecten* opened and examined by Thorson (unpublished) in the Frederikshavn laboratory in July 1951 he found a cluster of egg capsules of the gastropod *Turritella communis.* This was the first find of eggs of this snail in Danish waters, although it is very common in the Kattegat as well as in the northern part of the Øresund.

In my Frederikshavn material the eggs of a number of other gastropods were also found (Table 12).

Hundreds of *Hydrobia* egg capsules, attached mainly to bivalve shells and distributed in at least 91 *Astropecten,* were found, although this species usually attaches its egg capsules to other specimens of its own kind (Meyer & Möbius, 1872; Lebour, 1938). The capsules were not found on "dead" shells alone, but more frequently on shells of bivalves which clearly had been alive when swallowed.

TABLE 12. Finds of gastropod eggs in the stomachs of 322 *Astropecten irregularis* collected off Frederikshavn, Kattegat, in June-July 1952.

Group	Species	Number of sea-stars with eggs	Remarks
Prosobranchia	*Cantharidus clelandi*	1	Found free in stomach.
	Rissoa membranacea	4	On shell fragments.
	Hydrobia ulvae	91	On living bivalves, empty shells and shell fragments.
	Turritella terebra	10	Found free in stomach.
	Bittium reticulatum	1	Attached to *Zostera* leaf.
	Clathrus turtonis	1	Found free in stomach.
	Nassa sp.	1	Attached to shell fragment.
	Lora turricola	1	Attached to empty shell.
Tectibranchia	*Philine aperta*	2	Found free in stomach.
	Philine scabra	1	Found free in stomach.
Nudibranchia	*Duvaucelia plebeja*	1	Found free in stomach.
Unidentified		2	Gelatinous egg masses found free in stomach.

Among these were not just such relatively sluggish species as *Venus gallina*, but also the much more vivacious *Spisula subtruncata*. Usually, quite a number of capsules were found together on a substrate. Fig. 3 shows a single valve of *Syndosmya alba* with egg capsules attached to both sides of it. Egg capsules of *Hydrobia* were also found in the Frederikshavn winter material and in the sea-stars collected in the Hornbæk Bay.

Since these capsules look like small, irregular patches of sand grains when viewed from the upper side, many were probably overlooked, especially among those detached from the original substrate. Eggs shed in gelatinous masses, as e. g. those of *Cantharidus clelandi*, *Philine* spp. and *Tritonia plebeja*, must be digested so fast that the chance of overlooking remains of them likewise must be considerable.

Fish eggs were mostly encountered in *Astropecten* collected in the North Sea. These are also easily overlooked, and no sincere attempts were, therefore, made to count all eggs present. However, in one case I counted about 120 eggs in a single stomach.

"*Detritus*": Eichelbaum (1909) found "Bodenmaterial" in a good number of 29 *Astropecten* from the North Sea. In the North Sea material treated by me there was likewise, but in relatively fewer specimens, a substance present reminding one of bottom material or what many would call detritus.

Blegvad (1914), whose material, except for one specimen, came from the Kattegat, expressly states that *Astropecten* does not swallow detritus, and that any

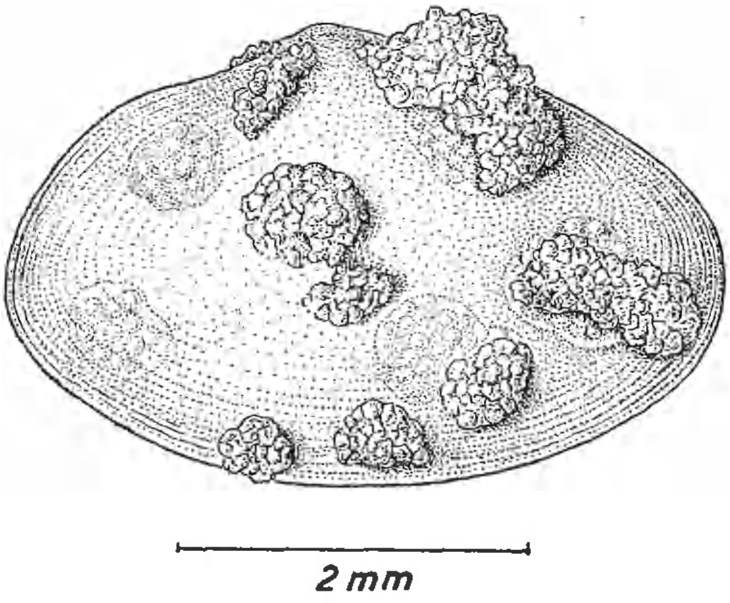


FIG. 3. Valve of *Syndosmya albida* with attached egg capsules of *Hydrobia ulvae* on both sides. Found in the stomach of an *A. irregularis* collected off Frederikshavn. Drawn from preserved material by Poul H. Winther.

present bottom material derives from swallowed detritus feeders. I found very little detritus in stomachs of *Astropecten* collected in the Kattegat and the Hornbæk Bay. In most cases it could be seen that the material originated from deteriorating polychaete tubes, particles from the inside of dead bivalves and gastropods swallowed because something edible were attached to them, sand particles attached to the byssus threads of juvenile *Mya,* foraminiferan tests built of sand or mud, and faecal pellets. Bottom particles may also be "accidentally" pushed into the stomach during ingestion of prey. Even in laboratory experiments it was occasionally observed that specimens ejected sand particles along with empty shells of digested prey.

On this background it seems justifiable to conclude that the higher amount of "detritus" found in the North Sea specimens is due mainly to two interrelated factors, viz the depth and the nature of the fauna present. Eichelbaum's material came from a mean depth of about 86 metres (range: 25-300 metres) whereas Blegvad's material (38 specimens) came from an average depth of 25 metres and my own material from inner Danish waters from an average depth around 20 metres. A quantitative comparison between the prey composition found in the sea-stars taken in the North Sea (Tables 3-5) and off Frederikshavn (Tables 7 & 8) also shows that there were fewer detritus feeders in the latter material. There were even fewer in the Hornbæk Bay material taken during the period of regular sampling (Table 10). However, as noted earlier, the detritus feeder *Echinocardium cordatum* was exceedingly abundant in other samples and totally dominating in one (Table 33).

Miscellaneous items: Eichelbaum (1909) noted a small piece of alga in two *Astropecten* and obviously thought that the sea-stars had picked them up as food.

Similar items were very occasinally found in my material. In the Frederikshavn material, for example, 14 specimens contained fragments of *Zostera*-leaves or algae. Contrary to Eichelbaum, however, I do not think that any of these items are actually digested by the sea-star.

A number of the gastropod eggs found were adhered to a piece of *Zostera* (Table 12), and in the sea-stars collected in Hornbæk Bay, the few pieces of *Zostera* found all had an epifauna of foraminiferans. Pieces of *Fucus* with attached barnacles fed to *Astropecten* in the laboratory were ejected in a completely undigested condition (p. 48). On this basis one must conclude that pieces of *Zostera* and algae are only swallowed when acting as a substrate for epifauna organisms or other edible matter.

Kisch (1958) found many strange items in his material: small pieces of coal, small stones, fish bones, ear stones of fishes, and leaves from land plants. He concludes that *Astropecten* cannot determine what is edible before it has swallowed the item. This cannot be correct, and Kisch must have failed to observe any attached organisms, or else these had already been digested or detached from the substrate. All the mentioned items have also been found in *Astropecten* from Danish waters in addition to fish scales and empty tubes of ampeliscid amphipods. It should be noted in this connexion that molluscan shell fragments were exceedingly more abundant in the Frederikshavn material than in the Øresund sea-stars in which, furthermore, fragments of "naked" echionid test pieces were completely absent. This fits well with the fact that attached egg capsules were very scarce and barnacles completely absent in the latter material.

Kjerskog-Agersborg (1918) found stones with barnacles in the stomach of the giant sun-star, *Pycnopodia helianthoides*, but this is to my knowledge the only case reported in the literature for other sea-stars than *Astropecten*.

Size of prey

The remarks given in Tables 3-5 show that the large majority of the prey found in the sea-stars collected in the North Sea belong to the meio-fauna as defined by Mare (1942). Micro-fauna organisms were not found. This size distribution fits well with the more comprehensive data from inner Danish waters.

Table 13 shows that about 30 % of all prey specimens swallowed by the *Astropecten* collected off Frederikshavn in June-July belonged to the meio-fauna. However, 75 % of the prey was less than 3 mm long and only about 3.5 % exceeded a length of 5 mm. All these sea-stars had an R of 30 mm or more (Table 1, mean about 45 mm), i. e. they were mostly adults with the large majority having a size equal to or larger than the largest specimens from the Øresund. Sea-stars collected in the latter locality had R's ranging from under 10 mm to less than 45 mm with a mean of about 20 mm (Table 1). About 96 % of the prey animals swallowed by the Øresund sea-stars belonged to the meio-fauna (Table 14).

TABLE 13. Size distribution of the majority (about 87 %) of all prey animals found in 322 *A. irregularis* collected off Frederikshavn, Kattegat, in June-July 1952. For size of 250 swallowed barnacles see text.

Shell height or length, carapace length, or disc diameter in mm.	<1	1-1.9	2-2.9	3-3.9	4-4.9	5-5.9	6-6.9	7-7.9	>8	Per cent of meio-fauna size
Prosobranchs	1	23	28	6	14	7	2	.	4	28
Retusa umbilicata	1	363	331	.	.	.	.	.	.	52
Nucula nitida	11	38	36	13	5	.	3	3	3	44
*Mysella bidentata**	13	130	494	131	5	1	.	.	.	18
Venus gallina	4	76	286	321	112	13	7	7	32	9
Spisula subtruncata	81	469	592	171	31	6	2	7	1	40
Mya truncata ?	8	51	25	9	7	.	.	.	.	59
Corbula gibba	.	43	126	69	22	2	.	.	.	16
Other bivalves	6	33	41	14	6	4	1	1	1	39
Cumacea	.	1	7	11	21	3	5	11	31	1
Ophiura albida	5	3	11	4	.	.	.	.	.	17
Total number of specimens in each size group	130	1230	1977	749	223	36	20	29	72	
Total number of meio-fauna size		1360 = 30.5 %					Total number of macro-fauna size =			3106 69.5 %

* Including about 20 *Montacuta ferruginosa.*

It is doubtful whether the data reflect a true prey-predator size relationship. In the Øresund, the *Astropecten* collected in 1960 had only had recently settled *Spisula subtruncata* to feed on, mainly because larger specimens were all but absent and because other attractive prey were scarce.

Off Frederikshavn the sea-stars had obviously had access to *Spisula* which had survived to become larger than they generally do where *Astropecten* occurs in the Hornbæk Bay.

Other facts also speak against the existence of a prey-predator size relationship *sensu stricto*, but a newly settled sea-star cannot, of course, swallow as large a prey as an adult specimen. Tables 13 and 14 show that the Øresund sea-stars on an average contained larger *Corbula* than the Frederikshavn sea-stars and smaller specimens of *Corbula* were definitely present in the Øresund. Furthermore, the average sizes of the prey swallowed by the smallest and the largest sea-stars taken on the same day were very similar. Finally, it should be noted that although the sea-stars taken in the North Sea were intermediate in size between those taken off Frederikshavn and those taken in the Øresund, the percentage of meio-fauna prey must have been as high or nearly as high as in the Øresund material (Tables 3-5).

No proper live material, i. e. including meio-fauna specimens and small juve-

TABLE 14. Size distribution of the majority (over 92 %) of all prey animals found in 1051 *A. irregularis* collected in the Hornbæk Bay, Øresund, from January 1960 through June 1961.

Shell height or length in mm	<1	1-1.9	2-2.9	3-3.9	4-4.9	>5	Per cent of meio-fauna size
Rissoa spp.	116	159	4	1	.	.	98
Other prosobranchs	64	41	17	2	1	10	78
Nucula spp.	1	3	1	.	.	1	67
Mytilidae	76	32	1	.	.	.	100
Mysella bidentata	14	48	16	7	.	1	72
Cardium spp.	16	13	3	.	.	.	86
Cyprina islandica	87	91	6	3	5	6	86
Venus gallina	13	8	2	.	2	1	81
Tellina spp.	1	4	1	.	.	.	83
Syndosmya spp.	6	40	11	1	.	2	77
Cultellus pellucidus	9	17	12	12	4	5	94
Spisula subtruncata	6703	1985	68	2	1	4	100
Mya truncata?	396	262	113	42	15	3	79
Corbula gibba	35	21	12	11	12	26	48
Other bivalves	90	6	.	.	.	1	99
Total number of specimens in each size group	7627	2730	267	81	40	60	
Total number of meio-fauna size	10357 = 95.8 %		Total number of macro-fauna size		448 = 4.2%		

niles, were available to test the conclusion drawn experimentally. In two experiments in each of which two *Astropecten* were offered equal numbers of half-grown (7-10 mm long) and adult (14-17.5 mm long) specimens of *Spisula subtruncata* the results indicated a distinct preference for the smaller specimens (Table 15). One should, however, be cautious in interpreting these data. It is easier to swallow small specimens, and fully adult specimens succeed more often to escape by the well known flight response of this species.

Hunt (1925) found only molluscs of macro-fauna size, ranging in length from about 2 to about 15 mm, with an average of about 8 mm, in a material collected throughout a year in the English Channel off Plymouth. It is, however, possible that Hunt overlooked smaller specimens hidden between the numerous folds of the stomach. The average number of prey specimens per sea-star was less than four, and the most abundant bivalves belonged to genera (*Venus, Nucula* and *Corbula*) which also in my material were larger on an average than other bivalves (Table 13). In the 1960 collections from the Øresund the average number of prey specimens per sea-star was 12.6. The much larger sizes of the prey found by Hunt must mean that the amount of organic matter present as food was high,

TABLE 15. Results of two experiments in each of which two *A. irregularis* (R: 37.0-40.0 mm) were fed with *Spisula subtruncata* of two different size groups. Temperature: 15° C.

Exp. No.	Duration of experiments in days	Size range of *S. subtruncata* in mm	Number of bivalves given	Number of bivalves eaten	Number of bivalves in stomachs
1	13	7.5- 8.9	25	22	0
		14.2-17.0	25	11	0
2	11	7.6- 8.8	25	21	0
		13.7-16.2	25	14	0

but it should be pointed out that in contrast to the Øresund material the large majority of the prey organisms were species of *Venus, Nucula, Corbula,* and *Natica* which are retained for several to many days (Table 19) and which, except for *Nucula,* often are thrown out again alive. The presence of *Echinocyamus pusillus* in 65 of the sea-stars indicates, furthermore, that these were taken on a shell-gravel bottom where the possibility of obtaining suitable small-sized prey may be significantly reduced. An example of this can be deducted from the data on stomach contents of 14 *Astropecten* collected on a gravel ground off the Gullmarfjord (Table 6). Except for *Laevicardium norvegicum,* no "first class" food was present as could be seen from the contents of the dredge hauls in which the sea-stars were taken. Since, furthermore, hardly any specimens of meio-fauna size were available, the sea-star was "forced" to feed on larger specimens (Table 16).

TABLE 16. Size distribution of the two dominating molluscan species found in the stomachs of 14 *A. irregularis* collected near Bonden island (cf. Table 6).

Shell height or length in mm	1-2.9	3-4.9	5-6.9	7-8.9	9-10.9	11-12.9	13-14.9	>15
Natica pulchella.............	1	7	5	2	.	.	.	.
Laevicardium norvegicum	13	11	16	5	3	1	3	1

General remarks

The results of the stomach analyses are essentially in agreement with earlier findings by Eichelbaum (1909), Blegvad (1914), Hunt (1925), Kisch (1958), and Bouchet & Le Campion (1962). Except for Eichelbaum, who in 29 specimens from the North Sea found echinoderms and bivalves to be about equally abundant, all other authors found bivalves to be more common than any other prey group (cf. grouping in Fig. 1) with respect to number of specimens, in most cases being more numerous than all other prey specimens combined.

Kisch (op. cit.) expresses the opinion, however, that *A. irregularis* feeds indiscriminately on whatever it comes across, thus implying that the stomach contents simply reflect the abundance of potential prey species where the sea-stars are collected. As we have seen, field data alone suffice to show that this is not the case, and experimental evidence are given in other sections of the present paper.

Stomach analyses of predators have often been used to calculate the relative consumption of different prey species. Provided that proper attention is given to prey size, this is permissable if (1) all ingested prey specimens will be digested, (2) all prey species are digested equally fast, and (3) all empty molluscan shells etc. found in the stomachs represent animals swallowed with all internal tissues present. None of these requirements are fulfilled in the present case.

If one was to go a step further and try to calculate the relative food value obtained from different prey groups or species, attention must also be paid to the fact that large variations exist with respect to contents of dry organic matter (cf. Thorson, 1957).

From all this it is evident that a proper interpretation of data obtained by stomach analysis cannot be given without a thorough background knowledge of the biology of the sea-star as well as the organisms on which it subsists.

Some of the necessary information is available in the literature, but laboratory observations and experiments had to be carried out concerning many points, especially with respect to the sea-star.

PERIODS OF DAILY FEEDING ACTIVITY

Power (1857) kept specimens of *A. auranciacus* in out-door tanks with a sandy bottom layer at Messina and observed that this species displays two periods of daily activity. Her specimens came out of the sand in the morning, dug themselves into it again around 9.00 hrs, and came out again at about 16.00 hrs "when the heat of the sun was diminishing". She thus implied that temperature is a governing factor, and although this explanation is difficult to accept, there is no reason to doubt the observation itself.

Furthermore, both Weber (1965) and Massé (1966) also observed that *A. auranciacus* is a diurnal feeder, at least in shallow water (up to 10 m depth). According to these authors it feeds mainly at twilight hours, both in the morning and in the evening.

Mori & Matutani (1952) kept 79 *A. polyacanthus* in a large tank with a sandy bottom. They recorded the activity of the sea-stars every three hours and more frequently during periods of peak activity. In addition the activity of 5 specimens was recorded on a kymograph for 7-9 days. The sea-stars generally came out of the sand early in the morning and again around sundown, searching for food, whereas the large majority remained buried during the intervening periods. The activity was more pronounced in the morning than at sundown and increased significantly when there was little or no food available. Furthermore, in this situation a rising number of sea-stars became active also during daylight hours. Under constant darkness the regularity of the periods of activity ceased after 2-3 days, thus strongly indicating that light is the primary governing factor. Temperature changes did not have any effects on the daily rhytms of activity.

Zavodnik (1967) states that *A.spinolosus*, a species not entirely tied to sandy bottoms, apparently exhibits diurnal feeding migrations. It can be found in 3-4 times greater numbers on the leaves of *Posidonia* at night time than during daylight hours.

As for *A.irregularis*, Weber (1965) observed by diving that the Mediterranean variety *pentacanthus* also is a diurnal feeder with the same periods of activity as *A.auranciacus*. These periods shifted with light intensities and no specimens were observed out of the sand on clear days in full sunlight, which shows that light must be a governing factor. All available evidence shows that this applies also to the main form. On many occasions I smoothed the surface of the sand in many aquaria before leaving the laboratory, usually between 16.00 and 17.30 hrs. Coming back, either the same evening (most often between 22.00 and 23.30 hrs.) or next morning, there were practically always tracks as well as burrows left in the sand showing that the sea-stars had been active in the meantime. Conversily, in most aquaria, of which I had over 20 during one stage of the work, one would rarely observe more than a few sea-stars out of the sand all day unless they were starving. It was also found that dead shrimps placed on the surface of the sand during the day in aquaria with satiated *Astropecten* were not eaten before the following evening or night.

Thus, there is no reason to doubt that *A.irregularis* is a diurnal feeder, even if quite different light conditions must exist in nature where it lives. In addition to light, the amount of food is also a governing factor. There is nothing in the literature or in my own observations indicating that the main prey organisms are more active and thus perhaps more vunerable at twilight hours.

PERCEPTION OF FOOD

It is commonly accepted that sea-stars possess an olfactory or chemical sense enabling them to percept food at a distance although no specialized organs for this purpose have been found (Feder & Christensen, 1966). Loosanoff & Shipley (1947), however, concluded from field experiments that *Asterias forbesi* finds its prey by accidental contact when moving over the bottom.

Recent studies by Castilla & Crisp (1970) show, on the other hand, that *Asterias rubens* senses water-born odors of living mussels and barnacles, its normal prey in the Menai Strait, and heads towards these in a Y-maze or in a shallow tank.

For the genus *Astropecten*, Preyer (1886-87) was able to lead *A.pentacanthus*, but not *A.auranciacus* and *A.bispinosus*, in any direction he choosed by holding a piece of fresh crab meat in front of one of the arms. He adds, however, that the specimens observed of the latter two species probably were full. Mangold (1908) later observed that *A.auranciacus* promptly came out of the sand when fish meat was placed in the aquarium containing it. Whether the sea-stars were fully buried is not clear. Hartman (1956) caught significant numbers of *A.californiensis* in traps baited with dead fish.

A behaviour similar to that seen by Mangold was once observed for *A.irregularis*. A bivalve, *Astarte elliptica*, was placed in an aquarium on the half-shell to induce buried *Nassa reticulata* to emerge. This goal was promtly achived, but within a few minutes a half-buried adult *Astropecten* emerged 15-20 cm away and headed straight for the mutilated *Astarte* with great speed.

It will be noted that the *Astropecten* in all cases reacted to stimuli emitted from the serrated surfaces of mutilated crabs, molluscs or fish. These stimuli cannot, however, be identical with those given off by living, healthy prey where the stimulatory substances no doubt consist of one or several metabolic end products. Hence differences in response to these essentially different stimuli may be expected.

Many investigators apparently consider mutilated prey to be more attractive than unharmed prey. This seems to be true in some cases as e. g. for the sea-star *Luidia sarsi* (Fenchel, 1965) which has been known to be a voracious predator for a long time (Mortensen, 1927). Conversily, Castilla & Crisp (1970) have shown that *Asterias rubens* shows a tendency, though not a statistically significant one, to avoid effluents from molluscan flesh, so one cannot generalize on this point. Cases involving other predators are pertinent also. A healthy oyster (*Crassostrea virginica*) attracts the oyster drill, *Urosalpinx cineria*, much more effectively than substances released from a mutilated specimen (Federighi, 1931; Sizer, 1936). Likewise, Hathaway & Woodburn (1961) found that the conch *Melongena corona* showed preference for live oysters over shelled oyster meat.

Any set of experiments designed to elucidate the possible significance of distance perception to a true predator should, therefore, primarily be carried out with living, healthy prey as potential attractants.

Since moving water, carrying any possible stimulating substance from a potential food source to a predator, cannot be controlled in conventional aquaria, a 120 cm long, narrow "current aquarium" (Fig. 4) was used for practically all the experiments recorded in the present section. In this aquarium it is possible to create a uniform, laminary current along the bottom, which in my experiments was covered with a layer of sand thick enough to allow normal burrowing activities of the sea-stars and their bivalve prey. A valve at the inlet end enables one to regulate the speed of the current.

To test whether rheotaxi is of any importance, 40 experiments were carried out with practically as many specimens of *Astropecten*, which in each case were

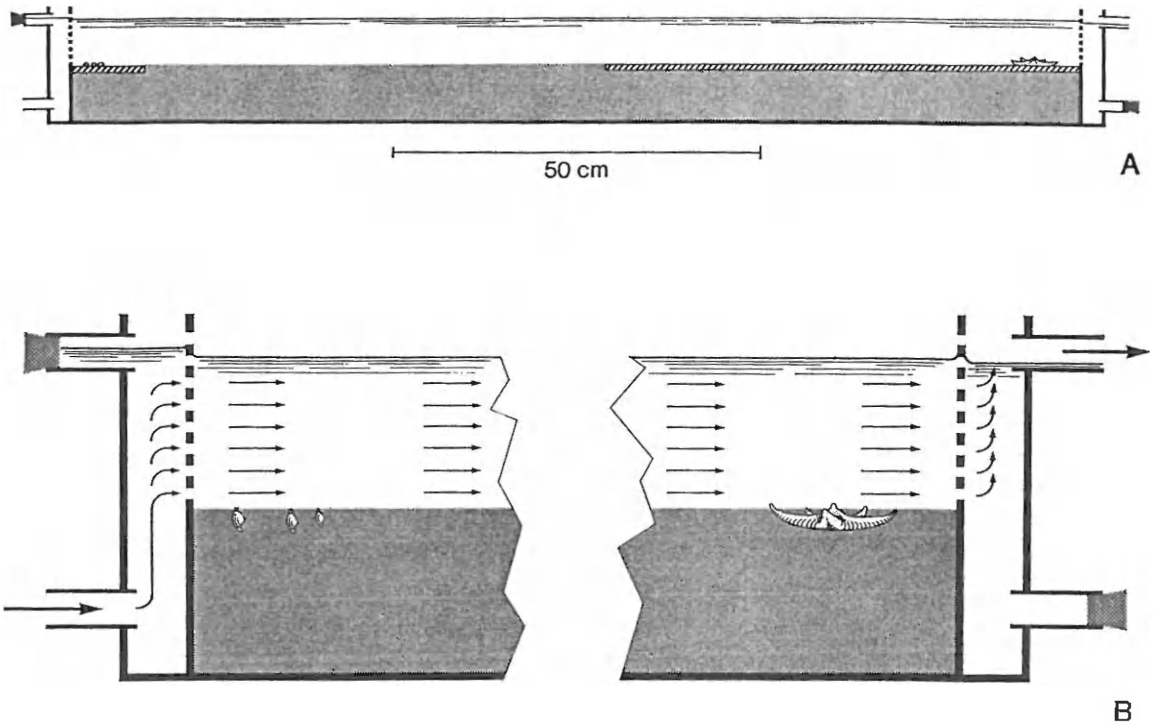


FIG. 4. "Current" aquarium designed by E. Kanneworff (unpubl.). A, Whole aquarium shown with plastic plates placed flush with the sand surface (cf. text). B, Details of inlet and outlet ends, showing direction and lamination of the water flow. One *Astropecten* and three *Spisula subtruncata* are shown in natural position in the substrate.

placed in the middle of the current aquarium. The sea-stars moved against the current in 19 cases and with the current in 21 cases. A rheotaxi seems therefore not to exist. In nearly all cases the sea-stars dug into the sand after moving for a short distance only.

A varying number of *Astropecten* were often left in the current aquarium without food for periods lasting from two to several weeks. As in the experiments by Mori & Matutani (1952) with *A.polyacanthus* this often induced specimens to become active for shorter or longer periods during daylight hours. When this happened I took the opportunity to test whether crushed bivalves (*Mytilus, Spisula* or *Venus*) placed upstream affected the sea-stars. In most cases they obviously sensed the potential food, but although many moved towards it, few continued to do so and the bivalves were in nearly all cases left untouched.

In other instances, "juice" prepared from grounded bivalve tissue was pipetted into the current passing over the bottom. The sea-stars reacted to this stimulus too, but only as long as the juice passing over them was "strong".

Both types of experiments as well as general observations in other aquaria lead to the conclusion that a non-buried *Astropecten* usually only reacts to crushed prey which still is "bleeding" heavily or is situated within a short distance of the sea-star. Both factors will, of course, influence the concentration of the stimulating agent(s).

Buried sea-stars, which were present in the aquaria during practically all experiments referred to above, reacted only very rarely to any of the mentioned stimuli.

Since *A. irregularis* is known to prefer *Spisula subtruncata* to all other bivalves occurring in its natural habitat in Danish waters (A. M. Christensen, 1962 and present paper), this species was used in experiments with life prey.

In the first experiment, 7 adult *Astropecten* were left without food for 14 days. Then, at a time when all were buried in the sand, four *S. subtruncata* of about 1 cm length were placed on the sand close to the inlet end. The bivalves proceeded to dig into the substrate, but before this was completely accomplished, one *Astropecten,* situated close to the outlet end, came out of the sand and headed towards the prey, this sea-star having had at least one arm tip above the sand when the bivalves were added about 2$^1/_2$ minutes earlier. Another specimen, situated in the middle of the aquarium, came out of the sand about 5$^1/_2$ minutes after the start of the experiment at a time when one of the *Spisula* was still not completely buried. The remaining sea-stars, all of which had at least an arm tip or two as well as the tip of the dorsal cone uncovered, remained buried although two of them were situated within 20-30 cm of the bivalves. It happens, although very rarely, that an *Astropecten* is completely covered; in most cases a careful observation will show that at least the center of the dorsal cone is uncovered, but it may, of course, make a difference whether the tip of the cone projects above the sand into the water current or is situated flush with the surface or even in a hollow in the sand.

These experiments indicated that even hungry *Astropecten* do not easily respond to stimuli emerging from living prey some distance away from them, at least not when they are buried in the substrate, i. e. resting. It also appeared that it might make a difference whether the prey is situated on the surface or, perhaps more correctly, in the act of digging into it.

Since the presence of digging bivalves is not the normal situation in nature, the 14 other experiments were carried out with the water flow stopped until the bivalves had buried themselves completely. In one case a sea-star, with two arm tips and its central cone free of the sand, apparently sensed the prey during this phase anyway and headed towards it, and the bivalves were picked up again. However, although a total of more than 70 sea-stars were used only 5 came out of the sand and headed towards the prey within 15 minutes after the start of the water flow, which had a speed of between 3 and 5 metres per minute. Furthermore, one of these specimens dug itself into the substrate again before reaching the prey. All the reacting sea-stars as well as all but a few of the non-reacting specimens had one or more arm tips and/or the central cone projecting above the surface of the sand.

Six similar experiments were carried out with 2-4 *S. subtruncata* placed on a plastic plate lying flush with the bottom surface at the inlet end (cf. Fig. 4). Of

21 sea-stars involved only two reacted within 15 minutes of the start of the water flow. At the end of the 15 minutes, or in some cases as long as about one hour later, the bivalves were crushed in situ on the plates, but this had little effect, in so far as only two of the remaining 19 sea-stars were observed to emerge and head towards the prey within the next 15 minutes, and none responded immediately when the main bulk of crushed particulate matter reached the places where they were dug down.

Similar experiments where the sea-stars were placed on a longer plastic plate at the outlet end (cf. Fig. 4) were inconclusive since an *Astropecten* placed on any hard surface starts to move in one direction or another, and the sea-stars moved away from the buried prey practically as often as towards it. Among those moving towards the prey the majority dug into the sand just after leaving the plate. This is not due to the handling of the sea-stars. Even satiated specimens will proceed to ingest a *S. subtruncata* if placed by hand on top of the bivalve. If placed on its dorsal side, the sea-star will in fact start to swallow a *Spisula* before it rights itself.

Various functions have been attributed to the central cone, which has a permanent character in 0-group specimens (Süssbach & Brechner, 1910), but Gislén (1924) is probably correct in believing that it mainly serves a respiratory function. A resting, fully adult *Astropecten* will usually be buried under a 1 to 2 cm thick layer of sand, except for the narrow cone projecting from the center of the disc and – at times – one or more arm tips. In this situation it seems likely that the cone and especially the arm tips might enable *Astropecten* to sense prey at a distance, but the laboratory observations and experiments do not indicate that this plays any significant role in nature.

This is not to be expected either since *Astropecten* essentially is an active hunter, which comes to the surface when searching for food. Even in this situation, however, the indications are that "long-distance" perception is of no real importance, whereas "short-distance" perception plays a very decisive role.

Once a period of feeding activities has begun, *Astropecten* moves over the bottom, apparently more or less at random, until it senses a suitable prey. When the prey is situated on the sand surface the moment of perception of it may at times be clearly seen; the sea-star suddenly starts to move faster and the leading arm or arms are lifted somewhat (more) from the ground. If such prey is situated more than about 10 centimetres away the sea-star may now and then stop moving for a few seconds before continuing again.

The distance at which perception is possible must vary with a number of factors (see review by Feder & Christensen, 1966), but in general, *Astropecten* seems to be unable to determine the exact direction towards the prey unless within 10-15 cm of it, and this applies, furthermore, only to unburied prey. As Fenchel (1965) states, with reference to *Luidia sarsi,* this is probably because the sea-star is unable to register a difference in stimulation between the arm tips at greater distances. The statement implies that large sea-stars can locate a potential prey at greater distances than juvenile specimens.

Since a good number of *Astropecten* species are known to subsist mainly on infauna prey it is not surprising that they are able to detect the presence of them. This ability is known to exist even in such genera as *Asterias* and *Pisaster* which almost exclusively feed on epifauna organisms (Loosanoff & Shipley, 1947; L. S. Smith, 1961), Several observations similar to those recorded by Smith (op. cit). suggest that *Astropecten* is unable to detect the exact location of a buried prey organism unless it passes directly over its burrow. One may observe a moving sea-star suddenly stop, move a few mm or more backwards and proceed to dig.

The following example shows the efficiency with which an *Astropecten* may survey the bottom for food. A circular dish with a bottom area of about 500 cm^2 was supplied with a 1.5 cm thick layer of fine sand and running sea-water with a temperature of about 14°C. Then 100 newly settled *Spisula subtruncata* (0.68-1.32 mm long) were spread evenly over the sand and allowed to dig into it. At 17.00 hrs a young *Astropecten* ($R = 17$ mm) was placed in the dish. Next morning at about 9.00 hrs, 78 pairs of ejected empty shells were found, and all the remaining specimens were inside the sea-star. The empty shells of these were ejected in two lots later the same day. A similar experiment with 72 juveniles *S. subtruncata* gave about the same result, whereas only 35 out of 65 were found as empty shells after a third experiment lasting 20 hours.

A similar experiment undertaken under the same conditions, but with juvenile *Venus gallina* as prey, gave a quite different result. Only 24 specimens (0.62-0.74 mm long) were used, and four sea-stars were placed in the dish. Yet, after a period of 48 hours there were still 10 living *Venus*.

This shows that one should be very careful when choosing prey species for experiments designed to test the ability of prey perception and, of course, feeding rates.

SEIZURE AND INGESTION OF PREY

When a prey is located the sea-star moves into a position above it and proceeds to dig down over it. Seizure and ingestion cannot be observed under these circumstances, and this is probably the reason why these processes seldom are referred to. Schiemenz (1896) must have observed it, however, in the case of *A. auranciacus*, as he writes: "Er hält sich mit Vorliebe an Meerenstellen auf, wo der Boden aus mehr oder minder tiefen Sande besteht, in welchem er halb eingegraben seiner Beute nachgeht. Diese besteht vornehmlich aus ebenfalls im Sande vergrabenen Muscheln und Schnecken, die er mit seinen dehnbaren Füsschen sich in seine ausserordentlich erweiterungsfähige Mundöffnung schiebt." Since *Astropecten* will also ingest food in aquaria with no bottom substrate, this renders it possible to observe these processes either directly from underneath or indirectly by mounting a mirror at a 45° angle under any aquarium with a glass bottom. If a suitable prey organism is used, one may in most cases simply place the sea-star on top of it, whereupon the sea-star will proceed to ingest it immediately.

Using this method it was repeatedly observed that *Astropecten* handles any type of food items quickly and efficiently with its tube feet, in spite of the fact that they lack suckers. They are sticky, however, as can be seen when the sea-star climbs up the side of the aquarium walls. Even unicellular organisms, such as foraminiferans are handled with ease and pushed into the stomach with the adhesive tube feet or – in some cases – by a single tube foot.

The pointed tube feet are also adhesive enough to allow an *Astropecten* to pick up a fairly large molluscan prey from the glass bottom and push it into the stomach without the prey specimen ever touching the bottom again. In one case a sea-star was seen to pick up a one cm long *Spisula* and move a considerable distance with it, keeping it suspended between the inner tube feet. In another case a mediumsized sea-star picked up seven small *Spisula* before it settled down to digest them. As the bivalves were being picked up, the sea-star gradually assumed a position somewhat like the well known "humped up" position of a feeding *Asterias*. Whether a substrate is present or not, *Astropecten* may also attempt to clamp down on a prey under certain circumstances, viz. when newly settled, vivacious bivalves are offered to it, or in the rare cases when it tries to food on juvenile *Ophiura*.

When an *Astropecten* encounters a fairly large prey placed on a sandy substrate, it will normally move over it "like a tank" and start to dig into the substrate immediately while beginning the act of ingesting the prey. A similar behaviour was observed for *A.auranciacus* by Power (1857) and Mangold (1908). If offered several prey specimens simultaneously the sea-star may, however, "hump up" during the process of ingestion and rest only partly buried in the substrate afterwards.

The fact that *Astropecten* digs into the substrate for food poses the question as to how far down it may seize its prey. When examining the stomach contents of the Frederikshavn summer material, it was realized that all the bivalves occurring in significant numbers (Table 7), viz. *Mysella bidentata, Venus gallina, Spisula subtruncata,* and *Corbula gibba* were all suspension-feeders with short siphons. They hence belong to the fauna which lives close to the bottom surface, except for *M.bidentata* which very often is associated with deep-sitting irregular echinoids. However, most of these were probably not swallowed as living animals (p. 23). *Mya truncata,* which is known to sit deeply buried in the substrate, also occurred in fair numbers, but the specimens found were all juveniles (Table 13). In this stage they are known to creep over the bottom, attaching themselves temporarily with byssus threads (Kellogg, 1899). Only one deposit-feeder occurred in notable numbers, viz. *Nucula nitida,* a species which, however, live close to the surface, searching for food with its labial palps (see for example Hunt, 1925). On this background it seemed reasonable to suspect that the deep-sitting deposit-feeders *Tellina* and *Syndosmya* were scarse in the stomachs because *Astropecten* cannot dig deep enough to seize them.

To test the hypothesis the following experiment was carried out in the Frederikshavn laboratory. A large number of adult *Nucula nitida* and half-grown *Tellina fabula* were placed in four aquaria, each of which was equipped with a 10 cm thick layer of sand. After a period of 14 days the sea-stars began to swallow and digest the *Nucula* at a rate of one to three per day until the experiment was terminated 17 days later. In one of the aquaria all the remaining *Nucula* were removed after four days, but in none of the aquaria was a single *Tellina* taken during the experiment.

More precise experiments were carried out in Helsingør with the two deposit-feeders, *Macoma balthica* and *Tellina tenuis*, in aquaria with running sea-water (Table 17). First it should be noted that the sea-star very willingly fed on *Macoma* since two specimens ate all 25 *Macoma* present within 6 days in an aquarium where no substrate was present. Hence the reason why fewer and fewer were taken with increasing depth of substrate can only be due to an inability of the sea-star to dig deep and fast enough to seize the prey. As the result of one of the experiments shows, even a substrate depth of 2-3 cm seems sufficient to offer some protection for *Macoma*. The three specimens caught in experiments with more than 8 cm sand were no doubt caught during a temporary ascent to the surface (see p. 43).

However, another factor interacts with substrate depth, viz. the ability of certain bivalves, as e. g. *Tellina fabula*, to move quickly and sideways in the substrate when a sea-star attempts to seize them (p. 63). *Astropecten* cannot move sideways within the substrate and is unable to ascend to the surface when covered with too much sand (Schäfer, 1956). This was confirmed in experiments carried out with sifted sand as well as the somewhat finer, natural substrate from the Hornbæk Bay. Even adult sea-stars were unable to ascend when covered with a 3-4 cm thick layer of these substrates. In contrast to the vivacious *Tellina*, about a dozen *Mya arenaria*, 12 to 16 mm long, were all caught within a week by three medium-sized *Astropecten* in an aquarium with a substrate about 8 cm thick. This bivalve is a slow burrower and is unable to move sideways in the substrate. Specimens of the stated size may, furthermore, be expected to ascend to the surface quite often (cf. Kellogg, 1899).

The small aquaria used increases the possibility of a bivalve being trapped against the walls and also ensures more encounters between the prey and the predator than would be the case in nature, where at least the Tellinidae tend to be spaced out evenly with fewer individuals per unit area once they have grown into the macro-fauna stage (cf. Holme, 1961). The field data seem to confirm that deep-sitting deposit-feeders are protected from predation by *Astropecten*. It seems highly unlikely that such common species as *Tellina fabula*, *Syndosmya alba* and *Macoma calcarea* should all the absent or scarse at one and the same time,

TABLE 17. The influence of substrate depth in aquaria on the ability of *A. irregularis* to seize deep-digging bivalves. The experiments marked with an asterisk were done in April-May 1961 with unfed bivalves; the others in October 1968 with fed bivalves. The R of the sea-stars ranged between 32 and 40 mm. The temperature was 14-15°C.

Duration of exp. in days	Number of sea-stars used	Depth of sand in cm	Species of bivalve(s) used	Size range in mm length	Number of bivalves offered	Number of bivalves eaten
6	2	0	*Macoma balthica*	5.4-13.5	25	25
8*	2	2-3	*Tellina tenuis*	11.3-17.3	8	6
5	3	2-3	*Macoma balthica*	6.5-11.5	25	13
			Tellina tenuis	13.7-15.0	3	1
8	2	8	*Macoma balthica*	3.5-13.0	30	6
39*	2	10	*Macoma balthica*	7.5-9.0	8	2
			Tellina tenuis	11.2-13.3	2	0
8	3	12	*Macoma balthica*	5.8-12.7	35	1

and that this should happen in both the major collecting localities, viz. off Frederikshavn in the Kattegat (Table 7) and in the Øresund (Table 10). Further support for this hypothesis came from 22 *Astropecten* sampled in the Øresund at a locality where Dr. Kirsten Muus had taken quantitative samples of the meiofauna the day before (Table 33). Deposit-feeders were practically absent in the *Astropecten* stomachs although they were very abundant in the bottom. The fact that the same was the case also for many of the suspension-feeding bivalves is due to a more or less pronounced "dislike" for these species (p. 61).

The reason why a few Tellinidae often are found in samples of *Astropecten* (Eichelbaum, 1909; Blegvad, 1914; Hunt, 1925) is probably that these bivalves come to the surface and move around to exploit the bottom more effectively for food or for other reasons (Yonge, 1949; Brafield & Newell, 1961). When a species is especially abundant, this will in itself increase the possibility of *Astropecten* encountering it on the surface, and the increased competition for food is, furthermore, likely to bring each individual specimen to the surface more often.

The suspension-feeding *Cultellus pellucidus* was rare in the Frederikshavn material. It has very short siphons and is hence situated fairly close to the bottom surface, but may escape from enemies by quickly retiring into its burrow or by digging further down (Ansell, 1962). Observations in the laboratory showed that *Cultellus* did not escape from being swallowed in the long run in any substrate depth, unless the specimens were so large that the sea-star would encounter difficulties in swallowing them. However, according to personal information from Dr. Ockelmann, the nature of the substrate may greatly influence the ability of Solenidae to dig efficiently (see also Trueman et al, 1966). And although all the *Cultellus* taken by *Astropecten* in the laboratory had dug into the sand as well as "natural" substrate with apparent ease they may not have been able to dig further

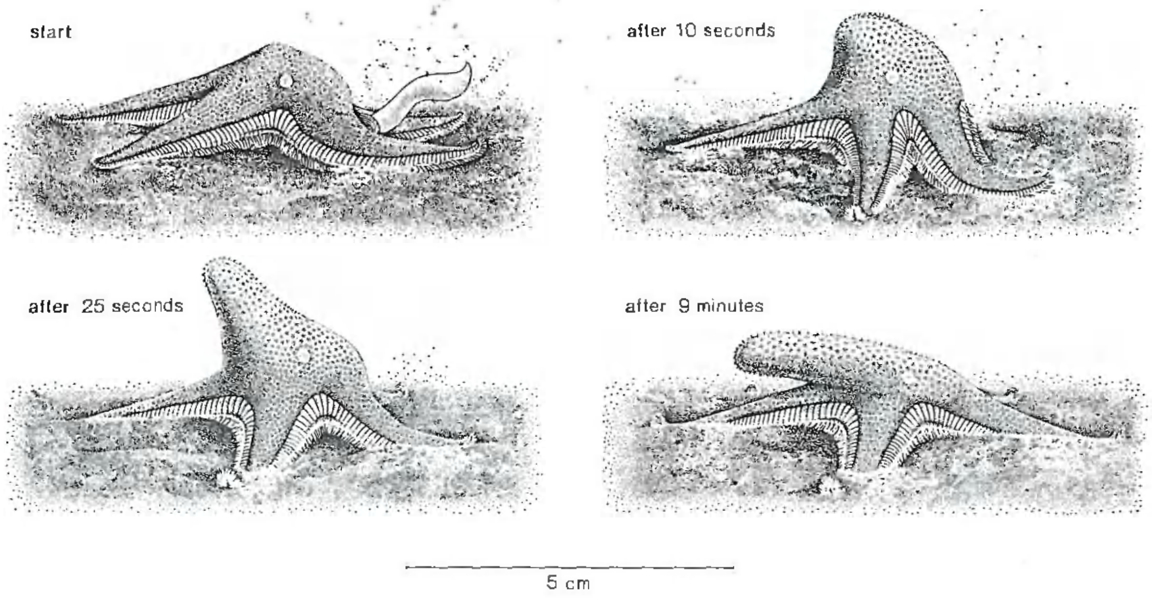


FIG. 5. *Astropecten irregularis* ingesting a *Cultellus pellucidus.* Drawn from life by Kai Olsen.

down with the same efficiency and speed as in nature. Some field data would seem to support this conclusion.

On 4 and 5 July 1960, hundreds of *Cultellus,* mostly between 5 and 12 mm long, were found in dredge hauls made in the Hornbæk Bay (depth: 16-21 m). In spite of this only a single specimen was found in 70 *Astropecten* collected on the same ground on 21 and 22 June and none at all in 48 specimens collected on 20 July. Furthermore, only 5 *Cultellus* were found in 22 *Astropecten* collected at a station where more than 600 of these clams were present per square metre (Table 33).

All the specimens of the related *Ensis* sp. found in *Astropecten* taken in the North Sea (Tables 3 & 5) were less than one mm long and, therefore, without doubt too small to be able to escape by digging.

In the dredge samples mentioned above hundreds of juvenile *Syndosmya alba* (2-6 mm long) were also present, yet only few were taken by *Astropecten* during the summer and fall of 1960 (Table 10).

Surprisingly large prey may sometimes be pushed through the highly extendable mouth opening, but successful ingestion is in these cases also dependent on the extraordinary elasticity of the stomach and the dorsal body wall. Fig. 5 shows how an *Astropecten* swallows a *Cultellus pellucidus* as long as its own radius (R). I have also observed an *Astropecten* with an R of 40 mm seize and swallow a 25.3 mm long *Macoma calcarea.*

The importance of the ability to swallow large organisms should not be overestimated, however, since the sea-star displays a decided tendency to choose prey of small size. The largest bivalve ever found in an *Astropecten* was a 17.6 mm long *Venus gallina.* It is conceivable, however, that local faunistic conditions may force *Astropecten* to swallow larger prey than is normally the case. Off the

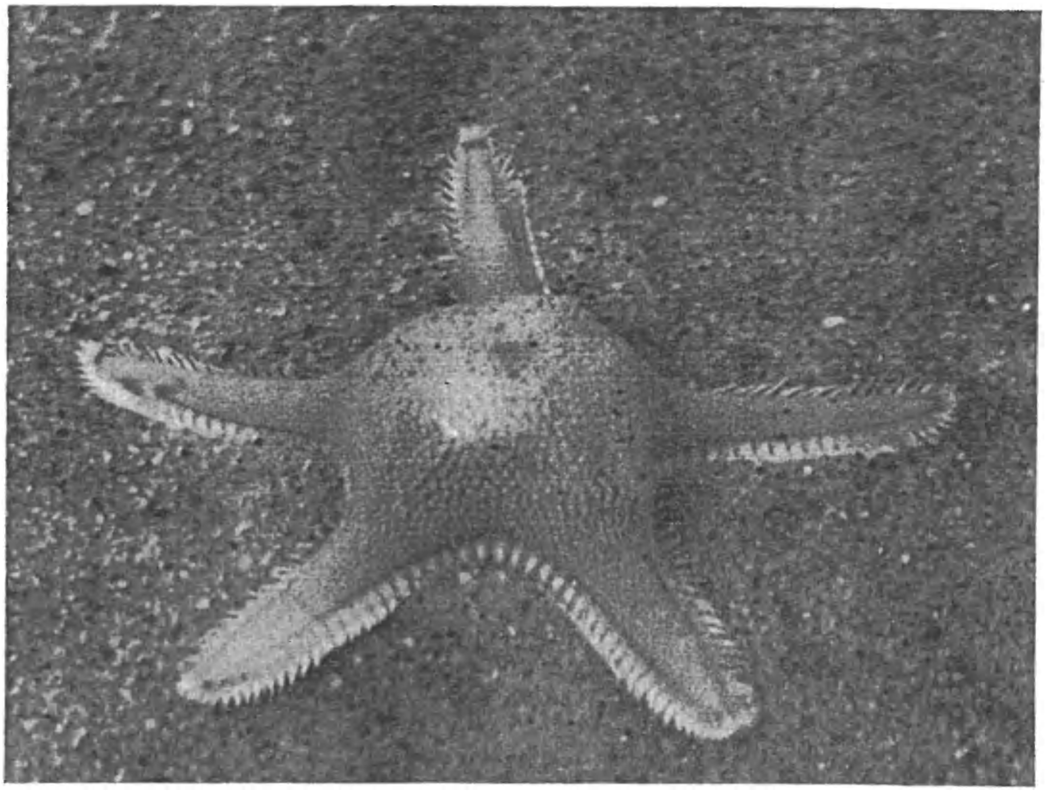


FIG. 6. *Astropecten irregularis* with a highly distended dorsal side caused by the swallowing of as large number of bivalves (cf. text). Photo, H. Knudsen.

Dutch coast fairly large specimens of the deposit-feeding *Donax vittatus* may be swallowed (Lems, 1951 & personal communication). This bivalve may come to the surface due to wave action and other causes, and it must be in this situation that it is caught even though it is very vivacious and capable of burying itself again with amazing speed (see Yonge, 1949; Ansell & Trevallion, 1969).

If prey specimens are accumulated in a heap, *Astropecten* may sometimes swallow so many that the elasticity of the stomach and the dorsal wall shows clearly up. Fig. 6 shows an *Astropecten* (R = 35,4 mm) which within 20 minutes swallowed nine *Nucula nitida* (8.8 to 10.5 mm long) and one *Cyprina islandica* (12.4 mm long). A similar case was never observed in any field material, but it has apparently been seen by Schäfer (1956).

Whereas it has been repeatedly observed that the stomach may be slightly everted in connection with the ejection of indigestible remains, there is no definitive evidence to show that it may be used either independently or as an aid in picking up food items through the mouth opening. Anderson (1954) implies that Cuenot (1891) and Ludwig (1899) have observed this, but I have been unable to find any statement to this effect in the cited papers. Prenant (1936) is likewise in error in citing Schiemenz (1896) for having this opinion. Bouchet & Le Campion (1962) state, however, that *A. irregularis*, although not very often, seems to evert

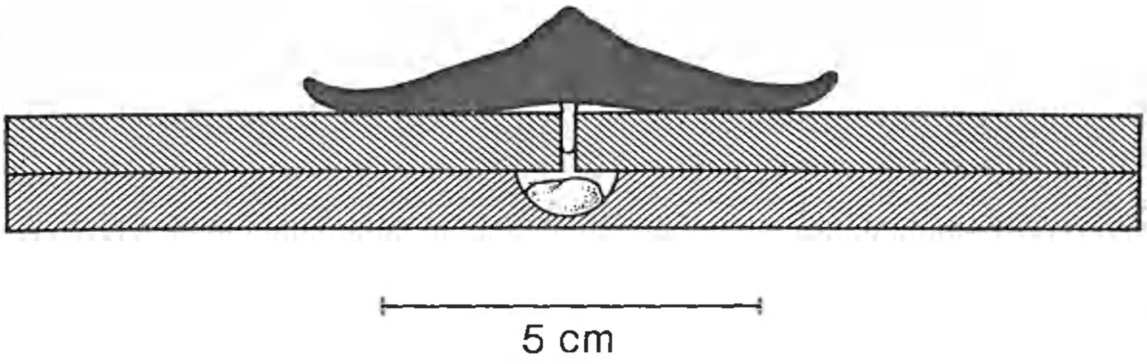


FIG. 7. Schematic drawing of *A. irregularis* with stomach lobe extending into a narrow hole, which leads to a chamber containing *Mytilus* meat (cf. text).

its stomach and bury it in the bottom underneath it. They make the suggestion that it may pick up micro-organisms in this manner.

This possibility was tested by use of a simple chamber filled with molluscan meat, which only could be reached through a narrow tube (Fig. 7). *Astropecten* did in fact in a number of cases evert a stomach lobe through the tube to the enclosed meat, but no digestion was observed. In a few cases, *Astropecten* has also been observed to evert its stomach slightly over bivalves on the half-shell, which were too large to be swallowed. In some of these cases the sea-star succeeded in picking up lumps or threads of disrupted tissue and push it through the mouth opening with its tube feet. Again, however, one cannot say with certainty whether any extraoral digestion took place, nor whether the stomach was used as an aid in picking up the food. I believe, however, that any successful attempt of extraoral digestion could not have escaped notice.

As indicated earlier, the speed of ingestion may be rather rapid, considering that any prey must be manipulated in position for swallowing and then pushed through the mouth opening by tube feet lacking sucking discs. As shown in Table 18, an ingestion period of one or three minutes is common for molluscan prey of a considerably larger size than those normally swallowed in nature (Tables 13 & 14). The ingestion period is here understood as lasting from the moment when a sea-star starts to handle the prey to the moment when the mouth opening is completely closed behind it. In all cases the sea-star was placed directly on top of the prey, and no sand was present in order to facilitate observations from beneath.

It is believed that prey can be swallowed faster under more natural conditions when the sea-star is able to move downwards over the prey while at the same time opening the mouth to admit it. Although it has not been directly observed – for obvious reasons – that the sea-star continues to guide and push a food item through the mouth opening with the inner tube feet while using the others for digging, this is without doubt the case. When one lifts an *Astropecten* out of the substrate under the mentioned circumstances it is always found holding on to the

TABLE 18. Time used by *Astropecten irregularis* to ingest different prey species in aquaria without sand.

Name of prey species used for experiments	Number of experiments	Length range of prey specimens in mm	Mean length of prey specimens in mm	Range of R (longest arm) of *Astropecten* in mm	Mean R of *Astropecten* in mm	Time range of ingestive process in seconds	Mean length of ingestive process in seconds
Nucula nitida	5	4-10	8	17-42	35	47-242	158
Cyprina islandica......	6	12-17	14	37-42	38	107-299	203
Venus gallina	5	9-13	10	37-41	39	162-352	264
Tellina tenuis	7	7-14	11	33-46	38	66-316	176
Cultellus pellucidus ...	3	17-27	22	32-46	39	118-545	269
Spisula subtruncata ...	12	10-16	13	37-47	42	100-765	240
Corbula gibba	3	7-9	8	28-43	34	62-158	119
Natica spp.	5	13-15	14	39-42	40	100-249	161
Echinocardium	7	9-12	10	33-42	38	92-689	321
Average for all 53 experiments			12		38		212

prey. It is also well known that individual or localized groups of tube feet can orientate and move independently of the remaining tube feet (J. E. Smith, 1950). Another advantage is also evident; prey such as bivalves situated naturally in the substrate will nearly always be more favourably oriented for swallowing by the sea-star than prey lying flat on a hard surface. In the laboratory it has been observed that some large specimens of *Cultellus* and *Macoma calcarea* which could not be handled when lying on a glass bottom were taken after being allowed to dig into 5-6 cm deep sand.

As earlier mentioned, *Cultellus* will try to escape by digging further down. Most bivalves, including the Veneridae, react, however, to danger by withdrawal of the siphons followed by shell closure (Ansell, 1962), a behaviour which offers no protection against *Astropecten*. Others, like *Spisula*, spp. exhibit a very characteristic escape response (see Feder & Christensen (1966) for references), but this does not seem to protect them against predation by *Astropecten* in the laboratory, nor in nature as far as juvenile specimens are concerned. The reason for this seems to be that an effective jump can only be carried out when the bivalve comes to the surface of the substrate, and the sea-star is in most cases over it too fast to allow this to happen. Adult *S. subtruncata* have, however, been observed to push even adult sea-stars up and escape from underneath.

DIGESTION OF PREY

In the laboratory it was soon found that *Astropecten* discriminated between the prey species present, and that the time it took before empty shells were ejected differed conspicuously for the different prey species. Whereas medium-sized *Spisula subtruncata* swallowed during the afternoon were digested and the empty shells found ejected next morning, odd specimens of such bivalve genera as *Venus, Corbula,* and *Astarte,* when swallowed at all, remained in the sea-star stomach for many days. Intriguing, moreover, was the fact that these bivalves in a good many cases came out fully alive after a prolonged sojourn in the stomach.

Since these phenomena also must exist in the sea it was decided (1) to determine the average periods needed for *Astropecten* to "digest" individuals of various sizes of prey species commonly found in their stomachs, and (2) to examine the state of digestion of all bivalves found in specimens collected in the field. The word "digest" is put in quotation marks to denote that it refers to the time between the moment of ingestion of a prey specimen to the moment of ejection of the indigestible remains. This period is here called the *retaining period.*

The retaining period

The fact that certain bivalves and prosobranchs may be retained for up to 2-3 weeks before the empty shells are ejected shows that the retaining period and the digestive period constitute two different concepts. The latter depends on temperature, the amount and kind of organic matter to be digested, and on how much of this the stomach wall of the sea-star may contact simultaneously. The retaining period depends on the duration of three phases, namely (1) the period between ingestion and start of digestion, (2) the digestive period, and (3) the period between the end of digestion and the ejection of the indigestible remains.

Many intertidal barnacles may close tightly and stay alive for many days out of water, and *B. balanoides* (size unknown) seems capable of surviving in deoxygenated water for at least ten days at 6-8°C (Dodgson, 1928). It was, therefore, tested how long *B. improvisus* may avoid being digested when taken by *Astropecten.* Six *Astropecten* were each offered a small piece (1-1.5 cm^2) of *Fucus serratus* with attached barnacles (base diameters between 0.9 and 4.2 mm) at a temperature of 10-11°C. Two pieces were ejected after about 24 hours with all (23) barnacles completely unharmed and with about 15 harpacticoids and halacarids crawling among empty *Membranipora* boxes. The third piece was ejected after 42 hours with all (21) barnacles alive. The fourth piece was ejected after about 72 hours with six live, two dead but undigested, and three digested barnacles. The 5th piece was ejected after about 114 hours with nine live and four digested specimens. The last piece, ejected after maximally 139 hours, had only one live barnacle, while seven were dead but undigested, and six had been eaten.

TABLE 19. Duration of time between ingestion of various prey species and subsequent ejection of indigestible remains in *Astropecten irregularis*. All experiments were carried out in aquaria without substratum.

Number of specimens tested	Prey species tested	Size range of prey in mm	Water temp. in °C	Range of retaining period in hours	Mean retaining period in hours
20	*Spisula subtruncata*	0.8- 1.3	13-15	7-11	9
13	*Spisula subtruncata*	2.8- 4.2	10-13	6-12	9
30	*Spisula subtruncata*	10.0-19.8	10-15	13-47	22
4	*Montacuta ferruginosa*	4.5- 5.3	16-17	12-19	15
32	*Spisula elliptica*	8.3-19.0	10-12	19-52	33
15	*Mya arenaria*	3.3- 5.2	15-17	7-15	10
6	*Mya arenaria*	9.3-15.5	11-12	25-74	39
6	*Cultellus pellucidus*	4.8- 8.5	14-15	5-6	6
6	*Cultellus pellucidus*	17.0-32.3	11-15	19-29	22
40	*Nucula nitida*	5.5-11.3	11-12	35-104*	64
8	*Cyprina islandica*	6.7-10.8	11-15	22-64	45
5	*Cyprina islandica*	12.5-17.4	10-15	110-311	181
5	*Venus gallina*	0.8- 1.2	13-15	28-117	61
7	*Venus gallina*	3.2- 5.8	12-16	31-205	88
10	*Venus gallina*	6.2-12.5	11-15	38-456	237
7	*Corbula gibba*	0.8- 1.0	15	-	17
6	*Corbula gibba*	6.2- 8.7	10-15	83-512	350
9	*Pectinaria koreni*	20.0-32.4	11-15	18-69	34
2	*Natica pulchella*	6.7- 9.5	10-13	65-157	111
4	*Natica pulchella*	10.0-15.1	10-15	242-362	286
6	*Echinocardium cordatum*	9.1-13.5	15	29-37	32

* In two cases the period was about 11 days, and in one case the *Nucula* was found fully alive after 13 days in the stomach; these cases are not included in the table.

A number of similar experiments with various prey species were carried out, especially with bivalves which constitute the main food of the sea-star.

Before discussing the results (Table 19) it should be pointed out that whereas the moment of ingestion could be accurately recorded, the moment of ejection of the indigestible remains in most cases had to be arbitrarily fixed as having taken place halfway between the last two checks. During normal working hours this period was seldom longer than two hours and most often much less, but in those cases where ejection took place during the night it was 8-10 hours. However, by starting the experiments at appropriate times for those species already known to be retained for relatively short periods, night ejections were largely limited to experiments with species normally retained for more than 24 hours. This made the error small in comparison with the rather extensive ranges in retaining periods recorded for most species.

Temperature-controlled experiments could not be carried out because sea-stars kept in standing, aerated sea-water did not thrive well. It is to be expected, however, that the retaining period will be more or less prolonged at low temperatures, partly because the digestive process itself must be affected, and partly because the ability of the prey to withstand anaerobic conditions will increase

Apart from difficulties in securing specimens of appropriate sizes, serious difficulties arose when trying to induce the sea-star to swallow specimens of *Cyprina*, *Venus*, *Corbula*, and *Natica*. This often took hours and more often than not the sea-star totally "refused" to do it. When a specimen of *Cyprina* was finally swallowed, it was in most cases also retained and digested, whereas specimens of *Venus* and *Natica* in most cases were ejected alive after a shorter or longer time. It was usually much more difficult to induce an *Astropecten* to swallow *Corbula* of macro-fauna size than equally large *Venus*, but they were not so commonly ejected alive. A comparison between the data in Table 31 and Table 32 indicates that this is true also for newly settled individuals.

In spite of the wide range in retaining periods for individual species, and the limited number of experiments in certain cases, the results presented in Table 19 leave no doubt that great differences exist between the species with respect to the mean retaining period. Apart from the general observations referred to earlier, direct and indirect evidence confirming this may also be found in the field data (p. 54) and the data derived from experiments on prey selectivity (p. 61). It may further be noted that the retaining period for the bivalve species tested increases in the reverse order to the degree of attractiveness of the species (cf. section on prey selectivity). For the individual species it usually also increases distinctly with size.

Whereas all sizes of *S. subtruncata* will be digested and the empty valves ejected within 24 hours, adult *Corbula* at the other end of the preference list are on an average retained for 14-15 days and may be retained for as long as 3 weeks at least. In one experiment two *Astropecten* were each fed with a *Corbula*, 8.0 and 8.7 mm long respectively, and after 21 days the bivalves were removed from the sea-stars through a slit made on the dorsal side and found to be fully alive. Incidentally, both sea-stars recovered from the operation and began to feed again about one month later. Newly settled *Corbula* are, however, retained for a significantly shorter time than newly settled *Venus*.

The stated tendency of *Astropecten* to eject certain bivalves alive raises the question whether the data on retaining periods in Table 19 in all cases are reliable. Although frequent checks were made it cannot be excluded that a prey specimen might have been ejected at night and picked up again before the next morning, but ejected live specimens were in fact most often found in the morning. However, I think the data are reliable. The data given in Table 20 show, moreover, that these species are capable of surviving anaerobic conditions for a much longer time than they have been retained in a sea-star stomach in the laboratory.

The fact that newly settled individuals of any species are retained for a shorter time than larger specimens was to be expected. However, the size-dependent differences in retaining periods for such species as *Venus gallina* and *Corbula gibba* shown in Table 19 are clearly so great that they cannot be explained simply by the different amounts of organic matter to be digested.

As has been hinted at earlier, the explanation for the phenomena recorded in Table 19 and other data given above must lie in a varying ability of ingested bivalves to sustain the conditions to which they are subjected once they are enclosed in a stomach fold of the sea-star. In this situation a bivalve will not be able to obtain any oxygen. However, as long as it can keep its valves tightly appended it cannot be digested, and the same applies to prosobranchs which possess a tightly closing operculum.

Although different species may exhibit a similar ability to withstand anaerobic conditions in sea-water they may well differ with respect to the time at which they first start to gape for any length of time. When held in a stomach pouch with no access to oxygen, it is of course the latter factor which is important.

Salanki (1966) studied the effects of KCl, $CdCl_2$ and gradual reduction of the oxygen content on shell movements in 12 bivalve species at Naples. It appears that different species react differently and that essentially three types of behaviour exist with respect to shell movements. In all cases he found that three species, viz. *Cardium tuberculatum*, *Ensis ensis* and *Pecten jacobaeus*, were unable to keep their valves closed for any length of time. This corresponds well with my findings, in so far that *Cardium edule* must be digested rather quickly (Table 12) and that *Cultellus pellucidus*, a close relative of *E. ensis*, exhibits a very short retaining period and was directly observed to gape widely shortly after being ingested by *Astropecten*. Among the other bivalves tested by Salanki only *Venus verrucosa* is related to a species of importance in the present context. This species may keep closed for 1 to 5 hours between periods of shell movements, and whereas *Cardium*, *Ensis* and *Pecten* died after some days (t = 21-22°C), *Venus* survived. All of this is in agreement with my own findings on related species. A third group of bivalves tested remained in the closed position for several days, showing a few active periods only before death. None of the genera belonging to this group were used in the present investigation, but it is feasible that *Corbula gibba* behaves in this manner (p. 54).

Of special interest is that Salanki's four species mentioned above each showed the same behaviour in all three types of experiments since a bivalve swallowed by an *Astropecten* is not only unable to obtain oxygen, but is also subjected to compounds released from the stomach wall.

It is, furthermore, evident that the extent of the gape, which also differs in different species (own observations), influences the length of the retaining period. In this connection it should be mentioned that Feder (1955) found that about 15 species of Californian clams with supposedly tight-closing valves actually have permanent openings in the posterior end large enough (0.1 mm or more) to allow *Pisaster ochraceus* to insinuate a stomach lobe. These openings are, however, (Feder, op. cit.) partially blocked by the pliable periostracum, and this must be pealed back by the sea-star before stomach intrusion can take place. *Astropecten* has no possibility of doing this, quite apart from the fact that the clams studied by Feder were very much larger than those ever taken by *Astropecten*.

Since newly settled specimens of a given species have a higher metabolic rate per unit body weight than larger specimens, and since this rate may be assumed to be more or less inversely correlated with their ability to sustain anaerobic conditions, it is understandable that juvenile *Corbula* on an average are retained for only 17 hours whereas the corresponding figure for adults is 14 days.

Prey species as *Cultellus pellucidus* which – regardless of size – exhibit permanent openings between the valves are, of course, susceptible to digestion immediately after being swallowed. This must be the main reason for the conspicuously small differences in retaining periods of specimens of *C. pellucidus* varying in length from 4.8 to more than 32 mm, but the fact that it gapes widely shortly after being ingested certainly plays a large role too. In this case it is, therefore, mainly the varying amounts of digestible matter which determine the length of the retaining period.

Since it is assumed that the differences found in retaining periods of bivalves with tight-closing valves are due mainly to a varying ability to sustain anaerobic conditions, it is of interest to see whether published data on species actually used in the present study supports this supposition.

Nikitin & Turpaeva (1957) tested the ability of *Spisula subtruncata* and *Venus gallina* to withstand anaerobic conditions at considerably higher temperatures than those found in the Helsingør laboratory. They were as high as 21-22° C for *Spisula* and 22-24° C (occasionally 27-28° C) for *Venus*. They found that an oxygen concentration below 0.5 mg/l was lethal for *Spisula*, i.e. they died as soon as the steadily decreasing concentration reached that level. *Venus*, on the other hand, could withstand a steadily decreasing concentration below the mentioned level for 10 days, and when they finally died, there was no oxygen left in the water. The related *Venus mercenaria* is also known to have a conspicuously low oxygen requirement (Mitchell, 1914). It may endure anaerobic conditions for as long as 16 days at 20° C, and for at least 35 days at only 5° C (Dugal, 1939). Dunnington (1968) found that the oyster (*Crassostrea virginica*) would survive under anaerobic conditions for 5 weeks or more at 5° C, whereas 18 out of 36 oysters died within 4 days at 25° C, and only one survived for a week. According to Dugal (op. cit.) the bivalves apparently resort to a glycolytic type of anaerobic metabolism, using the calcareous shell to buffer the resulting production of organic acids.

Brafield (1963) found *Macoma balthica* to be relatively intolerant of anaerobic conditions as it generally only survives 2-3 days (at room temperature?). This fits well with the observation (Table 17) that an *Astropecten* may accomplish to digest at least 12-13 medium-sized specimens within 6 days.

TABLE 20. Survival times of certain bivalve species in sea-water under anaerobic conditions. The initial oxygen concentration was 0.18-0.37 mg O_2/litre except for the experiments with *S. elliptica* where it was 0.52-0.68 mg O_2/l. Temperature 10-11°C. The maximum number of animals kept in one jar was six.

Species	Number tested	Size range in mm	Survival period in days
Spisula subtruncata	5	4.0- 6.8	2-3
Spisula subtruncata	15	7.0-12.0	2-5
Spisula elliptica	8	10.2-17.5	8-13
Nucula nitida	9	6.0-10.0	9-23
Cyprina islandica	9	4.5-12.0	28->57[1]
Venus gallina	6	6.0- 7.0	21-37
Venus gallina	4	13.0-14.5	24-28
Astarte montagui	5	4.0- 7.0	27-36
Corbula gibba	14	5.0- 8.0	47->57[2]

[1] One specimen was opened after 57 days and found to be alive.

[2] Nine ungaping specimens were after 57 days placed on a sandy substrate in a small aquarium wit running sea-water. One week later all had dug into the substrate.

These data and those of Salanki (1966) clearly demonstrate that there may be great differences in resistance to anaerobic conditions between different species, and that the duration of survival is highly dependent on the temperature level (see also Brand, 1946, Table 12).

Since information was lacking or meager on other species of interest to the present work, some experiments were carried out on the more important ones including also *S.subtruncata* and *V.gallina*. The reason for including these two species studied by Nikitin & Turpaeva was that the Black Sea populations could have differed physiologically from those found in the Øresund.

The method used has been described earlier (p. 10). From four to eight specimens were placed in each jar. The oxygen content at the start of each experiment was found to lie between 0.18 and 0.68 mg/l, i. e. it was negligible. The temperature at which the experiments were carried out (10-11°C) is close to the highest temperatures encountered where *Astropecten* has its main distribution in the Øresund. In the Kattegat collecting areas, however, the temperature exceeds 10° during June-October with a mean temperature for the warmest month (August) of 15-16° (Brattström, 1941, Table 16).

The results are shown in Table 20, with the species listed in order of increasing resistance to anaerobic conditions.

A considerable variation in survival time was found for most of the species. Generally, the largest specimens tested survived for the longest period, but exceptions occurred. *Corbula gibba* was never observed to gape prior to final death. However, due to the different morphology of the two valves and the presence of a marginal periostracum, a very slight gape may escape detection.

Most important, however, is the fact that there is a good correlation between retaining periods and abilities to survive anaerobic conditions (cf. Tables 19 & 20). It is true that the survival period for a given species in deoxygenated water is much longer than its retaining period, but this is to be expected. One reason for this is that temperatures differed in the two types of experiments, but the main reason is that a bivalve in practically all cases will start to gape long enough to allow stomach insertion long before it would die if left undisturbed.

That juveniles of a given species will suffocate sooner than adults is obvious, but even within the same size group rather wide ranges in the retaining period may occur. This is probably mainly due to three factors, viz. (1) that some specimens used may have been somewhat weakened and hence not as resistant as physiologically fresh animals; that (2) empty shells are not ejected "automatically" as soon as their contents have been digested, and (3) that not all experiments with the same species were done at the same temperature.

Among these factors the first mentioned is likely to affect species with a high metabolic rate sooner than others. The second factor does not seem to be completely independent of species either (p. 60). The effect of the third factor is obvious, but it may be added that the temperature in the Øresund, but not off Frederikshavn, is as low or lower during the main feeding season than the temperatures at which the experiments on retaining periods were carried out in the laboratory.

As already inferred, some of the prosobranchs found in the stomachs of *Astropecten* are also capable of withstanding a lack of oxygen for a considerable time. This was also noted by Kisch (1958) who observed that three different species were fully alive and unharmed after having spent at least 48 hours inside an *Astropecten* stomach. I have seen *Natica* spp. be ejected alive at least 80 hours after being swallowed. As noted in Table 19 the retaining period for *Natica pallida* may be as long as 14 days for larger specimens. It should be emphasized that the retaining period in these and other cases involving larger prosobranchs with normally coiled shells may be somewhat influenced by the difficulties in inserting a stomach lobe into the upper windings of the shell. If one drills a hole in the shell of a medium-sized *Natica pallida,* the sea-star will digest all soft parts and eject the empty shell within 24 hours.

State of digestion in field material

Since the retaining period varies so much for different species, it was to be expected that this fact would also manifest itself when the state of digestion of the bivalves found in *Astropecten* collected in the field was examined.

The stomach contents of the sea-stars collected at Frederikshavn (Tables 7

TABLE 21. The state of digestion of some bivalves found in the stomachs of 322 *A. irregularis* taken in the Kattegat off Frederikshavn in June-July 1953 and in 1068 specimens taken in the Øresund in 1960-1962.

Bivalves	Locality	Total number found	Number investigated	Number found digested	Number digested in %	Remarks
Spisula subtruncata .	Kattegat	1360	all	733	46.1	Only 80 specimens less than 2 mm long.
	Øresund	8775	7705	5113	66.3	Nearly all less than 2 mm long.
Mya truncata?	Kattegat	100	93	35	37.6	59 less than 2 mm long.
	Øresund	831	817	57	68.2	658 less than 2 mm long.
Venus gallina	Kattegat	858	all	33	3.8	Only 80 less than 2 mm long.
	Øresund	47	all	6	12.8	44 less than 2 mm long.
Corbula gibba	Kattegat	262	all	18	6.9	Only 43 less than 2 mm long.
	Øresund	135	all	41	30.4	61 less than 2 mm long, 39 of the 41 digested less than 1 mm long.

& 8) had been identified, measured and placed in individual tubes long before this suspicion arose. A re-examination of the material showed (Table 21) that not far from half of the *Spisula* and over one third of the *Mya* were digested, as against only 6.9 % of the *Corbula* and 3.8 % of the *Venus*.

The validity of these data depends, of course, on whether the bivalves originally were removed from the sea-star stomach in such a manner that any undigested meat were retained within the shells. As practically all undigested *Venus* and *Corbula* were found tightly closed and had to be probed open with a scalpel, these species presented no problem. The *Mya* were usually found slightly gaping, but the soft parts, when present, seemed to adhere rather well to the shells. Only *Spisula* gave reason for some doubt. Unless completely undigested they were often found gaping considerably, and the soft parts have been observed to "fall out" rather easily.

However, Table 21 also gives the data on the same species found in *Astropecten* collected in the Øresund, and with this material care was taken to note the state of digestion when the bivalves were removed from the stomachs. It will be seen that 66 % of the *Spisula* were found digested as against "only" 46 % of the Kattegat specimens. There is, therefore, hardly any reason to suspect that a significant number of the Kattegat specimens has been wrongly registered as having been digested. The percentage of digested specimens in the Øresund material was also higher for the other three species, but this was to be expected for at least two reasons. The Kattegat specimens were significantly larger, and their ability to resist anaerobic conditions must, therefore, have been higher. Although this factor cannot have played any real role for *S. subtruncata* (cf. Table 19) the larger volume of meat must have effected the digestive period *sensu stricto*. Furthermore, the Frederikshavn material was collected in the early morning before and around sunrise, whereas the Øresund material was collected mainly between 8.20 a.m. and 11.30 a.m., and on some occasions even in the afternoon. Since *Astropecten* feeds mainly at twilight hours it is to be expected that one finds more digested prey in specimens taken during the last mentioned periods of the day. This must especially be true during high summer when daybreak occurs around 4 o'clock in the morning.

Handling of food items in the stomach

A swallowed bivalve will under all circumstances sooner or later open up for shorter or longer periods. It is conceivable, however, that openings of short durations are not detrimental. This is primarily because the prey is not lying in a pool of gastric juice containing digestive enzymes or toxic substances. Already Conheim (1901) stated about stomachs carefully dissected out of *Astropecten auranciacus:* "Fürht man feste Nahrung in den Magen ein, z. B. zerschnittenes Musselfleisch oder Fibrin, so wird es nicht verdaut, da die Fermente nicht in den Magen gelangen«. Many years later, Anderson (1959) provided experimental evidence that no enzymes are produced in the stomach wall of *Patiria miniata,* but in the pyloric caeca, and this is probably true for all sea-stars. Digestive enzymes must be brought to the site of digestion by ciliary currents (see discussion in Anderson, 1966). Burnett (1960) found that although three clams had suffered partial digestion of their mantles after *Asterias forbesi* had had the opportunity to secrete digestive juice into the clams for two hours through a 1 cm^2 opening covered with bolting cloth (mesh size 40 μ), all other organs were completely unharmed and functional. A fourth clam was completely unharmed at the end of the experiment. This clearly indicates that a swallowed bivalve may open up a considerable number of times for short periods without being seriously harmed.

On preserved material it was observed that *Astropecten* handles food items by the non-everted stomach in the same manner as an *Asterias* or an *Evasterias* handles food with their everted stomachs (A. M. Christensen, 1957). A bivalve, for example, is held in a pouch of the stomach wall from which a fold or folds are insinuated in between the valves to contact as much of the internal tissue as possible. Especially in sea-stars preserved in formalin one may see spiral-formed lobes of the stomach wall protruding whereever a prosobranch or a pyramidellid snail is removed (see Fig. 8). Even such tiny animals as foraminiferans are digested

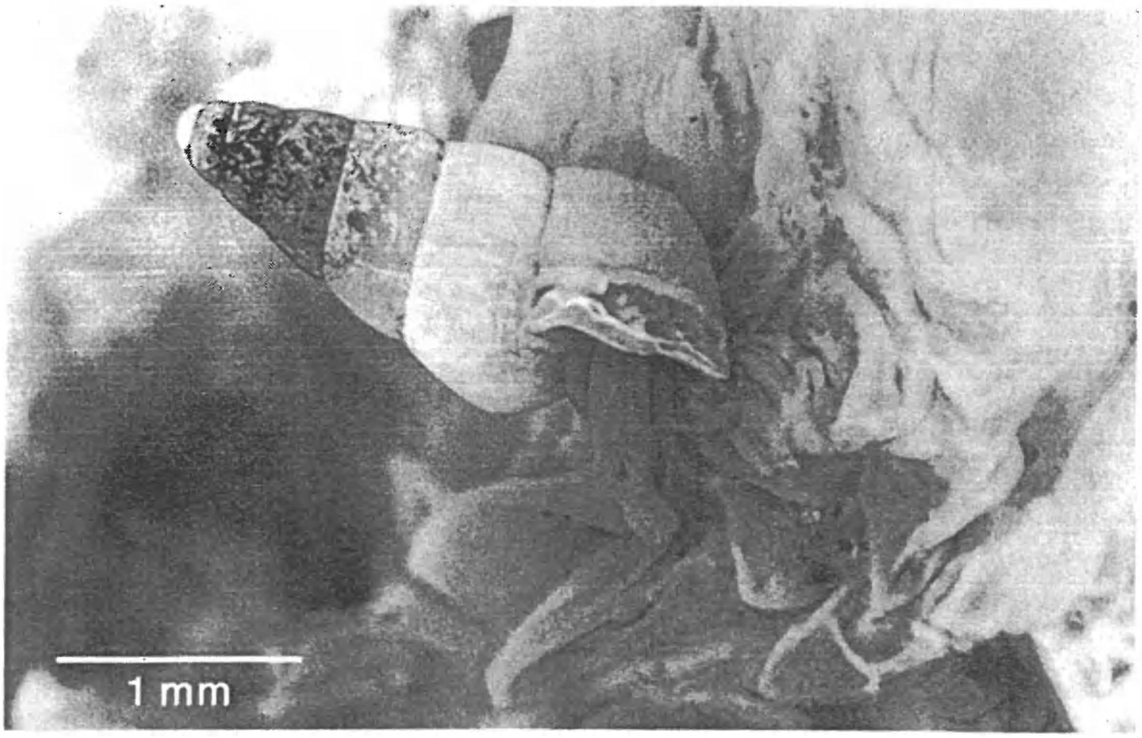


FIG. 8. *Odostomia* sp. in stomach of *A.irregularis*. Note lobes of stomach entering through the aperture. Photographed from preserved material by H. Knudsen. Slightly retouched.

by stomach entrance. Dr. W.C.Austin (personal communication) observed the same phenomenon in a number of *A.californicus* collected in Monterey Bay. In one specimen a fold of the stomach was found inserted between the valves of a swallowed *Nucula taphria*, inside of which the fold was expanded into a bulb.

Evidently, digestion takes place only where the stomach lining is in close contact with digestible tissue of the prey as is also the case for sea-stars with extraoral digestion (A. M. Christensen, 1957). Prey specimens found lying freely in the stomach of recently captured sea-stars, or in specimens preserved immediately upon capture, are also either completely undigested or consist only of indigestible remains, whereas prey removed from enfoldings of the stomach wall may be found in any state of digestion. Further proof was furnished by examining the state of digestion of large prosobranchs after ejection. In one case, for example, an *Astropecten* with an R of 39 mm after a long period of starvation swallowed a 15.1 cm long *Natica pallida*, and when the shell was ejected 10 days later the topmost part of the liver was completely undigested. The sea-star had obviously been unable to reach so far with a stomach lobe.

To further test the conclusions drawn above, 28 *Mya arenaria*, between 8 and 17 mm in length, were fed to as many adult *Astropecten*, which were then sacrificed while digestion supposedly still took place. Subsequent examinations of the bivalves revealed that, with the exception of the adductor muscle, any remaining tissue was localized at the posterior end, had sharp borders and was clearly without signs of having been affected by any digestive enzymes. The periostracum around the siphons is never digested.

Since direct contact between the sea-star stomach and the prey is necessary, another factor not yet considered may affect the digestive period. Since *Astropecten* is unable to exert any pull, a bivalve which gapes only very little before and after death will be difficult to handle as only a limited part of the internal organs may be digested at a time. Among such bivalve species are *Nucula nitida* and *Corbula gibba*. It has been shown earlier (A. M. Christensen, 1957) that sea-stars with extraoral digestion also have to use longer time to digest bivalve prey which the sea-star for one reason or another is unable to open, but where a permanent, narrow opening allows for the insinuation of a stomach lobe.

A surprisingly large number of small prey may be handled by the stomach wall and digested simultaneously. Thus, more than 400 newly settled bivalves may be found in the stomach of a medium sized *Astropecten* (Table 11), with the large majority being held in stomach pouches and undergoing digestion.

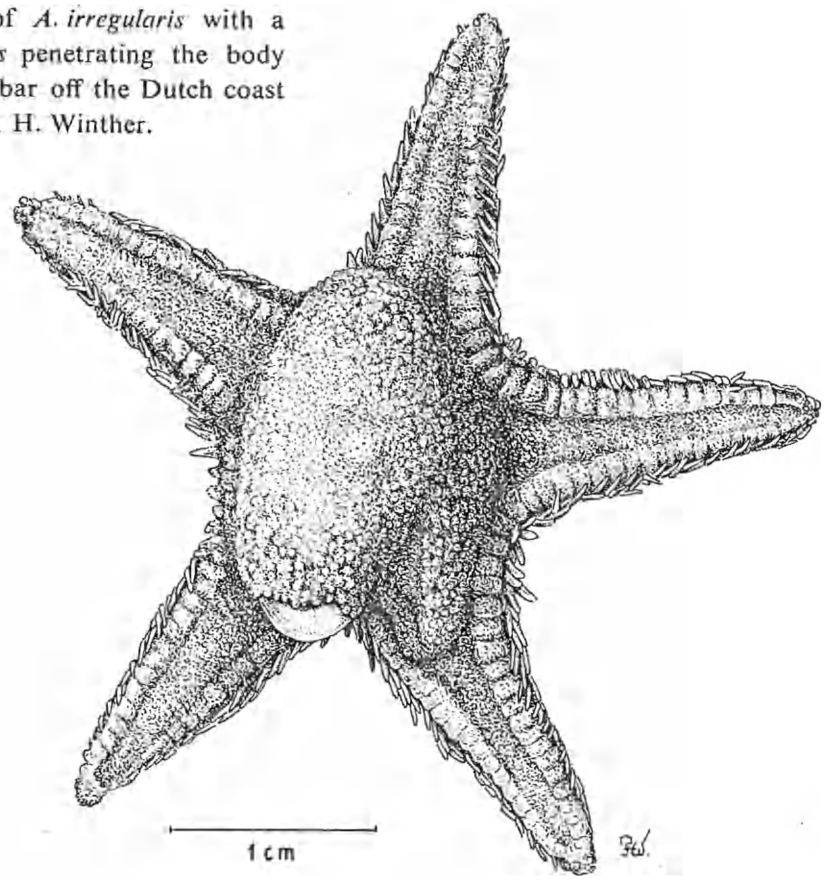
On the other hand, a stomach may also be so distended by swallowed prey that no lobes can be sent in between the valves of any present bivalve. In the case mentioned earlier (Fig. 6) four of the swallowed *Nucula* were ejected alive within 10 hours, and this was no doubt necessary to allow for stomach entrance into one or more of the remaining six bivalves.

EJECTION OF INDIGESTIBLE REMAINS

Once a prey has been digested, any indigestible remains such as molluscan shells, crustacean exoskeletons, polychaete tubes, echinoid tests, and foraminiferan tests must be ejected. Exactly how this process is carried out remains to be found out, but the stomach itself must play the major role. Small items are probably transported to the mouth opening by ciliary action and then pushed out by a lobe of the stomach, a small part of which may become everted in the process. Large items are carefully manipulated until they are oriented in the most favourable position for ejection. Shells of a *Cultellus* as large as that shown in Fig. 5 can be ejected without any damage, either to the sea-star or the rather thin shells of the bivalve, including the hinge and the elastic band. Also the very fragile tubes of the polychaete *Pectinaria koreni* are always ejected completely intact, regardless of size.

In view of these facts it may seem strange that several authors have reported damage to *Astropecten* spp. due to what they believe was the swallowing of a bivalve too large to handle when the valves began to gape following digestion of the soft parts (Sladen, 1879; Deinse, 1916, 1954; Prenant, 1936; Lems, 1951). These reports are all based on dead and, in most cases, dried specimens, however, and in view of my own observations, I am fairly convinced that the fissures

FIG. 9. Dried specimenof *A. irregularis* with a swallowed *Donax vittatus* penetrating the body wall. Collected on sand bar off the Dutch coast (cf. text). Drawn by Paul H. Winther.



in the body walls of these sea-stars are of postmortal origin. Fig. 9 shows such a specimen kindly sent to me by professor H. Engel from Holland and collected in the same area where Deinse and Lems secured their specimens. In accordance with my stated views, I can only agree with Engel (personal communication, 1953) that these *Astropecten* probably had their skin perforated by the swallowed *Donax vittatus* when the sea-stars were washed ashore on a sand bank and left to dry in the sun during low tide.

Astropecten may eject empty shells and other indigestible remains either while resting on the bottom or while it is buried in the bottom substrate. Judging from many laboratory observations, however, the latter procedure is the most common. One may often observe that the sea-star will stay buried in the same spot where it located the last prey during a period of feeding activity and gradually empty its stomach for indigestible remains before it emerges for the next period of activity. One may then find a small heap of empty bivalve shells, for example, just barely covered with bottom substrate.

Astropecten may selectively eject swallowed prey or empty shells while retaining other undigested prey (see also p. 40). Specimens have often been observed to eject swallowed prey belonging to species which rank low in the preference list while retaining those belonging to species higher on the list.

The fact that one may find completely empty, but otherwise fresh-looking shells in the stomach of *Astropecten* shows, however, that the indigestible remains are not always ejected immediately after digestion of the soft tissues.

To gain further information on the length of this period the following experiment was done. After 20 days' starvation, 26 adult *Astropecten* were each fed with a 9.5 to 13 mm long *Spisula subtruncata*. Between 11 and 16 hours later the sea-stars were opened from the dorsal side and the *Spisula* removed, except in six cases where the sea-star already had ejected the empty shells. Out of the remaining 20 shell pairs, 12 were completely empty, although most of them were still situated in enfoldings of the stomach wall. Eight pairs contained remains of undigested tissue. Considering these findings in relation to the average retaining period of 22 hours listed for adult *S.subtruncata* in Table 19, it is seen that empty shells may in some cases be retained for several hours after the digestion of the internal tissues.

The indications are that a time lag of only a few hours also applies to other bivalve species, but there are some noticeable exceptions.

Some of the *Astropecten* collected off Frederikshavn contained completely empty bivalve shells, notably *Nucula nitida,* tucked away in a narrow lobe of the stomach extending as much as halfway into an arm. It seemed as if these shells had been in the stomach for a long time. In the very much larger material from the Øresund, *Nucula* was very scarse (Table 10) and only few bivalve shells were found tucked away. Apart from *Nucula,* only *Corbula gibba* were found under similar circumstances. This species was also found in the arms of *A.africanus* by Cherbonnier (1966).

Failure to eject empty shells of *Nucula* was also observed in the laboratory. The 26 *Astropecten* used for the experiments referred to above had been fed for several months with *Nucula nitida* and then left without food for 20 days prior to being fed on *Spisula.* In spite of this fact, 14 pairs of empty *Nucula* valves were found enveloped in stomach lobes protruding more or less into the arms of the sea-stars.

Further examples are mentioned in the food notes to Table 19. One is left with the feeling that some *Nucula* may keep their valves almost closed even after suffocation, thus prolonging the digestive period considerably. Completely emtpy valves of ejected *Nucula* most often appear not to gape at all. It is conceivable that the range in the retaining period of *Nucula*, which obviously is much wider than listed in Table 19, has something to do with these facts, especially since similar observations concerning shell closure were made with respect to non-juvenile *Corbula gibba.* It is known that *Nucula tenuis* may survive anaerobic conditions for as long as 17 days, although not at which temperature (Moore, 1931). I cannot explain why these empty shells may be "tucked away" in the manner described but the phenomenon has not been observed in sea-stars offered a constant surplus of *Nucula nitida.*

In about a dozen cases the ejection of live molluscs or empty shells was directly observed. The necessary internal manipulations preceding this were for obvious reasons not seen, but the ejection itself is an even faster process than the ingestion. Once the shell has been passed through the mouth opening it is immediately dropped, and one may then see the slightly everted stomach be withdrawn rather slowly.

STUDIES ON PREY SELECTIVITY

Laboratory experiments

As already alluded to, the field data from the major areas investigated (Fig. 1) clearly indicate that bivalves are preferred to any other kind of prey. The data from the Kattegat off Frederikshavn (Table 7) and the Øresund (Table 10) further indicate a pronounced preference for *Spisula subtruncata,* but since both these collecting areas are inhabited primarily by a *Venus gallina* community where *S.subtruncata* may occur in immense numbers (cf. K. Muus, 1966) this apparent preference could in theory be due to this factor.

In the laboratory, however, the experiments recorded earlier (p. 40), showing that *Astropecten* would pick up numerous juvenile *S.subtruncata,* but very few juvenile *V.gallina,* revealed that *Astropecten* does indeed exhibit a distinct preference for certain prey species. Hence, further experiments were undertaken to test how refined the preference pattern might be.

Although the stomach contents of animals collected in the field show that *Astropecten* subsist mainly on prey of meio-fauna size or slightly larger, I was forced to undertake many of the preference experiments with prey specimens of larger sizes. It was practically only in the late summer and autumn of 1962 that a fair number of newly settled bivalves of several of the more important species became available at one and the same time. Even for older animals, it was by no means easy to secure sufficient specimens of the desired species at the same time, which made it necessary to undertake many of the experiments with specimens that had been kept in the laboratory for varying lengths of time, mostly without food. It is known that the suspension-feeding species always obtain a certain amount of food from algae present in the recirculating water in the laboratory, but *Nucula nitida,* which feeds beneath the surface (Yonge, 1939), must have been unable to secure any food from the clean sand used in the experiments. Consequently, some of the *Nucula* used may have been more or less starving and hence had a reduced metabolic rate, which in turn may have effected their attractiveness to *Astropecten.*

The substrate factor should also be considered. *Nucula nitida* is adapted to dig in a mixed substrate, and there are reasons indicating that it may be vivacious enough to escape in many cases under natural conditions. In the loose sand in

TABLE 22. Results of preference feeding experiments in which *Spisula subtruncata* were offered to *Astropecten irregularis* together with other bivalve species. All experiments were carried out in aquaria with a 5-8 cm thick bottom layer of sand and at temperatures between 11 and 16°C. All sea-stars used had an R of at least 35 mm.

Exp. No.	Duration of exp. in days	Number of sea-stars used	The (two) food species given to the sea-stars	Size range of bivalves in mm	Number of bivalves offered	No. of bivalves eaten
A1*	4	3	*S. subtruncata*	7.5-11.5	25	12
			Cardium edule	6.0-11.5	25	17
A2*	5	3	*S. subtruncata*	8.2-10.9	20	5
			Cardium edule	7.1-10.0	20	11
B1	6	2	*S. subtruncata*	7.8-12.2	20	15
			Mya arenaria	9.4-12.2	20	11
B2	5	3	*S. subtruncata*	6.8- 8.7	22	21
			Mya arenaria	6.0-10.4	22	20
B3*	4	2	*S. subtruncata*	8.5-10.5	25	24
			Mya arenaria	9.5-12.0	25	13
B4*	4	2	*S. subtruncata*	8.0-10.5	25	15
			Mya arenaria	7.1-10.5	25	8
C	13	2	*S. subtruncata*	12.0-14.3	30	23
			S. elliptica	11.7-14.0	30	4
D1	7	2	*S. subtruncata*	10.5-13.5	25	19
			Nucula nitida	9.0-11.3	25	5
D2	5	2	*S. subtruncata*	11.1-14.7	20	20
			Nucula nitida	8.8-10.5	20	8
D3	8	2	*S. subtruncata*	10.8-14.2	25	19
			Nucula nitida	8.7-12.0	25	5
D4	11	2	*S. subtruncata*	9.0-11.9	20	17
			Nucula nitida	8.1-10.0	20	3
D5	15	2	*S. subtruncata*	10.6-12.0	30	28
			Nucula nitida	8.5-10.8	30	8
E1	8	2	*S. subtruncata*	10.8-15.6	20	17
			Cyprina islandica	8.9-14.5	20	4
E2	8	2	*S. subtruncata*	?	20	17
			Cyprina islandica	?	20	1
E3	8	2	*S. subtruncata*	11.0-13.5	15	13
			Cyprina islandica	9.2-12.6	15	6
E4	7	2	*S. subtruncata*	10.6-15.8	17	17
			Cyprina islandica	8.6-15.0	17	1
F1	5	2	*S. subtruncata*	3.2-16.7	30	28
			Venus gallina	3.2-15.0	30	0
F2	7	2	*S. subtruncata*	15.3-18.0	19	17
			Venus gallina	10.0-15.4	27	0
F3	7	2	*S. subtruncata*	8.7-15.0	17	17
			Venus gallina	9.0-12.8	17	1
G	6	2	*S. subtruncata*	8.5-10.6	15	15
			Corbula gibba	8.4-10.2	15	0

* Fed prior to experiment

the laboratory it will not be able to do this with the same success. However, from the point of view of determining the relative attractiveness to *Astropecten*, it is only an asset that a possible ability to escape cannot be utilized. As for *Astropecten* itself it will not dig deeper in sand than in sandy mud. If it did, it would not be able to return to the surface (pp. 42-43). However, it was observed to dig somewhat faster into the loose sand than into the sandy mud found in the deeper parts of its habitat in Hornbæk bay. This might give certain fast-digging prey, as e.g. members of the Solenidae, a better chance to escape, but no species of this kind were used in preference experiments with non-juvenile specimens.

Table 22 shows the results of 20 experiments in which two or three *Astropecten* were offered the choice between *S. subtruncata* and other bivalve species. It is seen that *Astropecten* clearly prefers *S. subtruncata* to all other species except for *Cardium edule*. Furthermore, the preference becomes – broadly speaking – more and more pronounced over the other species in the order in which they are listed in the table. *C. edule* and *Mya arenaria* do not normally occur together with *Astropecten* in Danish waters, but a few have been found in specimens taken in the Øresund. The reason for including them was that several other *Cardium* species and *M. truncata* do occur on bottoms inhabited by *Astropecten*.

The results of 19 additional preference experiments given in Table 23 show that if *Astropecten* is given a choice between two of the species tested against *S. subtruncata* (Table 22), it shows a more or less pronounced preference for the species in the order listed in the last mentioned table. *Astarte montagui* seems to be just as unattractive as *Venus gallina* and *Corbula gibba*.

Table 24 shows the results of preference experiments carried out with juvenile specimens of *Spisula subtruncata, Tellina fabula, Nucula nitida,* and *Venus gallina*. It is again seen that *Astropecten* distinctly prefers *S. subtruncata* to any of the other species offered. Compared with the experiments with larger prey animals there is, however, a significant difference with respect to the relative numbers eaten of *N. nitida* and *V. gallina*. Whereas *N. nitida* very definitely is preferred to *V. gallina* when the specimens offered are well passed the meio-fauna stage (Table 23, experiments M1 & M2), this is apparently not the case when newly settled individuals are involved (Table 24, experiments 6, 7 & 8). However, a closer analysis of the data indicates that the real explanation lies in the substrate factor. *N. nitida* and *T. fabula* were eaten in fair numbers in dishes without sand, but not at all where sand was present. Apart from the fact that the layer of sand was only 1 to 1.5 cm thick, it did not seem feasible that newly settled *Tellina* bury themselves deep enough to escape from *Astropecten* with R's around 2 cm, even if larger specimens certainly may do so. Direct observations showed that their small size, smooth surface and pronounced vivacity make them extremely difficult to grasp by an approaching (sucker-less) tube foot as long as they have the possibility of "running away" in the sand. Even a layer of only a few mm sand seemed sufficient to enable them to do this.

TABLE 23. Results of preference feeding experiments in which different species of bivalves were offered to *Astropecten irregularis*. All experimetns were carried out in aquaria with a 5-8 cm bottom layer of sand and at temperatures between 11 and 16°C. All *Astropecten* used had an R of at least 35 mm.

Exp. No.	Duration of exp. in days	Number of sea-stars used	The (two) food species given to the sea-stars	Size range of bivalves in mm	Number of bivalves offered	Number of bivalves eaten
H*	12	2	*Spisula elliptica*	7.0-10.2	20	19
			Nucula nitida	8.0-11.9	20	2
J1	18	2	*Spisula elliptica*	14.1-16.5	12	11
			Cyprina islandica	12.0-14.4	12	1
J2	18	2	*Spisula elliptica*	13.8-16.8	20	9
			Cyprina islandica	12.0-14.3	20	7
J3	16	2	*Spisula elliptica*	15.0-18.5	20	13
			Cyprina islandica	10.9-14.2	20	5
K	10	2	*Spisula elliptica*	11.9-15.2	12	12
			Venus gallina	11.8-14.6	12	0
L1	14	2	*Nucula nitida*	7.0-11.3	25	24
			Cyprina islandica	6.6-12.1	25	9
L2	13	2	*Nucula nitida*	8.6-10.4	15	11
			Cyprina islandica	7.0-11.5	15	10
L3	25	2	*Nucula nitida*	9.0-11.6	17	14
			Cyprina islandica	6.3-11.7	17	9
M1	15	2	*Nucula nitida*	9.2-12.3	15	15
			Venus gallina	8.9-13.4	15	2
M2	19	2	*Nucula nitida*	8.5-11.8	18	18
			Venus gallina	9.2-12.5	18	1
N1	14	2	*Nucula nitida*	7.3- 9.5	20	17
			Corbula gibba	7.2- 9.3	20	0
N2	12	2	*Nucula nitida*	6.4- 9.0	28	20
			Corbula gibba	6.8- 9.6	28	1
O1	18	4	*Cyprina islandica*	7.4-12.6	15	12
			Venus gallina	8.0-12.8	15	5
O3	60	3	*Cyprina islandica*	10.3-15.6	10	8
			Venus gallina	12.38-15.0	10	3
O3	32	2	*Cyprina islandica*	9.6-14.7	13	13
			Venus gallina	10.2-14.7	13	4
O4	69	2	*Cyprina islandica*	6.0-11.6	20	14
			Venus gallina	6.2-12.6	20	4
P	32	2	*Cyprina islandica*	8.2-10.2	12	12
			Corbula gibba	8.7- 9.3	12	1
Q	54	2	*Venus gallina*	6.2-10.3	12	2
			Corbula gibba	7.0-10.0	12	3
R1	45	2	*Venus gallina*	6.1-15.3	15	5
			Astarte montagui	7.5-12.1	15	4
R2	58	2	*Venus gallina*	6.4-14.8	22	0
			Astarte montagui	5.9-14.3	2	4

* Fed prior to experiment

TABLE 24. Results of preference experiments in which two *A.irregularis* (R: 17-23 mm) were offered newly settled individuals of different bivalves in a round glass dish (500 cm^2) with and without a bottom layer of sand (1-1.5 cm thick). Temperature: 14-16°C.

Exp. No.	Duration of exp. in days	With (+) or without (—) sand	Bivalve species offered to the sea-stars	Size range of bivalves in mm	Number of bivalves offered	Number of bivalves digested	Number of bivalves in stomach
1	1	—	*Spisula subtruncata*	0.6-1.2	44	28	5
			Tellina fabula	0.6-1.1	44	8	5
2	1	+	*Spisula subtruncata*	1.0-1.4	22	19	1
			Nucula nitida	0.8-1.3	22	0	0
			Venus gallina	0.8-1.3	22	0	2
3	3	—	*Tellina fabula*	0.7-0.9	15	11	1
			Venus gallina	0.7-1.0	15	7	6
4	4	—	*Tellina fabula*	0.6-1.0	17	11	5
			Venus gallina	0.8-1.0	17	4	8
5	4	+	*Tellina fabula*	0.8-0.9	28	0	0
			Venus gallina	0.7-1.0	28	6	5
6	9	—	*Tellina fabula*	0.7-1.0	20	16	4
			Nucula nitida	0.8-1.3	20	10	7
			Venus gallina	0.7-1.0	20	9	8
7	9	+	*Tellina fabula*	0.7-1.0	20	0	0
			Nucula nitida	0.8-1.2	20	0	1
			Venus gallina	0.7-1.0	20	7	6
8	14	+	*Nucula nitida*	0.7-1.1	16	3	1
			Venus gallina	0.7-1.1	16	10	0

Recently, Caddy (1969) describes how juveniles of the related *Macoma balthica* may bury themselves 1 to 3 mm into muddy sand within 5-10 seconds and proceed to move horizontally through the soil without making contact with the surface. He further states that before siphonal development, these juveniles must make use of interstitial water for respiratory purposes. If this is true also for juvenile *Tellina,* this factor will also make it difficult for *Astropecten* to detect them by chemoreceptive means.

In the case of juvenile *Nucula,* "running away" beneath the surface was not directly observed. However, the fact that about equal numbers of *Nucula* and *Venus* were taken in experiment 6 where sand was absent, whereas only very few *Nucula* were taken in experiments 7 & 8 where sand was present, indicates that it is not a question of preference, but of an ability of the juvenile *Nucula* to escape, although apparently not with the same efficiency as juvenile *Tellina.* This is probably because they are not able to move horizontally through the substrate with the same speed as *Tellina.*

Table 25 shows the results of a preference experiment in which only *T.fabula* and *N.nitida* juveniles were present during the first week, whereupon juvenile

TABLE 25. Results of feeding experiment with three *Astropecten* (R's about 20 mm) being offered newly settled specimens of three bivalves ranging in length between 0.68 and 1.30 mm. Bottom covered with sand, 1.5 cm thick. Temperature: 13-14°C.

Date (1962)	Food species	Living	Digested	In stomachs	Added after inspection
6. xi	*Nucula nitida*	30	0	0	.
	Tellina fabula	30	0	0	.
9. xi	*N. nitida*	28	0	2	.
	T. fabula	29	0	1	.
13. xi	*N. nitida*	24	2	4	.
	T. fabula	27	3	0	.
	Spisula subtruncata	.	.	.	25
14. xi	*N. nitida*	24	0	4	.
	T. fabula	27	0	0	.
	S. subtruncata	13	9	3	12
15. xi	*N. nitida*	23	2	3	.
	T. fabula	27	0	0	.
	S. subtruncata	0	25	3	25
16. xi	*N. nitida*	23	0	3	.
	T. fabula	27	0	0	.
	S. subtruncata	0	27	1	25
17. xi	*N. nitida*	23	1	2	.
	T. fabula	25	0	2	.
	S. subtruncata	0	26	0	25
19. xi	*N. nitida*	23	0	2	.
	T. fabula	24	0	3	.
	S. subtruncata	0	25	0	25
20. xi	*N. nitida*	22	0	3	.
	T. fabula	24	1	2	.
	S. subtruncata	0	21	4	45
21. xi	*N. nitida*	22	1	2	.
	T. fabula	24	1	1	.
	S. subtruncata	0	42	7	.
					182

S. subtruncata were added. Digested specimens of the latter were, furthermore, replaced daily with about the same number of living individuals for the remaining 8 days of the experiment. As shown, only two *Nucula* and one *Tellina* were taken during the first week, whereas the three *Astropecten* practically "cleaned the table" for *Spisula* every day during the second week. The results of these experiments confirm those obtained in the other experiments, but indicate that juvenile *Tellina* are not 100 % protected in sand.

Hunt (1925) and Kisch (1958) found a fair number of *Natica* in the stomach of *A. irregularis*, and this is of interest in so far as the gastropod to some extent must compete with the sea-star for the same species of molluscan food. In my

TABLE 26. Results of preference experiment in which 3 adult *A. irregularis* were given the choice between the bivalve *Cyprina islandica* (7.9-14.0 mm long) and the prosobranch *Natica pulchella* (7.0-9.2 mm long). Initially 22 specimens of each were placed in the aquarium, and digested specimens were replaced on each census date. Thickness of bottom layer: 6 cm. Temperature: 15 °C.

Date (1961)	Number of *Cyprina* digested by		Number of *Natica* digested by	
	Astropecten	*Natica*	*Astropecten*	*Natica*
19. vi	0	0	0	0
26. vi	5	2	2	0
5. vii	10	2	2	1
14. vii	8	4	3	0
Total numbers	23*	8	7	1

* Four of the *Cyprina* digested by *Astropecten* bore marks of unfinished drill-holes.

material from the two main collecting localities, viz off Frederikshavn and in the Øresund, *Natica* is all but absent. However, in nine *Astropecten* from the North Sea as many as 31 *N. pulchella* were present (Table 5), and it was, furthermore, the second most common prey species found. Notable numbers were also present in the small number of sea-stars collected off the Gullmarfjord (Table 6) and in the Kattegat off the island of Læsø (Table 9).

Hence several experiments were carried out with *Natica pulchella*. In one experiment, two *Astropecten* (R: 33.5 & 35.0 mm) were placed in an aquarium with 25 *Natica* with shell heights from 7.0 to 11.4 mm. After 12 days only 6 *Natica* had been eaten, and after 28 days only 4 more had been taken, i. e. less than 0.2 *Natica* were eaten per day per sea-star. When 15 *Nucula nitida*, 7.8-11.4 mm long, were added on the 29th day, these were all eaten within 8 days together with one more *Natica*. No cannibalism among the snails took place in this experiment, whereas this was the case in the similar experiment involving *Cyprina islandica* listed in Table 26. Again a clear preference for the bivalve was shown, although *Cyprina* of the size used must be considered as rather undesirable for *Astropecten*. In a third experiment, two *Astropecten* (R: 35.5 and 37.0 mm) were placed in an aquarium with 5 *Natica* (shell heights: 7.5-9.0 mm) and 10 *Nucula nitida* (shell lengths: 7.3-9.0 mm). After 11 days (no checks in between), two *Nucula* were found with complete bore holes made by *Natica*, and the remainder had definitely been digested by *Astropecten*. None of the *Natica* had been eaten.

General observations from the storage aquaria on *Turritella terebra, Aporrhais pespelecani* (small specimens without "wings"), *Natica* spp. *Buccinum undatum,*

TABLE 27. Results of preference experiments in which *Spisula subtruncata* were offered to two *Astropecten* together with equal numbers of echinoderms. All experiments were carried out in aquaria with a sandy bottom layer. The R's of the sea-stars varied between 25.5 and 39.5 mm. Temperature: 14-15°C.

Exp. No.	Duration of exp. in days	Name of (two) food species given to the sea-stars	Size range of food specimens in mm	Number of food specimens given	Number of food specimens ingested
1	9	*S. subtruncata*	7.4-12.2	16	16
		Ophiura albida	2.8- 5.0	16	4
2	5	*S. subtruncata*	6.8- 8.2	20	18
		Echinocyamus pusillus	6.0- 7.5	20	2
3	6	*S. subtruncata*	6.7- 8.4	24	24
		Echinocyamus pusillus	5.3- 7.8	24	14

Nassa spp. and *Lora* spp., although only few with a length of less than 5-6 mm, also indicated that *Astropecten* pays little attention to prosobranchs.

Based on stomach investigations of 29 specimens collected in the North Sea, Eichelbaum (1909) states that echinoderms are as important as food for *A. irregularis* as bivalves. This is in disagreement with the findings of other authors as well as my own, but only when the results from all the investigated sea-stars are pooled. Exceptions occurred, both with reference to *Ophiura albida* and *Echinocardium cordatum* (p. 25). *Echinocyamus pusillus* was rare in my material, but was found in significant numbers by Hunt (1925).

It was not possible to secure living *Ophiura* of the very small size usually swallowed in nature, and only one experiment with fairly small *O. albida* was, therefore, carried out, whereas two experiments were done with *Echinocyamus*. Both species were tested against *S. subtruncata* and the results revealed a distinct preference for the bivalve (Table 27). In the case of exp. No. 3 it should be noted that all bivalves had been eaten and the empty shells ejected, which is no doubt the reason why a relative high number of *Echinocyamus* were taken as compared with exp. No. 2. Small *Echinocardium* were not available in sufficient numbers, and the few I had thrived badly and refused to dig into the substrate used.

The experiments clearly demonstrate an ability of *Astropecten* to discriminate between buried prey species. Although inherent in the information recorded about food perception, it should be emphasized that this discrimination takes place while the sea-star is crawling on the bottom, i. e. it does not dig at random in search of food. If one keeps the sea-star in aquaria with only *Venus gallina*, for example, the number of burrows made within a given period will be very small compared with the number made under otherwise identical conditions in aquaria with *Spisula subtruncata*.

Discussion of underlying factors

Having established that *A. irregularis* by and large preferentially selects its bivalve prey in the same order every time, one may ask how this selectivity is mediated. No attempts were made to study this aspect which inevitably will prove to require very refined and time-consuming biochemical work. There is, however, certain information in the literature which, in combination with the knowledge gained in the present study, points in a definite direction.

In reviewing the work carried out by earlier investigators on the attractiveness of different prey animals to the oyster drill, *Urosalpinx cineria*, Carriker (1955) points out that the studies by Haskin (1940, 1950) suggest that the metabolic rate of an oyster is more important than age in determining the degree of attractiveness of substances released by it. The fact that Stauber (1943) and Janowitz (personal communication) noted that confinement of prey for extended periods reduced their activity and their attractiveness to oyster drills points in the same direction. Inspired by the above information, Blake (1960) took up studies to determine whether the oxygen consumption of certain prey organisms was not in fact correlated with prey selection by *Urosalpinx*. Testing four factors affecting metabolic rate, viz. species, age, growth rate, and feeding, he found in each case that the more attractive animals had a proportionally higher respiratory rate. Having demonstrated that oxygen consumption is a valid index of attractiveness for the ages and species tested by him, Blake goes on to say: "It must be emphasized that respiratory rate of prey is not considered to be the motivating factor, but rather an easily measured index of the attractiveness of the organism to the predator; in other words, relative attractiveness and respiratory rate are similarly correlated with the actual predator stimulus. This relation may vary from one species to another in that the ratio between respiratory rate and concentration of attractant may vary, or different species may emit different kinds of attractants. Thus, the reported preferences of *Urosalpinx* for prey species other than oysters may be indicative of either quantitative or qualitative differences in attractants".

When the relative attractiveness to *A. irregularis* of the bivalve species listed in Tables 22 & 23 was discovered, it occurred to me that *Astropecten* also might select its prey among those with the highest metabolic rate. *Cardium edule* seems to have a very high metabolic rate (Spärck, 1936). Number two on the list, *Spisula subtruncata* has long been known to be a fast-growing species, whereas *Venus gallina* at the other end of the preference list grows at a much slower rate (Ansell, 1960b). The results of some recent studies in the Helsingør laboratory by Dr. B. Bayne (1968, unpublished) on the oxygen consumption of these two species are here given with his kind permission (Table 28). Dr. Bayne used both the closed chamber and the open chamber method, but further details will be published by Dr. Bayne elsewhere. As expected there is a difference in metabolic rate between the two species, although the data obtained seem to show that it is

TABLE 28. Determination of oxygen consumption of *Spisula subtruncata* and *Venus gallina* by Bayne (unpublished). In each of the 9 experiments, three equally large specimens were used, i.e. the measurements listed for dry weights and oxygen consumptions are average values for three animals. All experiments were carried out at a salinity of 17.6 ‰ and a temperature of 11 °C. The oxygen concentration varied between 5.21 and 5.94 ml O_2/litre at the start of the experiments.

Species	Dry weight (d.w.) in grams	Oxygen consumption		Mean oxygen uptake for each weight group
		ml/animal/hour	ml/gram d.w./hour	
S. subtruncata	0.011	0.0059	0.536	
–	0.011	0.0061	0.554	
–	0.011	0.0052	0.473	0.521
S. subtruncata	0.019	0.0096	0.508	
–	0.019	0.0091	0.479	0.493
V. gallina	0.012	0.0043	0.358	
–	0.012	0.0041	0.342	0.350
V. gallina	0.017	0.0032	0.189	
–	0.017	0.0039	0.229	0.209

smaller than one might have expected. This could be due to *Spisula* being affected more by lack of food prior to the experiments than *Venus* and further experiments, especially with juveniles of the mentioned as well as other prey species, are very much needed. It should be noted, however, that Spärck (op.cit). also found a low oxygen consumption for *Venus gallina* as well as for *Astarte montagui* which is "disliked" by *Astropecten*.

Finally, although exceptions may occur, the ability of a bivalve to sustain anaerobic conditions must be more or less inversely correlated with its "normal" metabolic rate, and a comparison between the data listed in Table 20 with those in Tables 22 & 23 shows that, when given a choice, *Astropecten* will always display a tendency to feed primarily on species with the least resistance to anaerobic conditions.

Since the metabolic rate decreases in starving animals, lack of food should affect such a species as *S. subtruncata* sooner than species with lower metabolic rates. Although an attempt was made to use as fresh animals as possible, it is, therefore, fairly certain that under normal conditions the preference shown by the sea-star for *S. subtruncata* would have been even more marked than indicated in Table 22. In fact, some of the data in the mentioned table lend support to such a conclusion.

It is seen that no clear preference for *S. subtruncata* over *M. arenaria* can be deducted from experiments B1 & B2. In experiments B3 and B4, however, which were carried out in 1968, both prey species were fed with a suitable mixture of algae right up to the start of the experiments, and here the preference shown for *S.subtruncata* is clearly significant. This result fits well with the fact that *M.arenaria* is known to have a relatively low metabolic rate (Thamdrup, 1935, p. 66).

M.arenaria does not normally occur on *Astropecten* grounds, where it is replaced by the closely related *M.truncata* which, judging from the stomach finds (Tables 7 & 10), ranks as high or higher on the preference list as its shallow-water relative. This is not surprising since *M.truncata* probably has a significantly higher metabolic rate than *M.arenaria* (cf. Spärck, 1936). As seen in Table 10 *Astropecten* starts to feed on *M.truncata* as soon as this species starts to settle in late winter. However, later when *S.subtruncata* starts to settle, this species is distinctly preferred as judged from the fact that numerous *M.truncata* were still present in the bottom samples taken from "Thelma" in early July the same year. Further evidence is rendered by the data given in Table 33, which directly indicates a pronounced preference for *S.subtruncata* over *M.truncata*.

Blake's hypothesis was tested using *S.subtruncata* starved for two-three weeks in running, filtered water and others fed every day with three suitable species of unicellular algae. Painted spots were used to differentiate the two groups. The paint did not affect attractiveness in so far as the results were similar whether starved or non-starved specimens were marked.

The results did not support the hypothesis, since equal or almost equal numbers of each group were ingested in the five experiments carried out. Since actual metabolic rates of the groups could not be tested at the onset of the experiments it is not certain, however, that the results are reliable. Seven successfull flight responses observed were all made by non-starved specimens, so it is also possible that a preference for these may have been masked by this factor.

As stated by Blake (1960) the metabolic rate can only be used as an index for attractiveness, i.e. it is in some way correlated with the actual predator stimulus. Later, Blake (1961) undertook comparative biochemical studies of the metabolic end products of the oyster, *Crassostrea virginica*, a mussel (*Modiolus demissus*), and a barnacle (*Balanus balanoides*), all of which are preyed upon by *Urosalpinx* in nature, and tested their attractiveness to the snail. The attractant was not completely identified, but the results suggested that it consists of two fractions, viz. (1) a highly volatile fraction, most probably ammonia, which stimulates initial movement and preliminary orientation of the predator, and (2) a protein or peptide fraction, which is responsible for final identification by the snail.

In free-living flatworms a similar pattern is known to exist, with different chemoreceptors being responsible for long and short distance perception (see review by Passano, 1957), and there is evidence that the same is true for a number of other invertebrates (Jahn & Wulff, 1952).

Another interesting aspect noted by Blake (1961, p. 37) is that the attractants from mussels and oysters are very similar, if not identical, whereas barnacles excrete a more distantly related compound.

This may indicate that differences in attractiveness is only of a quantitative nature as long as we are concerned with systematically related prey species such as bivalves. On the other hand, certain species may possibly give off metabolic end products which makes them non-attractive to a predator, regardless of metabolic rate and the accompanying quantity of a substance or substances which normally would make them attractive.

Carr (1967) studied chemoreception in the gastropod *Nassarius obsoletus* by use of stimulatory substances extracted from a shrimp, but found no volatile substances responsible for perception. However, this snail is a scavenger, feeding on anything it comes across, i.e. it is neither a predator, nor a selective feeder. In contrast to *Urosalpinx* which, as mentioned earlier, reacts much more positively to substances released from living prey, it is well known that species of *Nassarius* are highly attracted to substances released from mutilated or decaying organisms (see review by Kohn, 1961). Hence it is not to be expected that the two snails discussed should possess the same chemoreceptive properties. Blake, in fact, was well aware of this. He tested the responses of several gastropods to effluents from actively metabolizing oysters. Three species failed to react positively, viz. two species of *Nassarius* and *Terebra dislocata,* none of which feed on living oysters. Four species of *Murex, Urosalpinx perrugata, Fasciolaria hunteri,* two species of *Thais, Polinices duplicatus,* and *Eupleura caudata,* all known to be oyster enemies, reacted, however, just as positively as *U. cinerea.*

Astropecten may swallow carrion (p. 27), but is nevertheless first and foremost a predator, and its chemoreceptive properties are most probably rather similar to those of *Urosalpinx.* At least they both prefer bivalves with a high metabolic rate. It is, of course, not justified to imply that non-bivalve prey species are rejected or only taken in small numbers due to low respiratory rates and that others, such as *Retusa umbilicata* which occasionally occurs in large numbers (cf. Table 8), are taken because of high respiratory rates.

THE INFLUENCE OF AVAILABLE PREY SPECIES ON FOOD UPTAKE IN THE LABORATORY

When undertaking the preference experiments it was soon found that the time it took to arrive at decisive results differed considerably, depending on prey species present. Whereas experiments involving maximally 20 *S. subtruncata* and as many of any other species usually could be carried out in 8 days or less (Table 22, column 2), it took from about one to more than two months to carry out experiments when such species as *Cyprina islandica, Venus gallina, Corbula gibba,* and *Astarte montagui* were paired in the experiments (Table 23, column 2). It should be noted that four sea-stars were used in experiment O1 and three in O2 which means that the duration of these experiments should be counted as 36 and 90 days, respectively, to compare them with the other experiments listed in the table. Furthermore, in spite of the long experimental periods, very few bivalves were eaten, and the sea-stars were obviously starving. A calculation of the food uptake based on the last 8 experiments (O1 to R2 incl.) shows that each sea-star ate only one bivalve per 10 days, and in the last three experiments only one bivalve per 17 days. Conversely, in the first five experiments listed in Table 22, where such "favourite" food species as *S.subtruncata* and *Mya arenaria* were present, each sea-star ate between one and three bivalves per day.

Apart from some of the experiments lasting 14 days or more, no checks were made on food uptake during any of the experiments listed in Tables 22 & 23. Based on the knowledge obtained on retaining periods (Table 19) each experiment was usually terminated when a significant result could be expected.

Another experiment involving the three prey species *C.islandica, V.gallina,* and *S.subtruncata* was carried out with checks being made each morning except for some days just after the start of the experiment on 21 February 1961 and on 8 March (Table 29). As shown in the table, *C.islandica* was as usual preferred to *V.gallina,* but it was only eaten at the rate of about 0.2 bivalves per day per sea-star. When – after 29 days – all the *Cyprina* had been eaten, there were still five *Venus* present in addition to four that had been swallowed. *Venus* was often ejected alive, even during the long period from 22 March to 16 May when it was the only species present in the aquarium. Furthermore, during this period only four *Venus* were eaten, and two specimens present in the sea-star stomachs were ejected alive when 12 *Spisula* were added to the aquarium on the last mentioned date. These very large *Spisula* were then digested and the empty shells ejected within 8 days, thus showing that the sea-stars had fed at an extremely low rate due to lack of suitable prey. It is also to be noted that whereas at least one *Venus* was inside a sea-star during all but one day from 27 February to 22 March, when the last *Cyprina* had been digested, none were picked up after the *Spisula* were added on 17 May before the last *Spisula* had been swallowed.

A similar experiment was undertaken with the same prey species, but with sand present (Table 30). Here checks were not carried out every day since remaining live bivalves in each case had to be given time to adjust in the sand before the sea-stars were returned to the aquarium. The results did not differ from those obtained in the preceding experiment. Equal numbers (13) of the three prey species were offered. Of these the 13 *S.subtruncata* were probably all digested within 8 days, whereas only 6 *Cyprina* and one *Venus* had been digested 12 days after the start of the experiment. It took about 70 days before the last of the *Cyprina* was swallowed, and only two *Venus* were digested during the same period. When 10 *S.subtruncata* were added on the 71st day, all were eaten in five days, whereas none of the 10 *Cyprina* added at the same time were taken.

The results of the two experiments conform strictly with the preference pattern

TABLE 29. Preference experiment with two *A. irregularis* (R's = 41.0 and 43.5 mm) first given the choice between equal numbers (12) of *Cyprina islandica* and *Venus gallina*, and later between the remaining *V. gallina* and *Spisula subtruncata*. The daily observations for the period 23 March-15 May are not included but are accumulated in the data for 16 May, when the *Spisula* were added. To facilitate daily observations, no substrate was present. The temperature range was 12.5 to 14.0° C.

Date (1961)	*C. islandica* (9.3-14.0 mm long)				*V. gallina* (9.9-13.8 mm long)			
	living	in stomachs	digested	ejected alive	living	in stomachs	digested	ejected alive
21. ii	12	0	0	.	12	0	0	.
22. ii	10	2	0	.	12	0	0	.
27. ii	5	6	1	.	10	2	0	.
28. ii	5	2	4	.	9	2	1	.
1. iii	4	3	0	.	8	3	0	.
2. iii	4	1	2	.	10	1	0	2
3. iii	4	1	0	.	9	2	0	.
4. iii	4	1	0	.	10	1	0	1
6. iii	2	3	0	.	9	2	0	.
7. iii	2	3	0	.	10	1	0	1
9. iii	2	1	2	.	8	3	0	.
10. iii	2	0	1	.	7	4	0	.
11. iii	1	1	0	.	8	3	0	1
12. iii	2	0	0	1	7	4	0	.
13. iii	2	0	0	.	8	3	0	1
14. iii	1	1	0	.	8	2	1	.
15. iii	1	1	0	.	9	1	0	1
16. iii	1	1	0	.	8	2	0	.
17. iii	1	0	1	.	7	2	1	.
18. iii	0	1	0	.	5	4	0	.
19. iii	0	1	0	.	7	2	0	2
20. iii	0	1	0	.	9	0	0	2
21. iii	0	1	0	.	8	1	0	.
22. iii	0	0	1	.	5	4	0	.
16. v	12 *S. subtruncata* (15.0-17.4 mm)				3	2	4	(17)
17. v	8	4	0	.	3	2	0	.
18. v	5	4	3	.	5	0	0	2
19. v	4	4	1	.	5	0	0	.
20. v	2	3	3	.	5	0	0	.
21. v	1	3	1	.	5	0	0	.
22. v	1	1	2	.	5	0	0	.
23. v	0	2	0	.	4	1	0	.
24. v	0	0	2	.	3	2	0	.

TABLE 30. Preference experiment with three *A.irregularis* (R's = 33.5, 36.0, and 37.5 mm) given the choice between three bivalve species. Prey size ranges in mm length are given in brackets. The temperature range was 15 to 13° C. Note that 10 *Spisula subtruncata* and 10 *Cyprina islandica* were added on 21 November. While these bivalves dug into the substrate the sea-stars were temporarily removed to another aquarium.

Date (1962)	*S. subtruncata* (11.4-13.8)			*C. islandica* (10.2-12.0)			*Venus gallina* (9.8-12.4)		
	living	in stomachs	digested	living	in stomachs	digested	living	in stomachs	digested
11.ix	13	0	0	13	0	0	13	0	0
13.ix	10	1	2	8	5	0	13	0	0
17.ix	2	0	9	8	0	5	12	1	0
23.ix	0	0	2	6	1	1	12	0	1
29.ix	0	0	0	4	1	2	12	0	0
2.x	0	0	0	3	0	2	12	0	0
6.x	0	0	0	3	0	0	12	0	0
13.x	0	0	0	1	0	2	12	0	0
18.x	0	0	0	1	0	0	12	0	0
24.x	0	0	0	1	0	0	12	0	0
6.xi	0	0	0	1	0	0	11	0	1
19.xi	0	0	0	1	0	0	11	0	0
21.xi	0	0	0	0	1	0	11	0	0
21.xi	10	0	0	10	1	0	11	0	0
26.xi	0	0	10	10	0	1	11	0	0
Total number digested		23 (of 23)			13 (of 23)			2 (of 13)	

discussed earlier and confirm the conclusion that food uptake depends to a very large extent on the prey species available.

Bivalves of the size used in the two experiments and in the preference experiments recorded earlier are rarely found in the stomachs of *Astropecten*, at least in Danish waters. The conclusions drawn are, nevertheless, supported by the results of the experiments done with newly settled specimens of a number of "key" species. Certain of the data recorded in Table 24 have been discussed earlier. In the present context reference is primarily made to the results obtained in dishes with a bottom substrate, since this was the case in all but one of the experiments where macro-fauna bivalves were used as food. Observing this prerequisite, it is seen from exp. 2 that each sea-star ate about 10 juvenile *S.subtruncata* in one day, whereas the combined data from experiments 5, 7 and 8 show that only about 0.2 juvenile *V.gallina* were eaten per day per sea-star, i.e. the rate of feeding on *Spisula* was about 50 times higher than the rate of feeding on *Venus*. The rate was even lower for the other species offered, viz. *N.nitida* and *T.fabula*.

TABLE 31. Feeding experiment using juvenile, 840-1240 μ long *Corbula gibba* as food for *Astropecten irregularis*. Temperature: 14-15°C. Experiment started in aquarium with 2 *Astropecten* and 16 *Corbula*. No sand.

Date (1962)	Hour	Number of *Corbula gibba*			Remarks
		Living	In stomachs	Digested	
31.x	11.00	16	0	0	
2.xi	16.00	4	6	6	← Empty shells removed here and at each following check
6.xi	10.00	1	1	8	
8.xi	16.00	1	1	0	
10.xi	9.00	0	1	1	
11.xi	17.00	0	1	0	
12.xi	9.00	0	0	1	

Even then the number of *Spisula* eaten in exp. 1 (and in exp. 2 where no sand was present) was low compared with the 35-100 specimens eaten by other small *Astropecten* in the one-day experiments recorded on p. 40, and the same is true for the number eaten of *Venus*, where about two juveniles were taken per day per sea-star in a two-day experiment. Since the sea-stars used were of about the same size in all experiments, and since the dishes and substrate used were the same, the most probable explanation for the apparent discrepancy lies in the temperature factor. In September 1968 about 25 *Astropecten* were collected to be used for a course in ecology. In a trial run prior to the course the animals seemed fully adapted to laboratory conditions and fed at a normal rate on *S. elliptica*, and at a temperature of about 15°C. However, when the temperature subsequently rose to over 16°C, the animals became inactive, and although they were without food for about a week they did not start feeding before five days after food was offered to them again. By then they had apparently adapted to the higher temperature. As noted in the heading to Table 24 some of the preference experiments carried out were in fact done at a temperature of 16°C.

Two experiments were done with *Astropecten* being offered only juvenile specimens of *Corbula gibba* and *Venus gallina*, respectively (Tables 31 & 32). To facilitate observations, no substrate was present, but the data on *Venus gallina* in Table 24 indicate that this should not affect feeding rate on this specices, and there is no reason to suspect anything different for *Corbula gibba*, which is also very inactive and displays no escape responses. As shown the feeding rate was less than one *Corbula* per day per sea-star. As for *Venus gallina*, seven specimens were eaten by four sea-stars during the first two days, which is also less than one prey organism per day per sea-star. The living specimens were removed 46 hours after the start of the experiment because two of the eleven specimens found to be swallowed at a check made the day before had been ejected alive again four hours later and another two during the following night. Of the seven specimens

TABLE 32. Feeding experiment using juvneile, 620-740 μ long *Venus gallina* as food for *Astropecten irregularis*. Temperature: 15-15.5°C. Experiment started with 24 bivalves and 4 *Astropecten*. No sand in aquarium.

Date (1962)	Hour	Number of *Venus gallina*			Remarks
		Living	In stomachs	Digested	
13.ix	11.00	24	0	0	
14.ix	13.00	7	17	0	
	17.00	8	16	0	
	–	8	15	0	One damaged specimen removed
15.ix	9.00	10	7	6	
	9.00	0	7	0	← Living specimens and empty shells removed at this and each following check. Note that specimens are very often ejected alive
	12.00	1	5	1	
	18.15	1	4	0	
16.ix	9.15	1	3	.	
	16.00	1	1	1	
	20.00	0	1	0	
17.ix	9.00	0	1	0	
	11.30	0	1	0	
	16.30	1	0	0	

still remaining in the sea-stars only two were in fact digested, whereas the remainder were all ejected alive. If ejected specimens had not been removed, they might have been picked up again, probably more than once, and the fact that even juvenile *Venus* may be ejected alive would not have been as clearly established. On this background it is strange that Massé (1966) did not observe ejections of live *Venus* less than about 8 mm long by *A. bispinosus*.

FIELD DATA ON STOMACH CONTENTS IN RELATION TO LABORATORY FINDINGS

It is not to be expected that the distinct preference pattern found in the laboratory should manifest itself as clearly in the quantitative composition of the food in a field material.

The reasons for this lie both in the conditions under which the laboratory experiments were undertaken (low food spectrum, "artificial" substrate, high prey densities etc.) and in the varying physical and biotic factors affecting the composition and densities of the fauna in any given locality (see next section). Whereas it is easy for an *Astropecten* to traverse the small area of an aquarium and pick up suitable prey, conditions are different in nature. When encountering a "second class" prey organism, the sea-star cannot "know" that a more suitable prey may be present just outside its range of perception. In this situation a starved animal may be more likely to accept such prey than a satiated specimen, as found for a number of predators (see Emlen (1966) for references). Laboratory observations and experiments indicate, however, that this is not the case for *Astropecten* (cf. Tables 29 & 30) when the most undesirable prey species are encountered, but other, less "despised" prey species may possibly be taken in significant numbers in the absence or scarcity of "first class" prey. Nevertheless, certain field data indicate that the sea-star may starve in the midst of numerous members of many potential prey species.

It is clear that many other potential prey species should be tested for attractiveness and a possible ability to escape, although the present study has comprised the majority of the most common prey found in *Astropecten* in inner Danish waters.

A sample of 22 *Astropecten* taken in 1964 made it possible to make a direct comparison between the stomach contents and the quantitative occurrence of potential prey species on the bottom by utilizing data supplied by Dr. K. Muus (unpublished). The data obtained (Table 33) are in every respect consistent with laboratory experiments and observations. They confirm (1) that the deposit-feeding Tellinidae, *Syndosmya alba* and (juvenile) *Nucula,* as well as the suspension-feeding *Cultellus* to a large extent are able to escape in their natural habitat, that (2) *Cyprina, Venus* and *Corbula* are only taken in negligible numbers, and that (3) *Spisula subtruncata* are traced down with great efficiency, considering that 35 were found in the sea-stars although only 75 were present per square metre.

It is also significant that only one specimen of *Philine* occurred in the sea-stars although this genus (mostly *P. denticulata*) was represented by more than 7000 specimens per square metre (see also Horikoshi, 1967).

Finally, the data confirm that *Ophiura* is taken in small numbers only, whereas *Echinocardium* is picked up in large numbers while belonging to the 0-group.

In addition, the data in Table 33 yield more information concerning *Mysella bidentata.* As seen, it was by far the most abundant bivalve, with more than 2000 specimens per square metre. In spite of this, maximally 22 specimens occurred in the sea-stars. Furthermore, on 29 October 1960, Ockelmann (unpublished) found 700-1100 *Mysella* per square metre at 19 metres depth in the Hornbæk Bay, yet only few and distinctly eroded shells were found in the sea-stars collected in the fall that year (Table 10). These facts strongly support the view that this species very rarely is swallowed alive (p. 23). This is in striking contrast to the findings concerning the related *Montacuta ferruginosa;* all 320 specimens taken by only 17 *Astropecten* in the Hornbæk Bay on 17 September 1962 (Table 10) were fresh looking specimens, with the majority still containing undigested remains of the internal organs. Furthermore, in 29 *Astropecten* collected off Frederikshavn on 10 July 1951, Thorson (unpublished) found *M. ferruginosa* to be the most abundant bivalve.

TABLE 33. Comparison between numbers of some common bottom animals found in 22 *A.irregularis* and in quantitative samples taken with the "mouse trap" on a *Venus* community station at 18 m depth in Hornbæk Bay. Nearly all molluscs taken belonged in both cases to the meio-fauna. *E.cordatum* were not measured, but all taken by the sea-stars were less than 4 mm long.

Family, Genus of Species	Total numbers found in 22 *A.irregularis* collected on 14.viii. 1964	Numbers found per square metre based on 5 samples collected by K. Muus (unpublished) on 13.viii. 1964
Nucula spp.	0	64
Mytilidae	3	342
Mysella bidentata	22	2033
Montacuta ferruginosa		107
Cardium spp.	22	128
Cyprina islandica	3	96
Venus gallina	11	567
Macoma calcarea	0	225
Tellina fabula	0	653
Syndosmya alba	0	182
Cultellus pellucidus	5	609
Spisula subtruncata	37	75
Mya truncata	2	54
Corbula gibba	8	770
Thracia spp.	0	96
Philine spp.	1	7233
Ophiura spp.	12	806
Echinocardium cordatum	921	1027
Total number	1047	

Another factor to be considered, when comparing field data and laboratory results, is the influence of the retaining period. The size distribution of the *Venus* found in the Frederikshavn material (Table 13) indicates that they represented the number taken during approximately three days (cf. Table 19). Conversely, more than 97 % of the *S.subtruncata* found in the same material had a size at which they in the laboratory were retained nine hours on an average and for maximally 12 hours. The temperatures at which the experiments were carried out in the laboratory were probably several degrees higher than the bottom temperature off Frederikshavn where the mean temperature for June, in which all but 20 of the sea-stars were taken, lies around 10° C (Brattström, 1941), but the consequence of this would only be a still larger difference in retaining periods between *Venus* and *Spisula*. Even without considering the latter aspect, the data available show that the number of *Venus* found should be divided by a factor of about six to compare the actual consumption of this species per time unit with the consumption of *S.subtruncata*. When this is done we find that the ratio is about 10 to 1 in favour of the latter species. Furthermore, we know that the number of *Venus* swallowed is not equal to the number that eventually will be digested since roughly 70 % may be ejected again fully alive (Table 32). One may ask why so many *Venus* were ingested at all in the Frederikshavn locality, when it is so "disliked" by the sea-star. Apart from factors mentioned earlier (presence of attached egg capsules, patchy distribution), the data given in Tables 22 & 29 show, however, that only in the immediate presence of the most desired prey, *Spisula subtruncata,* will *Astropecten* "refuse" to pick up *V. gallina* at all.

Many of the factors discussed above also play a role in evaluating the reasons why a fairly high number of *Corbula gibba* was found in the Frederikshavn material. In this case, however, the experiments on prey selectivity listed in Tables 22 & 23 are misleading since only adult animals were used. In contrast to *Venus,* newly settled *Corbula* never seem to be ejected (Table 31), and the average retaining period is only 17 hours as against more than 60 hours for newly settled *Venus.* The majority of the *Corbula* found in the Frederikshavn material were less than 4 mm long, but only 43 (out of 362) were of meio-fauna size, and none of the experiments carried out in the laboratory involved specimens in this size range. Nevertheless, the indications are that *Corbula* in the 2-4 mm size range are retained and digested to a considerably higher extent than *Venus* of the same size group. Apparently, circumstantial evidence may also be drawn from the data on state of digestion in field material (Table 21), but the difference in size distribution of the two species in the two materials makes it impossible to draw any conclusions in this respect, especially since practically all of the *Corbula* found digested in the Øresund material were less than one mm long.

Yonge (1931) as well as others have warned against determining what marine invertebrates feed upon by relying on their stomach contents, since they may lack enzymes necessary to break down certain parts of the food ingested. Whether this factor plays any role for *Astropecten* is not known, but based on our present knowledge of enzyme occurrences in other sea-stars as reviewed by Anderson (1966), this is hardly the case, i.e. all internal tissues of bivalves and snails as well as the external and internal tissues of echinoderms can no doubt be assimilated, and the same must apply to other less important food organisms (see also Heyde, 1923).

The results of the present study constitute a further warning against relying on stomach contents, especially when one deals with predators that are unable to mastigate their food and feed on molluscs able to protect their internal organs by tightly appending valves or an operculum.

To this must be added the great variations that one may find in stomach contents due to a number of factors discussed in the next section. To rely on samples from just one locality may lead to quite wrong results, especially if the samples are small and derive from certain seasons of the year only. Laboratory studies should be carried out in conjunction with field studies, but this has apparently not been possible for most of the authors which have published papers on food uptake by *Astropecten*. The data published by A. M. Christensen (1962), Massé (1966) and in the present contribution clearly emphasize how important this is when attempting to draw conclusions from field data. The recent studies carried out on all sea-stars occurring within diving depth in the Puget Sound region by Mauzey et al. (1968) serve to stress the same point.

VARIATION IN PREY SPECTRUM

The data depicted in Fig. 1 show that the prey composition may vary considerably from one area to another. However, the composition shown is, of course, not a static one. The majority of the North Sea sea-stars were taken during the settling season of *Pectinaria koreni*. The Frederikshavn material was collected at a time when the opisthobranch, *Retusa umbilicata*, must have occurred in enormous numbers, and the Øresund material happened to be taken mainly in a year (1960) when a tremendous spatfall of *S.subtruncata* took place. A change in just these three factors could have changed the prey composition in all localities to a considerable extent.

Nevertheless, in the long run *Astropecten* will probably ingest a comparatively lower number of bivalves in the North Sea than in the other localities, since the bottoms inhabited by them in the North Sea in general are more muddy and hence contain fewer suspension-feeding bivalves (see e.g. Yonge, 1956). The fact is also that the 54 sea-stars (out of 114) collected at the shallowest depths in the North Sea contained 82 % of all the bivalves found.

These remarks may suffice to stress that a number of biotic and physical factors may be responsible for apparent differences in food uptake at various localities and at different seasons of the year, as well as from one year to the next. In the following the most important factors will be treated and illustrated with examples from the collections made. It is obvious, of course, that many variations in food contents are not just due to one factor, but that two or more factors may be involved. It cannot be said, for example, whether the curious distribution of *Pectinaria koreni*, Harpacticidae and *Ophiura albida* in the sea-stars taken from three close localities in the North Sea (see remarks in Table 4) is due to a substrate factor or a patchy distribution of the mentioned food animals, or whether both factors played a role.

Regional differences in available prey

Since *A.irregularis* is distributed along the East Atlantic coast from Marocco in North Africa to Lofoten in northern Norway and may be found in depths ranging between 10 and 1000 metres (Mortensen, 1927), they do not everywhere have the same prey fauna from which to seek their food. Many of the species found by Kisch (1958) in his very large material from the French west coast do not occur in Danish waters at all, and a good number is not found in the North Sea either.

It is also well known that the Øresund has a fauna which is considerably poorer in species than any of the other localities from which material for the present study was obtained. Furthermore, among the species occurring in the Øresund many may be rare, whereas they may be common in other localities.

Patchy distribution within the collecting area

Since *Spisula subtruncata* plays a dominating role as food for *Astropecten* inhabiting *Venus gallina* communities, it is appropriate to mention the study by Davis (1923) who found a very distinct patchiness in distribution of this species in the Dogger Bank area in the North Sea. He also noted that settling took place in different patches from year to year. Later, Hagmeier (1930) found the same phenomenon off the German coast, and there are other statements in the literature to the same effect, both with respect to this as well as other species.

That such patchiness also occurs within a rather restricted area is indicated by the fact that even during July-August 1960, when *S. subtruncata* totally dominated the stomachs of *Astropecten* taken in the Hornbæk Bay (Table 10), one could on the same date find sea-stars containing 200-300 juvenile *Spisula* along with others containing none or only a very few specimens. However, within areas sampled from an anchored boat, the patchiness is not very pronounced (K. Muus, unpublished).

In the material collected off Frederikshavn, there were 47 *Astropecten* which contained *V. gallina*, but no *S. subtruncata*, and 68 where the reverse was the case. In many of those, which contained specimens of both species, the distribution was often skewed, in many cases with only one specimen of one of the species.

Finally, it can be seen in Table 5 that 6 *Astropecten* together contained 99 newly settled *Spisula solida*, whereas three others from the same station in the North Sea contained none.

Seasonal and annual variation in composition of prey fauna

Especially for a predator as *Astropecten* which preferentially feeds on newly settled invertebrates subjected to extermination within a few months (cf. K. Muus, 1966), notable changes will occur in prey species composition throughout the year.

The first "first class" food species to settle during the year in Danish waters is *Mya truncata*, which is a winter spawner (Thorson, 1946; K. Muus, 1966). When the temperature in the Hornbæk Bay rose above 4°C in February 1960 (Table 24), *Astropecten* started to feed on this species (Table 10). If some *Spisula subtruncata* had not survived from the preceding year, the number of *Mya* taken might well have been higher. When the former species began to settle later in the season, they completely dominated the stomach contents, especially in July-August.

The data for September 1962 (Table 10) show that *Montacuta ferruginosa* may be taken in large numbers at this time of the year when present. This brings out the influence of annual variations in prey composition on food uptake.

Contrary to 1960, settling of *S.subtruncata* apparently failed in Hornbæk Bay in 1961 (Table 10). In June 1961, *Mya truncata* and *Cyprina islandica* made up the bulk of the bivalves present whereas *S.subtruncata* accounted for over 70 % in June the year before. It is well known that this and other species with a short life span and planktotrophic larvae show great fluctuations in abundance from year to year (Jensen, 1919; Thorson, 1957). However, although the sea-urchin *Echinocardium cordatum* does not have a short life span (Ursin, 1960; Buchanan, 1966), it may be almost absent in *Astropecten* stomachs in some years and exceedingly abundant in others (p. 25). It is possible that this to some extent is a local phenomenon since recruitment of this species in the Øresund depends mainly on an inflow of larvae from the Kattegat or even the Skagerak (Thorson, 1946). Since this is true also for a number of other potential prey species and since the hydrographic conditions are rather unstable (Davidsson, 1962), annual variations in prey composition are probably greater in the Øresund than in other localities from which *Astropecten* were collected.

Variations due to nature of bottom substrate

Massé (1966) noted that the food of *A.auranciacus,* a Mediterranean species, varied according to the type of bottom on which it was collected. Although *A. irregularis* prefers a more or less clean sandy bottom and is a recognized member of the *Venus* community, it has already been pointed out that it may be found on other substrates too. A look at the species swallowed by the animals collected in the Øresund (Table 10) shows that a number of the bivalves, as well as some species from other groups, do not belong to a typical *Venus* community, but rather to the *Syndosmya alba* community. Unfortunately, the collections were made in such a way that the sea-stars taken from the two communities could not be separately handled. This is largely because the *Venus* community and the *Syndosmya* community are present only as narrow strips along the coast north-west of Helsingør. It is even a question whether the latter community exists in the Hornbæk Bay area except as spots cramped in between the *Venus* community and the deeper *Amphiura* community. Sampling along the coast at about 20 m depth, it is not uncommon to find animals from all three communities in one and the same dredge haul.

However, the collections made at Læsø in the Kattegat on a so-called *Amphioxus* bottom (*Venus fasciatum-Spisula elliptica-Branchiostoma* community in

Thorson, 1957) clearly show the influence of the substrate factor. On this bottom practically none of the prey species preferred by *Astropecten* are present, at least not in notable numbers. The sea-star seems to react to this situation by feeding, although not extensively, on almost anything available, including some of the most undesirable species (Table 9). *Natica* spp. were present in 17 out of the 45 sea-stars collected, but nearly all specimens were of meio-fauna size. Most numerous in the stomachs was *S.elliptica,* a species which does not belong to those most desired by *Astropecten,* but all specimens found were less than 2 mm long and may, as discussed earlier, rank as "first class" food at this stage.

The small collection made off the Gullmarfjord (Table 6) on a gravel ground also shows a prey composition quite different from that found in *Astropecten* collected from a *Venus gallina* community. Here *Laevicardium norvegicum* was the most abundant prey species with 53 specimens found in the 14 sea-stars. Next came juvenile *Pagurus* sp. with 22 specimens, and, as in the Læsø material, quite a few *Natica* were present.

A gravelly substrate, and especially a shell-gravel substrate dominated by large shells of *Cyprina* for example, is in itself disadvantageous to *Astropecten* since it in many cases may prevent it from digging effectively into the substrate when sensing a potential prey organism. Under such circumstances more energy than normal will be used, both in unsuccessful as well as successful digging attempts, and the sea-star may also have to traverse more ground in seaching for food than on other bottom types. In the Øresund, however, *Astropecten* has never been taken on bottoms which, as judged from the contents of dredge hauls, consist entirely of shell gravel.

Variations due to possible differences in preference pattern

The variations in stomach contents so far discussed have been based on the influence of regional, seasonal and annual effects on presence or absence and relative density of acceptable and accessible prey species. In addition, differences in size distribution of prey species present also plays a role.

However, one cannot be certain that only these factors are responsible for differences in stomach contents at various localities, or even within the same locality.

As we have seen, the specimens collected in the Øresund and fed in the laboratory preferred bivalves, and did this with a fairly clear order of preference. However, it is reasonable to ask whether other populations of *Astropecten* would exhibit the same selectivity pattern if the same faunal composition existed throughout its distribution range. Orton (1929) made some experiments with specimens of the boring gastropod *Ocinebra erinacea* from three different English localities and found that specimens taken from a locality where oysters (*Ostrea edulis*) were absent or extremely rare would eat very few of these in the laboratory, whereas snails deriving from an oyster bed fed heavily on them. He concluded that a fixed difference in feeding habit existed between the two populations due to environmental conditions, i. e. the food organisms to which the snails had become accustomed.

Wood (1968) made a comprehensive study on another boring snail, viz *Urosalpinx cinerea,* along the U. S. east coast. He introduced the concept of "ingestive conditioning", that is that the predator will prefer a certain prey species after it has fed on it for some time. Many of the arguments used by Wood to explain the background for the occurrence of this phenomenon cannot be applied to predators which swallow their prey whole and are unable to gain access to the internal tissue by force. *Urosalpinx* uses different methods of attack, depending on type of prey, and these are apparently learned by individual specimens, which by concentrating upon a single prey species probably increase their attack efficiency. It should be stressed also that Wood's results do not invalidate those obtained by Blake (1960, 1961), whose main conclusion is that *Urosalpinx* among prey of the same type or the same species selects those with the highest metabolic rate.

Recently, Castilla & Crisp (1970) suggested that ingestive conditioning may occur in *Asterias rubens* and it cannot be ruled out entirely for *Astropecten,* especially in habitats where more or less equally attractive prey species may occur in oscillating densities, but none of the available data supports the idea. Sea-stars fed on *Nucula nitida* for many months, for example, will show the same preference for *Spisula subtruncata* as specimens fed wholly or in part on the latter species. In the Øresund, this species may fail to settle for several consecutive years, yet the preference for it is clearly upheld.

Sigalas (1922) states that *A. irregularis* prefers to feed on the gastropods *Nassa reticulata, Trochus* spp. and *Bittium reticulatum,* but refuses to feed on small *Cardium edule.* Especially the last statement seems hard to believe since the sea-star feeds voraciously on this bivalve in the Helsingør laboratory. That the statement is fallacious is indicated by the fact that Bouchet & Le Campion (1962) in their studies of 53 *Astropecten* collected in the same area (Arcachon, France) found that bivalves constituted by far the largest prey group. Curiously enough, however, *Venus gallina* was the most abundant bivalve, but a look at the list of the other species found shows that the sea-stars were mainly taken on a rather coarse bottom as also indicated by the authors themselves. Thus, *Laevicardium norvegicum* and *Lucina* sp. followed next in abundance.

The author is well aware of the danger in assuming that a predator displays the same feeding behaviour throughout its geographical range, but in the present case it seems obvious that evolution would not favour a population feeding on bivalves and gastropods which cannot be digested before several days or even weeks after ingestion of them.

The sea-star is, on the other hand, not so specialized in its feeding habits that it runs the risk of starving to death when settling of the most preferred prey species fails, but it may well influence its reproductive capacity (p. 97). The fact

that it may stay alive without any food at all for more then a year (Fig. 21) at a temperature range higher than that found in any Danish *Astropecten* locality constitutes further proof of its ability to survive for long periods when "first class" food may be lacking.

Whether it is able to obtain any supplementary "food" by "skin-digestion" as described for other echinoderms, including sea-stars, by Ferguson (1963, 1967) and Pequignat (1966) is not known. The same applies to the possibility of ciliary (flagellary) feeding as suggested for *Astropecten* by Gemmill (1915) and Gislén (1924). Both methods of securing supplementary food might prolong the life of an otherwise starving sea-star.

Other possible factors

Dickie & Medcoff (1963) showed that *Asterias vulgaris* in the Gulf of St. Lawrence benefits from the fact that one of the prey species, *Placopecten magellanicus*, does not tolerate the local temperature extremes as well as the predator. In the case of *Astropecten* it seems possible that a potential bivalve prey species may be the beneficiary because inactivity (limited or complete cessation of ciliary activity) of a bivalve will lower its metabolic rate and hence its attractiveness. This statement is made on the assumption outlined earlier that metabolic rate is a valid index for attractiveness.

THE INFLUENCE OF TEMPERATURE AND PREY PREFERENCE ON SEASONAL FEEDING RATES

In the following account relative feeding rates are expressed in terms of number of prey specimens swallowed per sea-star. This is permissable since the majority of prey specimens found belonged to a restricted size range and since the retaining periods of the species taken during peak periods of feeding are among the shortest found in the laboratory. In other words, if differences in retaining periods were considered, it would only further accentuate the differences found between periods of high and low feeding rates.

The relevant data on bottom temperatures, number of macro- and meio-fauna prey specimens swallowed, and percentage of empty stomachs for each month of collection in the Hornbæk Bay from January 1960 through June 1961 are given in Fig. 10 and Table 34. Before discussing these data it should be noted that temperature conditions below 20 metres depth usually are very stable, whereas this is not the case at 15 metres depths (Horikoshi, 1967). Since some of the *Astropecten* were taken between 15 and 20 metres depth, this may have had an influence on the feeding rate of some of the sea-stars analyzed for stomach contents, although there is nothing in the combined data which indicates anything in this direction.

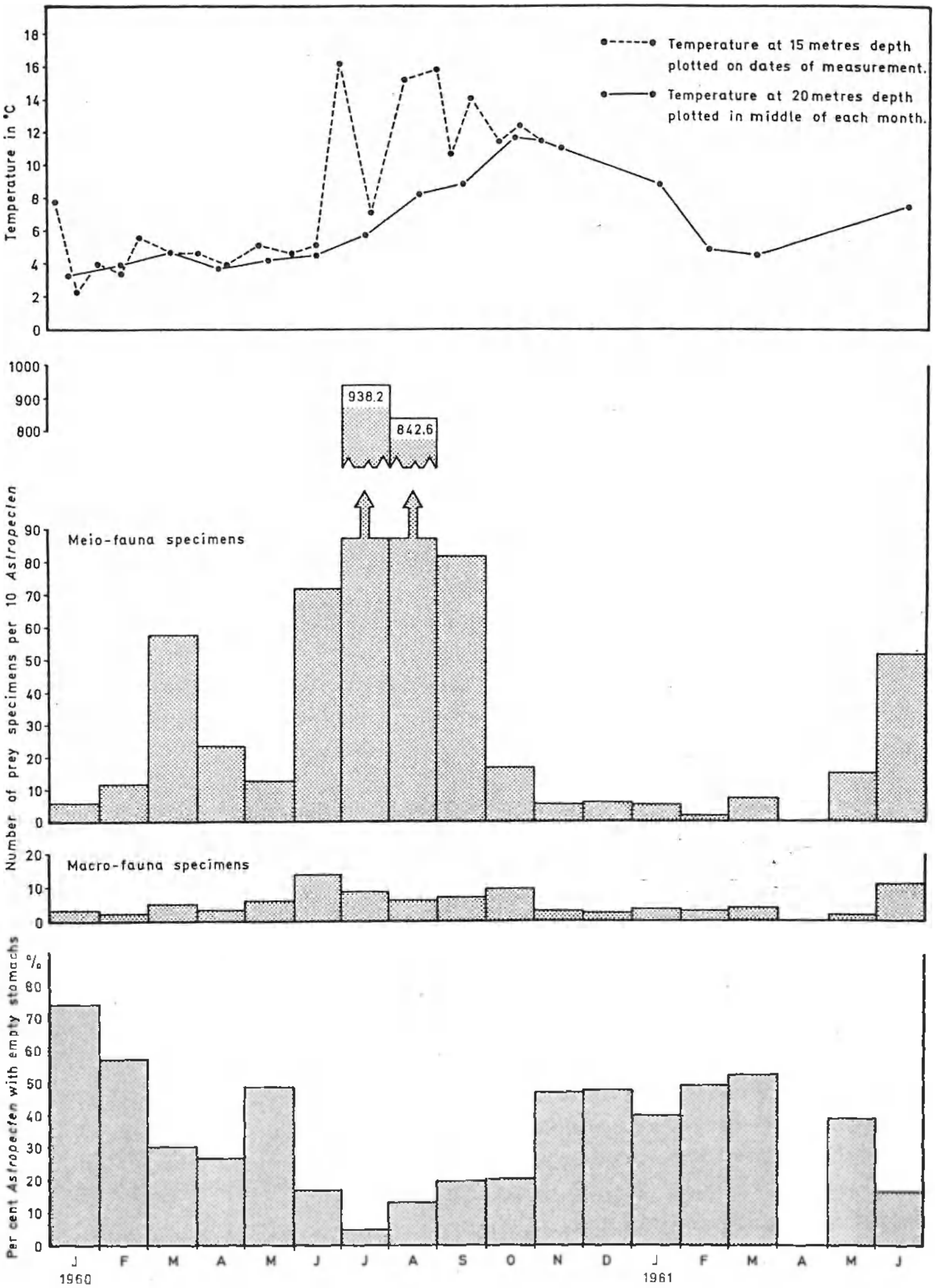


FIG. 10. Data on stomach contents of *Astropecten irregularis* collected in Hornbæk Bay (Øresund) from January 1960 through June 1961. Numbers and percentages given for each month are based on one to three collections of varying numbers of sea-stars (cf. Table 34). Temperatures at 15 metres depth were not available for the whole collecting period.

TABLE 34. Data on number of empty stomachs, total number of prey, number of bivalves, and temperature (in part) for each collection of *A. irregularis* made in Hornbæk Bay, Øresund, from January 1960 through June 1961. Temperatures mostly after Schram (1962), who generally made his measurements a few days before or after my samplings.

Date	Number of *Astropecten* collected	Number with empty stomachs	Number with empty stomachs in per cent of sea-stars taken	Number of prey specimens in stomachs	Number of prey specimens per stomach	Number of bivalves in stomach	Number of bivalves in per cent of total number of prey	Temperature at 20 m depth measured within 3 days of sampling
1960								
13.i	4	4	100	0	.	.	.	3.4
27.i	11	7	64	13	1.2	7	54	3.0
12.ii	75	48	64	44	0.6	22	50	3.6
19.ii	74	38	51	172	2.3	144	84	4.3
14.iii	53	14	26	292	5.5	235	80	4.8
30.iii	32	0	0	244	7.6	205	84	4.5
26.iv	59	16	27	159	2.7	126	79	3.8
10.v	42	23	55	76	1.6	50	66	4.3
27.v	52	23	44	110	2.1	67	61	4.3
9.vi	92	12	13	457	4.9	294	64	4.6
21+22.vi	70	16	23	939	13.4	830	90	4.5
20.vii	48	2	4	4549	94.8	4337	95	5.8
9.viii	11	1	9	1793	163.2	1754	98	6.1
15.viii	12	2	17	332	27.7	266	80	8.8
22.viii	14	2	14	1018	72.7	967	95	7.6
9.ix	43	16	38	645	15.1	621	96	8.2
22.ix	52	3	6	200	3.8	93	47	9.6
5.x	23	7	30	73	3.2	40	54	9.8
20.x	19	2	11	46	2.4	14	30	13.8
27.x	31	6	19	75	2.4	35	45	.
4xi	21	9	43	14	0.7	5	36	11.2
8.xi	15	7	47	23	1.6	11	48	.
18.xi	12	7	58	6	0.5	0	0	.
21.xii	27	13	48	24	0.9	10	42	.
1961								
4.i	12	6	50	7	0.6	2	29	.
8.i	20	6	30	25	1.3	4	16	8.9
26.i	20	9	45	16	0.8	5	31	.
15.ii	8	4	50	4	0.5	1	25	5.0
1.iii	11	6	55	9	0.8	3	33	4.5
16.iii	17	4	24	41	2.4	20	49	.
29.iii	19	15	79	4	0.2	2	50	4.9
26.v	5	2	40	8	1.6	6	75	.
26.vi	47	8	17	298	6.4	228	76	7.6
Total and mean values	1051	338	32	11716	11.1	10395	89	.

The bottom temperature at all depths from which *Astropecten* were collected was unusually low in the winter of 1959-60, reaching a minimum of 2.3°C in January. It is no wonder, therefore, that about 75 % of the sea-stars collected had empty stomachs, and that the mean contents of prey specimens found per sea-star was less than one. However, although the temperature only rose slightly above 4°C in February this was apparently enough to induce the sea-stars to start feeding on newly settled *Mya truncata* which, judging from larval data acquired by Schram (1962) must have been present, also in January. In March the feeding rate on *Mya* became higher and the sea-stars also started to feed more extensively on *Spisula subtruncata* from the 1959 settling. Less than 20 % had empty stomachs whereas 55 % had empty stomachs in March 1961. Furthermore, the mean number of prey specimens per sea-star was about five times higher in 1960 than in 1961, although the temperature was at least as high as in March 1960. This points to a complete absence of *S. subtruncata* and a scarcity of *Mya truncata* in March 1961 (cf. Table 10), where the 47 sea-stars had been collected. The presence of a notable number of the latter species in the June collections of 1961 indicates that the distribution was patchy, since they almost certainly had settled before March.

In April 1960 the temperature dropped once more below the 4°C level, and this may be the main reason for the low feeding rate in this and the following month. Another factor could have been the severe decimation of the remaining *S. subtruncata*, but *M. truncata* was still present. Hence it is highly feasible that *Astropecten* practically stops feeding at temperatures below 4°C in the Øresund. The few food animals found may have come mainly from specimens collected between 15 and 20 metres depth.

With the rising temperatures in June and the new spatfall of *S. subtruncata*, the feeding rate rose to a very significant peak in July-August, when the average content of prey specimens per sea-star stomach amounted to over 93 and 84, respectively (over 90 % *S. subtruncata*, Table 10). On one collection date, viz on 9 August, the average content per sea-star was as high as 163 prey specimens (Table 34).

In spite of a steadily increasing temperature the feeding rate in September was below 10 % of that found in August, and in October, when the maximum temperature (11.8°C) of the year was recorded, the feeding rate was as low as in April, although there were somewhat fewer sea-stars with empty stomachs. The reason for this must be that the *Spisula* population was almost completely exterminated by early September (cf. Table 10), and that no other species ranking high on the preference list were present.

A comparison of the data for September 1960 and September 1962 (Table 10) supports this conclusion. In 1962 there was evidently a heavy spatfall of *Montacuta ferruginosa* as well as an extensive settling of *Echinocardium cordatum*, with the result that the average number of prey specimens per sea-star stomach became as high as 42.4, i. e. over 5 times as high as that found for September 1960. This fact and the neat correlation between feeding rate and abundance of *S.subtruncata* in 1960 give no reason to suspect that a decline in feeding rate may be connected with breeding as known for several sea-stars. It is, furthermore, doubtful whether *Astropecten* reproduces in the Øresund exept in in very favourable years.

From November 1960 through March 1961 about half of the collected sea-stars had empty stomachs and the numbers of prey animals found in the remainder were very low. Many of the sea-stars only contained a few skeletal remains of ophiuroids, and one specimen collected on 16 March contained in fact more than one-third of all prey specimens found in the 47 sea-stars collected in that month. Furthermore, practically all the bivalves and snails found during the mentioned period had an eroded appearance and were full of sand, indicating that they had either been swallowed many weeks earlier or had been picked up as "dead" shells.

In June 1961 the percentage of empty stomachs was the same as in June 1960, but the number of swallowed prey animals was about 25 % lower although temperature conditions were much more favourable than one year earlier (Table 34). An apparent complete absence of *S.subtruncata* in 1961 and a scarcity of other suitable prey almost certainly account for this difference.

One final example of the influence of prey selectivity on feeding rate in the Øresund may be mentioned. In spite of a very low density of *S.subtruncata* in the Hornbæk Bay in August 1964, a high density of newly settled *Echinocardium* resulted in an average content of more than 47 prey specimens per stomach (Table 33). Had the latter species been absent, it is very likely that *Astropecten* would have all but starved during a month of the year at which feeding activity was at its highest in 1960. A clear example of such a negative influence caused by the absence or scarcity of suitable prey species can also be deduced from the unpublished data by Thorson on 29 *Astropecten* collected at 15 metres depth off Frederikshavn on 10 July 1951. In spite of favourable temperature conditions, only 111 prey animals were found, corresponding to an average of 3.8 per sea-star. Of these, 36 were *Montacuta ferruginosa,* which must have been scarce considering its rank as "first class" food (p. 000). Among the others were 17 *Venus gallina,* 20 *Corbula gibba* and 25 *Cingula semicostata,* but not a single *Spisula.* Obviously even this very low content of potential food found in the sea-stars in the midst of the main feeding season exceeded by far the amount of food actually assimilated per day.

Some information on the effect of temperature on feeding rate may also be gained from other field data as well as from the literature.

Out of 105 *Astropecten* taken off Frederikshavn in February 1952 only 20 contained food, and the total number of prey animals was as low as 24, in addition to a small number of *Hydrobia* egg capsules. Since bottom temperatures at 15-20 metres depth off the island of Læsø east of Frederikshavn ranged between 2 and

4.1° C from 4 February and well into March (Nautical-Meteorological Annual, 1953), this fits well with the conclusion that feeding practically stops below a temperature of 4° C.

It will be recalled that the fishermen at Frederikshavn normally catch very few specimens during the late winter months. In 1957, for example, they caught only 8 specimens over a period of seven weeks in February-March. The fishermen believe that the sea-stars either migrate to deeper waters or stay buried during this period. There is every reason to accept the latter point of view, i.e. the sea-stars are probably "hibernating" more or less constantly at temperatures below 4° C. This also agrees with the observation by Ursin (1960), who noted a distinct decimation of the *Astropecten* population in the eastern North Sea following the severe winter of 1946-47, when bottom temperatures below 3° C were recorded for a considerable period of time, indicating that such low temperatures may even be lethal for the sea-star if lasting too long (see also Wolff, 1968). Nowhere does it seem to occur at lower winter temperatures than in Danish waters (Ursin, op.cit.).

The eight sea-stars referred to above had an average stomach content of only 1.4 prey specimens although bottom temperatures in February 1957 probably exceeded 4° C most of the time (Nautical-Meteorological Annual, 1958).

Out of 20 *Astropecten* collected in February within 40 km of the German and Danish west coast (18) and the south-west Norwegian coast (2), ten had empty stomachs, seven contained next to nothing, and only three contained remains of more than one prey animal (Eichelbaum, 1909). The data given by Ursin (1960, p. 12) show that all these collecting stations are situated where the mean bottom temperature for February lies between 3 and 4° C. Thus, the findings of Eichelbaum are also in full agreement with those obtained in the present studies.

Blegvad's (1914) material from the Kattegat were taken during three consecutive years between early June and early September. His limited data point to a maximum feeding rate in August.

Usually sea-stars seem to have their optimum feeding rate at a temperature lying a few degrees below the mean temperature of the warmest month in the area where they live (Feder & Christensen, 1966; MacKenzie, 1967). In the case of *Astropecten* the pronounced preference of newly settled specimens of a limited number of species, settling at different times of the year, may lead to the paradox that food uptake becomes very limited under the most favourable temperature conditions. This is especially true in the Øresund, where the hydrographic conditions are rather intricate and strongly influence the pattern of larval settling, both in time and space (cf. Thorson, 1946).

There is bound to exist an upper temperature limit at which *Astropecten* becomes inactive and stops feeding, a limit which no doubt will differ throughout its long longitudinal distribution range. This limit has not been established in Danish or any other waters, but it has been noted once that it took about two weeks to adapt a number of *Astropecten* to feed in the laboratory at 17°C, although they were collected at a time of the year (September) when bottom temperatures at 20 metres depth and below are approaching the highest level of the year (cf. Fig. 11). If kept for a long time they will feed willingly at 18°C, which was the highest temperature recorded in the running sea-water system of the laboratory.

The lethal temperature has not been established, but the species does not seem to occur in Danish waters where the mean summer temperature exceeds 16°C (Ursin, 1960). In the laboratory no mortality was observed for specimens accidentally left for two-three days in stagnant water at room temperature (20-22°C).

RATE OF FEEDING AND GROWTH

Introductory remarks

If the retaining periods for different sizes of all prey species at different temperatures were known, it would be possible to estimate the total number of specimens of all species consumed by a population of *Astropecten* throughout a year of regular sampling. This is not the case, but rough calculations on the daily consumption of some of the more common prey species may be made. Reliable figures on amounts of organic matter or the calorific value for most of the meiofauna organisms, constituting the majority of the ingested prey, are lacking, and no attempts have, therefore, been made to analyse the field data from this point of view. In either case it must be emphasized that any results obtained would only apply to one particular year and only for the restricted area investigated.

Fenchel (1965) was able to follow the growth rate of a single year-class of *Luidia sarsi* in the Øresund over a period of about 18 months, and by determining the growth efficiency in the laboratory, he could then make a crude estimation on its food uptake in nature, based on the justified assumption that it feeds mainly on *Ophiura albida,* which always occurs in more than sufficient numbers.

It is obvious that such a procedure could not be applied in the present case. Based on present knowledge one may with some accuracy estimate how the stomach contents of collected *Astropecten* are related to daily consumption. However, unless a population is sampled daily or almost daily it is not always safe to estimate seasonal feeding rates on this basis. This can only be done if one is assured that suitable food has been abundant between sampling dates.

In the following subsection it is also assumed that all swallowed prey specimens can be handled simultaneously by the stomach wall. Only in rare cases may an *Astropecten* swallow too many or too large specimens to allow for this.

It should not be overlooked that although an *Astropecten* may well have to "wait" several days or even weeks before it can start to digest large prey of certain species it will also, if and when this happens, be able to assimilate an amount of food equal to that found in many hundred newly settled individuals. Macro-fauna specimens of species which are neither highly attractive nor distinctly disliked by the sea-star may, therefore, play a considerable role, since they are seldom ejected alive and have a fairly short retaining period. Thus, *Nucula nitida*, with a retaining period of 2-3 days for adult individuals, becomes an important food source when swallowed to the extent found by Hunt (1925).

Due to both species and size distribution these factors played a very small role for the Øresund population of *Astropecten* throughout the whole period of regular sampling, but this may not necessarily be a static phenomenon in the area.

Feeding rate in nature

For obvious reasons each prey species must be treated separately, and only the more common ones will be dealt with. The bivalves will be discussed first, beginning with the most preferred species. Other prey groups will be treated briefly since most of the necessary information on these were given in the section on stomach contents.

Spisula subtruncata: Based on the data in Table 19 it is justified to conclude that the average stomach contents of about 83 *S. subtruncata* per *Astropecten* in the Øresund samples from July-August 1960 (Table 10) represent less than the number swallowed and digested per day. The facts that over 66 % of the *Spisula* removed from the stomachs were digested (Table 21) and that a notable number of sea-stars (13.5 % in August) had empty stomachs point in the same direction. At Frederikshavn, where the sea-stars were collected very early in the morning, only 5 out of 322 specimens had empty stomachs. In the laboratory; *Astropecten* will feed at a fairly steady rate for many months when given suitable prey to feed on, so it is very unlikely that it should not pick up food every day during periods when its favourite prey is exceedingly abundant. The empty sea-stars had probably ejected their stomach contents in preparation for the next period of feeding activity. In a number of cases, sea-stars were removed from the Sigsbee trawl or the dredge with their stomachs everted. Whether they were caught while ejecting food remains or were induced to this in the collecting gear is not certain, but since so few had empty stomachs in the Frederikshavn summer material, where the hauls lasted much longer, the first possibility seems more likely.

In the laboratory a small sea-star may pick up all of 100 *Spisula* spat present within an area of about 500 cm^2 (corresponding to a density of about 2.000 per m^2), digest the meat and eject the empty shells within 19 hours (p. 40). Adult specimens may digest between 200 and 300 spat simultaneously (p. 58).

On this background it seems justifiable to conclude that each of the *Astropecten* caught during July-August 1960 in the Øresund on an average must have eaten more than 100 newly settled *Spisula* per day. In other words, the number of

Spisula actually found in the sea-stars represent significantley less than the number destroyed per day.

Apart from the distinct preference for *S.subtruncata* shown by *Astropecten*, the density of this prey species is the most important factor determining the number destroyed per day. The data given in Table 10 and indirectly in Fig. 10 indicate that the settling and survival pattern in the Øresund in 1960 was the same as that found for 1965 in the same area by K. Muus (1966), and it is quite clear that the sea-star made very good use of this food resource right until the population was as good as exterminated. In fact, the data in Table 33 strongly suggest that if any threshold density exists, at which *Astropecten* no longer seeks this prey species, it must be very low. If *Echinocardium* had not been so abundant at the same time, thus reducing the need of *Astropecten* to traverse much ground in search of acceptable food, it is conceivable that an even higher ratio of *Spisula* consumed to *Spisula* present would have occurred.

The comparatively lower number of *Spisula* found in the Frederikshavn summer material (Table 9) must be due to the density factor, since only a reduced population, deriving mainly from the preceeding year, was available.

Spisula elliptica: Although this species definitely is less acceptable than its relative, *S.subtruncata* (Table 22), and seldom occurs together with it, it ranks higher on the preference list than *Nucula nitida* (Table 23) upon which *Astropecten* thrives very well in the laboratory. There are also indications that it is much preferred to other species living in coarse substrates (Table 23). However, in the only area in the Øresund, where *S.elliptica* is constantly abundant, viz on a long stretch of shell gravel bottom off the Swedish coast north and south of Höganäs, *Astropecten* seems to be absent.

Also *S.solida* may be picked up in large numbers in the North Sea (Table 5), and in one case, 67 specimens were found in a single sea-star. In view of the relative short average retaining period of 33 hours for the "large" specimens listed in Table 19, it may be assumed that the usually very small *S.elliptica* and *S.solida* swallowed in nature are digested within 24 hours irrespective of numbers present.

Montacuta ferruginosa: This species was seldom taken during the period of investigation in the Øresund, but when a successful spatfall occurs, it is taken by *Astropecten* in considerable numbers (Table 10, last column). Since it also seems to have a short retaining period (Table 19), there is every reason to suspect that any numbers found in a stomach represent less than the numbers actually digested within a 24 hour period.

Mya truncata: As implied earlier this species seems to be at least as attractive to *Astropecten* as *M.arenaria*. Nearly all specimens found in the investigated sea-stars were less than 5 mm long (Tables 13 & 14), and this seems, therefore, to be about the maximum size taken in nature. Hence all stomach finds of this species must represent less than what may be consumed within a 24 hour period (cf. Table 19).

Solenidae: Although species of this family usually are rare in the stomachs of *Astropecten* the dominance of an *Ensis* sp. in a material from the North Sea (Table 3) shows that exceptions may occur. As the retaining period of *Cultellus pellucidus* up to a size of at least 8.5 mm is as short as 5-6 hours (Table 19), it is quite certain that stomach finds of newly settled members of the Solenidae – and only these are taken in nature – represent considerably less than what may be digested per day.

Cyprina islandica: Juveniles of this species occasionally occur in considerable numbers in *Astropecten* stomachs, especially in the North Sea (cf. Table 4). It was not possible to secure specimens of this size for experiments on their retaining period, but it is bound to be considerably lower than the average period of 45 hours for specimens ranging between 6.7 and 10.8 mm in length (Table 19). A period of about 20-24 hours for 2-3 mm long specimens and still less for smaller specimens is to be expected in view of the very large difference in retaining periods between the two size groups tested (Table 19). In other words, stomach finds of juveniles of this species probably represent just about what may be eaten within 24 hours.

Nucula nitida: This species was all but absent in the many sea-stars collected in the Hornbæk Bay (Table 10) in spite of the fact that it was very common in the bay during the whole collecting period in 1960-61. However, it did occur in the Frederikshavn material (Table 7) and was, along with two other species of *Nucula,* present in significant numbers in the *Astropecten* investigated by Hunt (1925).

As will be recalled (p. 60) the empty shells may often be retained for a long time. However, if the shells look fresh and are not found "tucked away" in the arms of the sea-star as described elsewhere, it may be assumed that half-grown and adult specimens represent 2-3 days consumption.

Venus gallina: The predation on this species in relation to that on *S. subtruncata* has already been discussed in detail earlier (p. 75), so a few remarks may suffice here. It is evident that the stomach contents of *Venus* in the "best" case, i.e. when only juvenile specimens are ingested and all are presumed to be retained and digested, represent several days consumption. However, since about 70 % of all swallowed specimens are apt to be ejected again alive, at least in Danish waters, one may estimate that stomach finds of this species on an average represent 2-3 weeks consumption, depending on temperature and size of the specimens.

Corbula gibba: With our present knowledge it is difficult to estimate what stomach finds of macro-fauna specimens "stand for". It is probably not far from the truth, however, that they – on an average – represent 10-14 days consumption. The longer retaining period – as compared with *V. gallina* – must be compensated for by the higher percentage of specimens retained and digested (see also Table 31). Since fully adult specimens are able to withstand anaerobic conditions much longer than any other species investigated (Table 20), it is conceivable that 3-5 weeks may pass in these cases before the clam may be digested (see also p. 50).

Pectinaria koreni: Among polychaetes, only juvenile *Pectinaria koreni* were found in significant numbers, notably in North Sea materials (Tables 3 & 4). Since adults containing many hundred times the amount of organic matter are retained for only 34 hours on an average (Table 19), it is certain that newly settled individuals are digested in a few hours. Hence stomach contents of these must represent considerably less than the number digested within 24 hours.

Retusa umbilicata: Although the majority of the *Retusa umbilicata* found in the Frederikshavn material (Table 8) were undigested, the small size and the direct access to the internal tissues indicate that they may be digested and the empty shells ejected within a day or two. Stomach entrance is not as simple as in the case of newly settled bivalves, but since the maximum number found in any stomach was 28 (Table 11), an adult sea-star should have no difficulty in digesting these at one and the same time, unless a significant number of other prey is also present.

Echinocardium cordatum: Since specimens around one centimetre in length are retained for only 29-37 hours, it can be taken for granted that newly settled specimens up to the length of 5 mm are digested within 24 hours. Whether all the internal tissue is digested could not be determined from the field material, but this may not be the case. Larger specimens ingested in the laboratory have been ejected as bare tests with all the spines detached, but with some internal tissue left undigested. If, moreover, no attempts are made to ingest all the internal tissue by stomach entrance through the rather narrow mouth opening, it is conceivable that even the maximum number of 165 specimens found in a single sea-star may be disposed of within 24 hours. This depends on whether notable numbers of other prey species are present at the same time, which was not the case in the Hornbæk Bay in August 1964 (Table 33) and this may no doubt often happen in the Øresund. If *Montacuta ferruginosa* is abundant, as in September 1962 (Table 10), such high numbers of *Echinocardium* may probably not be swallowed, even if this species also is abundant.

In summing up the data given and discussed in the present subsection, one may state that *Astropecten* is obviously capable of destroying a three-figured number of prey specimens daily during peak periods of feeding, and that the actual figure is more dependent on the kind of species present and their density than on any other factor. Even at a temperature of only 6-7° C, one may find over 160 *S. subtruncata* per sea-star stomach, which was the case on 9 August 1960, indicating a daily consumption of over 200 specimens. It would probably be higher at more favourable temperatures. However, these figures should not mask the fact that the amount of food obtained in terms of dry organic matter may well be modest when all the prey swallowed is newly settled specimens.

Growth in nature

From the data given in Table 2 it is seen that size frequency distribution of the sea-stars caught in the Øresund cannot be used to differentiate year classes and hence rate of annual growth. Moreover, the material was collected with different types of gear which tend to retain different size groups of sea-stars. Thus, 42 specimens caught with a dredge on 10 May 1960 had a mean R of 15.5 mm (Table 34) whereas 28 specimens taken the same day with a Sigsbee trawl, had a mean R as high as 27.7 mm. None of the collecting gear used ever yielded specimens with an R of less than 5 mm.

It is clear, however, that growth in the Øresund must be extremely slow. This is also indicated by the data on mean sizes (R) given in Table 2, showing that almost no growth took place in 1960. Whether the slightly higher figures for 1961 and the significantly higher figures for the two collections made in 1962 and 1964 reflected the growth of the population sampled in 1960 is uncertain, but it may well be the case. The slow growth is not surprising considering the modest annual food uptake. The sea-stars are definitely undernourished in this area in the sense that they would eat much more if suitable food species were more abundant and available throughout longer periods of the year. Compared with the Frederikshavn area there is a shorter period with "summer" temperatures and the temperature level reached is several degrees lower (Brattström, 1941), and these conditions will in themselves lead to a lower annual food uptake. More important, however, is that the density of preferred prey seems to be low in the Øresund during the period when the highest temperatures prevail. This was the case in 1960, and from the data given by K. Muus (1966, and personal communication) as well as the general impression from nearly ten years of more or less intense sampling by staff members from the Helsingør Laboratory in the area there is every reason to believe that it will be the case practically every year. In fact, in years when *S. subtruncata* fails to settle, it is easy to envisage that *Astropecten* may not secure food enough to grow, let alone to reproduce.

In this connection it may be pointed out that Thorson (1946) found only seven *Astropecten* larvae during his regular survey of the plankton off Ven during the years 1936-1939, and that Schram (1962) did not find any at all in 25 500-litre samples taken just south of the Hornbæk Bay in 1959-1960. The facts that sea-stars weighing about one gram may reach a weight of nearly 18 grams in one year in the laboratory and show an increase in R from about 17 mm to about 47 mm (Fig. 12) during the same time also show that growth is hampered in the Øresund. Only a lack of adequate food can explain this, although the temperature factor, of course, plays a significant role too. The data become even more illustrating when it is pointed out that no *Astropecten* weighing over 13.7 grams were caught in the Øresund during the present studies and that only very few specimens taken had an R of 43 mm or more in spite of the fact that even under the much higher temperature conditions in the laboratory, the sea-star may attain an age of at least $9^1/_2$ years.

It is well known that many invertebrates do not reach the same size in the Øresund as elsewhere. In the case of *Astropecten* this was already pointed out by Brattström (1941), but it has never been demonstrated that the primary cause for this is an insufficient food source, a fact which should not obscure that the indirect reason for this is the peculiar hydrographic conditions which exist in this area.

The North Sea specimens studied were also small compared with those collected off Frederikshavn (Table 1), although practically all of them were collected by trawling. Ursin's data (1960) also indicate that only few North Sea specimens reach a size comparable with the majority of those taken in the northwestern Kattegat. It is generally accepted that production of potential prey animals is significantly lower in most parts of the North Sea than in the Kattegat (Petersen, 1913; Stephen, 1933; and others), and *Astropecten* is, furthermore, all but absent from such a rich fishing ground as the Dogger Bank (Ursin, op. cit.). On this background it seems that also in the North Sea there is not a suitable prey population large enough to allow the same rate of growth and reproduction as in the northwestern Kattegat. Consequently, it is also doubtful whether Ursin (op. cit.) is correct in suggesting that specimens with an R of 20-29 mm in the North Sea may belong to the 1-group. In my opinion they may well be several years old.

The *Venus* community off Frederikshavn offers much better conditions for *Astropecten* than the Øresund. Summer temperatures are higher and other hydrographic factors more stable. The area supports a large population of plaice, which has been fished by seiners for many years. Since the preferred bivalve food species of this fish and that of *Astropecten* largely are identical (Hunt, 1925), ample food must be available in most years, and it is, therefore, not surprising that the sea-star reaches a very large size in the area. Its rate of growth is probably also considerably faster than in any other area from which material have been obtained. In the laboratory, specimens collected in the Øresund may easily reach the same size when given an unrestricted food supply.

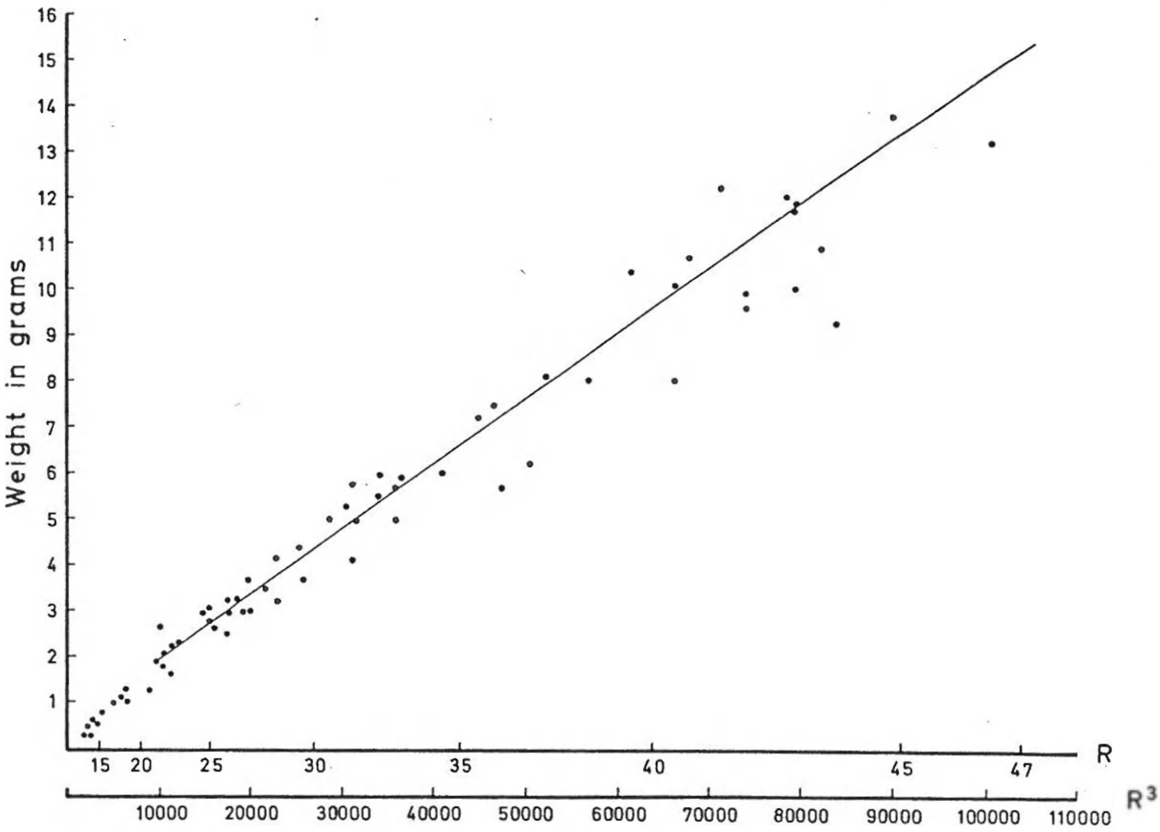


FIG. 11. Weight-length relationship and weights plotted against R^3 for 63 *Astropecten irregularis* collected in Hornbæk Bay in January, April, October, and November 1960. Regression line fitted by eye.

In Fig. 11 the weights of 66 specimens collected at different times of the year in the Øresund are plotted against the third power of R. Since the points are scattered evenly on both sides of a straight line for all but the smallest individuals growth is probably isometric. The same is likely to be true for specimens living in other areas, but the slope of the line would no doubt be steeper when based on material collected in richer areas such as off Frederikshavn. Furthermore, specimens from richer localities can "afford" to use much more of their energy intake on reproduction, which would result in a wider scatter around the regression line. In the laboratory, equally large specimens may vary much more in weight than specimens of the same size just collected in the Øresund, depending mainly on state of nutrition and stage of development of gonadal material. The latter factor is especially notable in females. After spawning the weight may be reduced by more than 25 %, whereas an accompanying reduction in R is almost negligible (cf. Fig. 13).

Growth and feeding rates in the laboratory

All feeding experiments on juvenile bivalves discussed earlier were obviously of such short duration that feeding rates in terms of numbers taken daily over a longer period cannot be deducted from them. However, they did clearly show that the rates of feeding on different species differ greatly, also when newly settled specimens are involved, and that non-attractive juveniles may be ejected alive to about the same extent as macro-fauna specimens. Moreover, all the field data, as already discussed, agree entirely with the laboratory findings. In other words, quantitative studies on feeding rates in the laboratory may justifiably be carried out with macro-fauna specimens since the rank of attractiveness is linked primarily to species and only secondarily to size of prey.

In feeding experiments designed to show how much food an *Astropecten* will ingest under optimal feeding conditions it is, of course, necessary to use prey species which are both attractive and accessible to the sea-star. Since they also preferably should be of common occurrence in the natural habitat of the sea-star, this further reduces the number of species which may be used.

With due consideration to these prerequisites there was really only one ideal species available, viz *S.subtruncata* which could be dredged in large numbers in 8-12 metres depth in certain spots along the coast north-west of Helsingør where part of the population may survive to reach adult size. In addition, *Nucula nitida* was also used.

It was not possible with the technical facilities then available to carry out feeding experiments at constant temperatures for any length of time.

Consequently, only the experiments carried out in aquaria supplied with running sea-water will be recorded and discussed.

During the major part of the year the temperature was significantly higher in the laboratory than in the locality from which the animals were taken. Besides raising the metabolic rate of the prey species, the higher temperature also in some cases induced epidemic spawning in *S.subtruncata,* which thereby must have lost a significant amount of organic matter. The sea-stars can compensate for this by ingesting a larger number of prey specimens, but the point becomes important if an attempt is made to express daily food uptake in terms of dry organic matter based on determinations of freshly caught specimens of the same size as those eaten by the sea-stars. It is equally important if one tries to estimate how many newly settled specimens should be ingested to account for the same amount of dry organic matter as that of a prey specimen of known size swallowed in the laboratory. However, although rough estimates probably could be made in both directions, the main purposes of the experiments were to study growth under laboratory conditions, and to test the conclusions drawn from other evidence that the sea-stars would grow much faster in the Øresund if more suitable prey were present in sufficient numbers during the warmer season of the year.

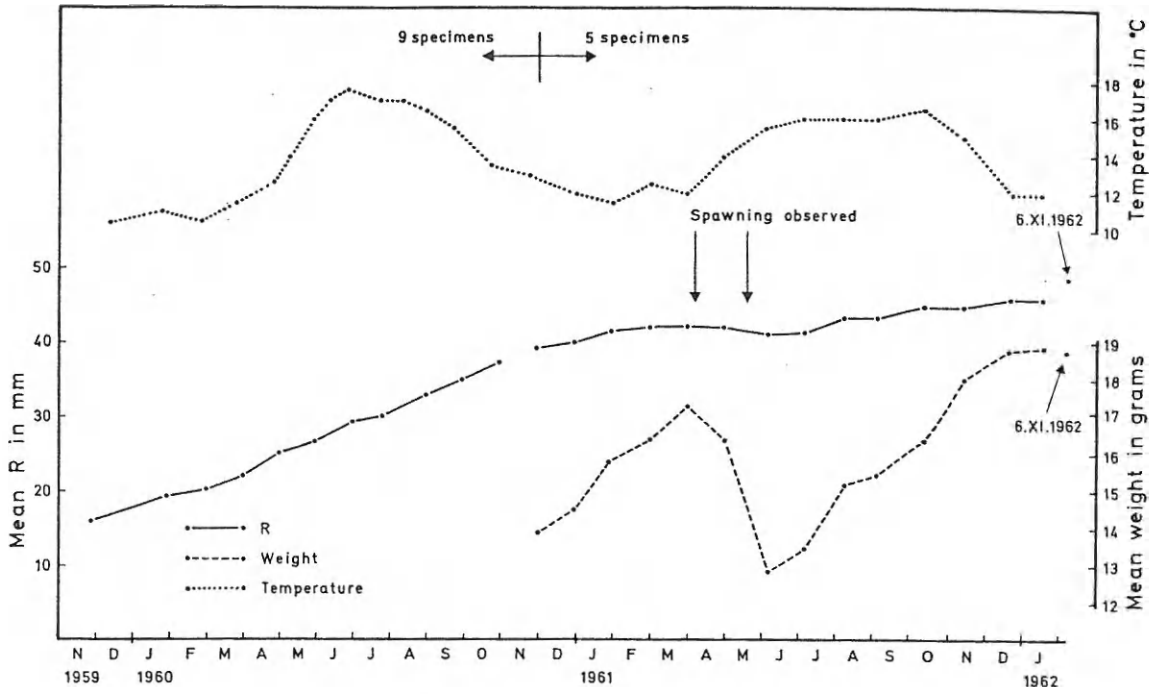


FIG. 12. Results of feeding experiment F-I (cf. text).

As it could not be supposed that too much handling of the sea-stars would not influence their feeding rate and hence rate of growth, the first experiment (F-I, Fig. 12) was carried out with 9 juvenile *Astropecten* being given an unrestricted food supply, consisting mainly of small *S.subtruncata* and *M.arenaria,* without disturbing them unnecessarily. Thus, the number of swallowed specimens was not determined as this requires sifting of the sand, but empty shells found on or just below the surface were picked up now and then. The sea-stars were only picked up, one at a time, for a few minutes once a month to measure their R's, whereas the rather rough treatment necessary in weighing them was avoided. As shown, the average R of the sea-stars increased from 16 mm to 39.5 mm in one year and apparently at a rate not visibly influenced by changes within the rather high temperature level (10.5 to 17.5°C). After this first year, the sea-stars, which must have had an average weight of about one gram at the start (cf. Fig. 11), were weighed and proved to have attained an average weight of almost 14 grams, i.e. they had already reached the weight found for the heaviest (and considerably larger) specimens taken in the Øresund. Four specimens were then removed to make better room for the remaining sea-stars in the aquarium, and from then on the animals were weighed at intervals of about one month as also shown in Fig. 12. This was done because spawning had been observed in other specimens of this size in the laboratory, and we shall soon see that this decision was well motivated. During the first four months with only 5 sea-stars present, the average weight increased from 13.9 grams to 17.3 grams, whereas the average R only increased from 39.5 to 42.5 mm. If one compares these data with the data in Fig. 11 it is seen that field specimens with R's of the mentioned lengths only weigh around 10-11 grams. The reason for the modest size increase which in fact came to a standstill in February-March, became evident later when it was found that the animals – as expected – had been using most of their energy intake in building up their gonads. As the temperature rose in April-May, two spawnings were observed, one on 6 April when two males released sperm, and one on 18 May when all sea-stars spawned simultaneously. It was then found that the other three specimens were females. Other spawnings may have occurred during these spring months without being observed.

As could be expected, a subsequent reduction in weight took place, and it is in the present connection important to note that it took the sea-stars about seven months to regain the lost weight. The size of the animals were also affected, although only very slightly, and the subsequent growth was very moderate. About 26 months after the start of the experiment, i.e. in January 1962, the sea-stars had attained an average R of 47 mm and an average weight of nearly 19 grams. Almost 11 months later the average R was 48.5 mm and the average weight was practically unchanged. In all likelihood another spawning had taken place in the meantime, but since the animals were left completely undisturbed during the mentioned period, no definite proof is available. Fig. 17 shows, however, that an isolated adult female may reach the astounding weight of 32.8 grams by steadily producing eggs, which it apparently "refuses" to release in the absence of sperm in the water.

Alone on the basis of the experiment described above (Fig. 12) in which the sea-stars constantly had an abundant food supply and were kept at temperatures much more favourable than those existing around 20 metres depth in the Hornbæk Bay, it can be safely concluded that it must take *Astropecten* living in the Øresund many years to reach a size with an R of 45 mm or more. As we already know (see also Brattström, 1941) very few specimens do in fact become so large in this area.

Another experiment (F-II, Fig. 13), with four sea-stars of the same size as those used in experiment F-I, gave even higher growth results, although these sea-stars were subjected to weighing once a month from the start and each time kept in a separate aquarium until all prey specimens had buried into the substrate. Also in this case an unrestricted food supply, mainly of *Spisula subtruncata,* was offered. In one year the average increase in R was 27 mm as against 23.5 mm, and the average wieght increased from one gram to 17.5 grams as against 13.9 grams in the first experiment. The four sea-stars also attained an average R of 40 mm after only eight months, whereas it took a full year in experiment F-I. It will be noted that both experiments were started about the same time of the year, the first one in November 1959 and the second in December 1960. The different results of the experiments are probably due to individual variations in feeding behaviour.

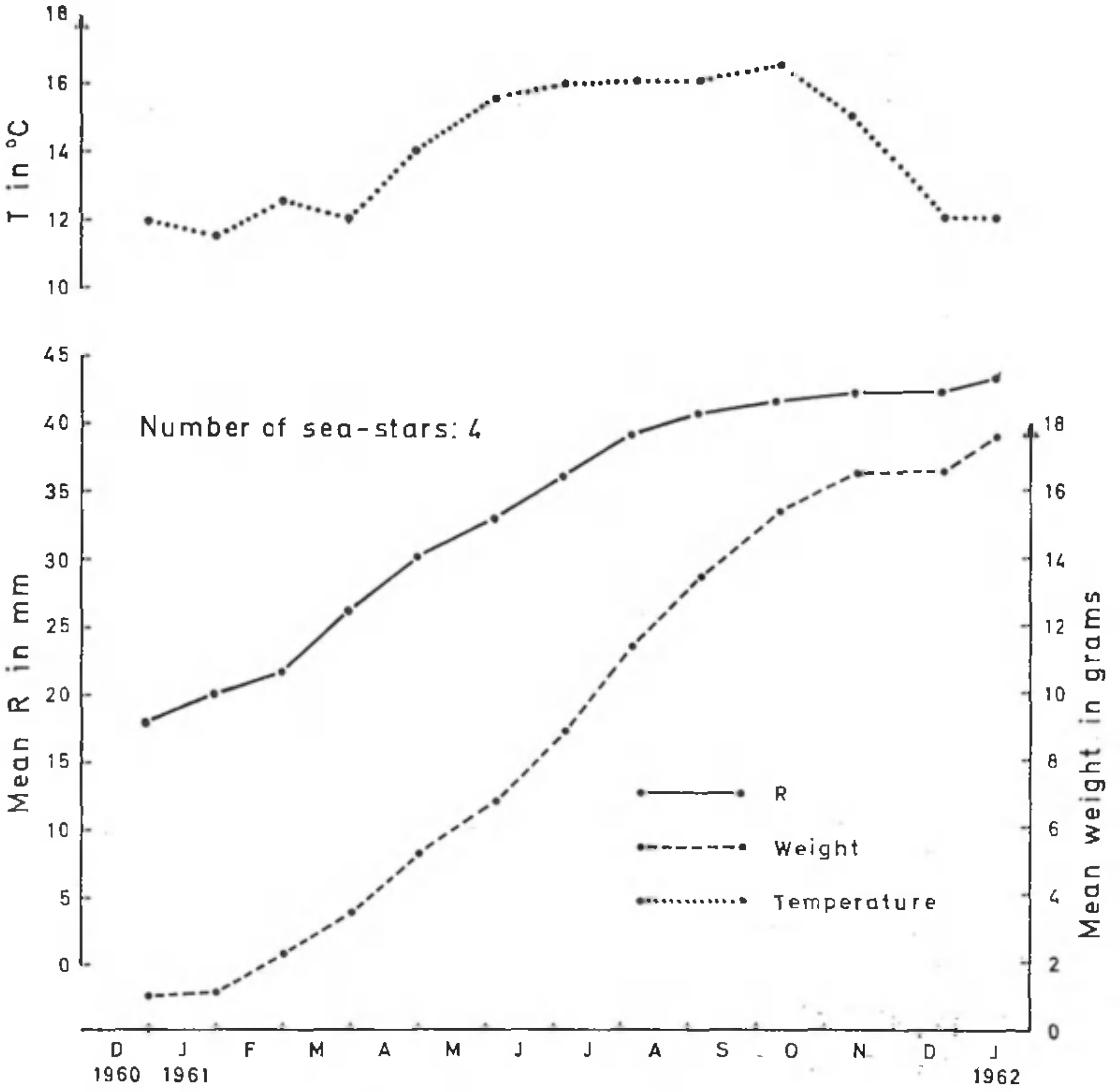


FIG. 13. Results of feeding experiment F-II (cf. text).

In the experiments described below, feeding rates were calculated in terms of prey specimens of known sizes eaten daily per sea-star as determined by checks made at intervals of about 14 days.

In Fig. 14, the results of two experiments (F-III & F-IV) are compared. They indicate that *Astropecten* under otherwise identical conditions will assimilate a more or less "fixed" amount of organic matter daily irrespectively of the prey specimens being offered, provided that these do not differ too much in attractiveness and are unable to escape being caught. It will be noted that feeding on *Spisula subtruncata* and *Nucula nitida* resulted in roughly the same rate of growth although the sea-stars feeding on *Spisula* ate more than twice as many specimens than those feeding on *Nucula* which, furthermore, had a significantly smaller average length. The reason for this could well be the considerable difference in nutritive value between the two species. As mentioned earlier, *Spisula* also sometimes

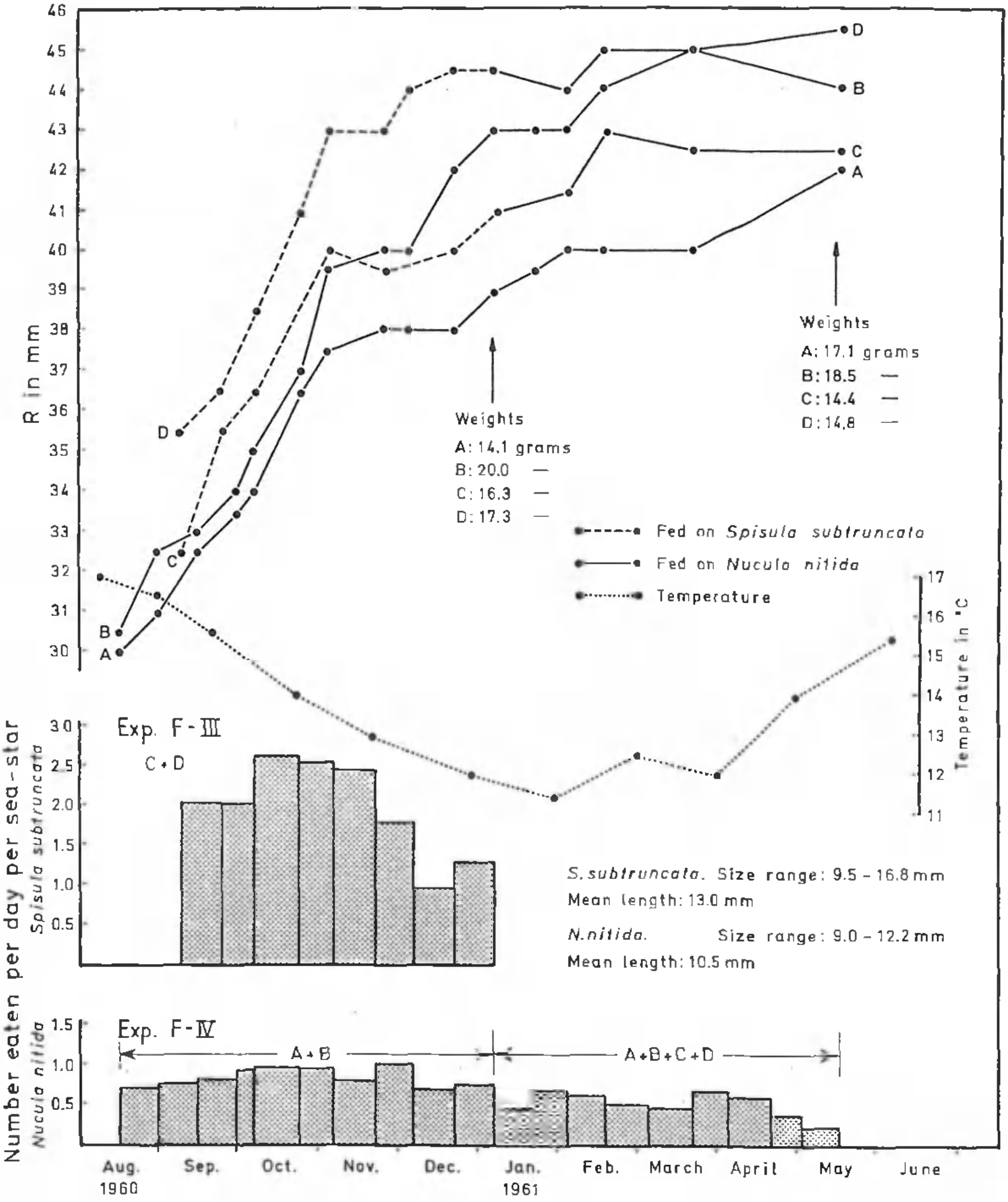


FIG. 14. Results of feeding experiments F-III and F-IV (cf. text).

spawned when brought into the laboratory, thereby loosing further in nutritive value.

From early January 1961, all four specimens were fed on *Nucula*, but still kept in two separate aquaria. As noted in the figure, the daily food uptake fell, but this was true for both pairs, i.e. it was not due to specimens C and D eating less because they had been "adapted" to feed on *Spisula*. In fact, these specimens had lowered their feeding rate very significantly while still feeding on *Spisula*.

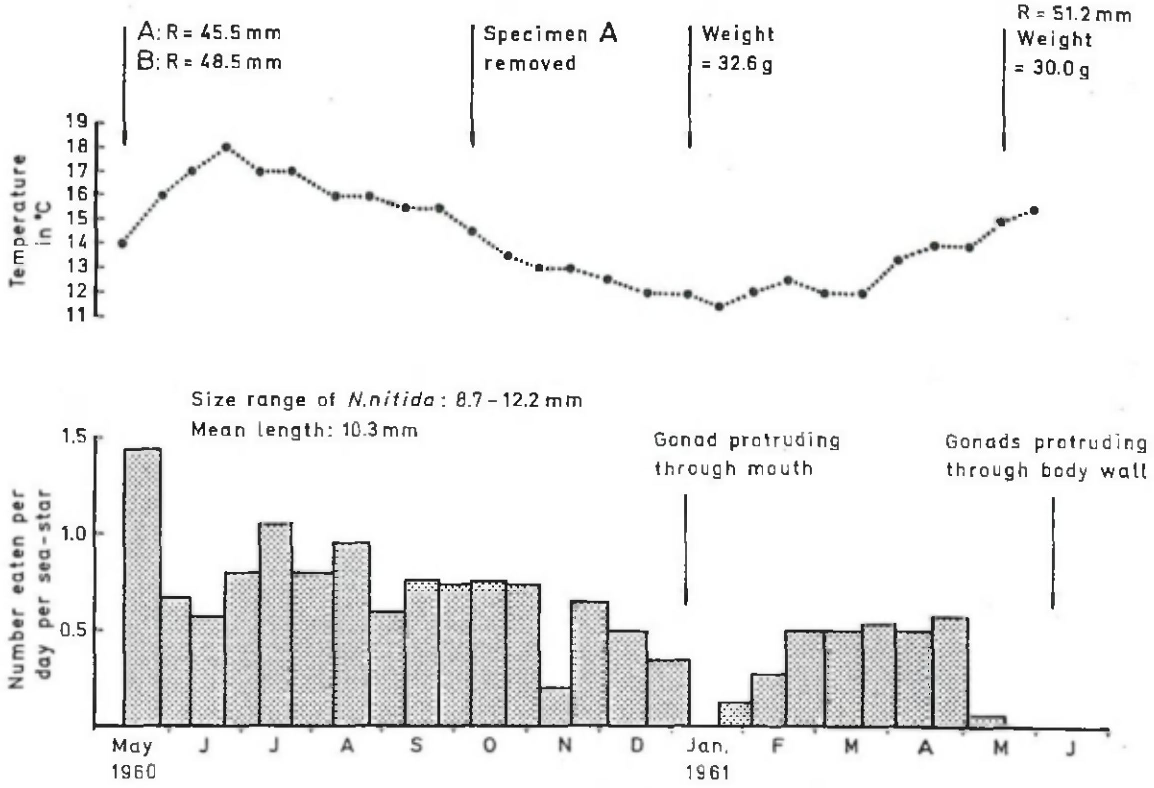


FIG. 15. Results of feeding experiment F-V (cf. text).

The observation that three of the specimens lost in weight while feeding on *Nucula* from early January to the middle of May suggests that they may have spawned during this period, presumably after the temperature began to increase towards the end of January. The fact that growth levelled off or even became negative is also in accordance with the observations recorded in Fig. 12. On this background it is reasonable to ask whether the reduced feeding rate could be connected with the reproductive cycle. Such an effect has been recorded for two species of *Asterias* (Galtsoff & Loosanoff, 1939; Hancock, 1958; MacKenzie, 1967). Since the reductions in feeding rate shown in Fig. 14 coincide with declining temperatures (except for late April and May), and since any animal will feed less voraciously when approaching maximum size, the results of the experiments do not, however, warrant any conclusions in this direction.

Fig. 15 shows the feeding rate of two specimens which already had reached about the maximum size attained in the Øresund (experiment F-V, prey species *Nucula nitida*). Unfortunately, one specimen became infected with an unknown skin disease and had to be removed about five months after the start of the experiment. It turned out to be a female, as was the other specimen. A gradual decline in feeding rate is again apparent, but this coincided with declining temperatures, and when the temperatures began to rise in the middle of January 1961 the feeding rate increased once more although not to the level recorded from May to

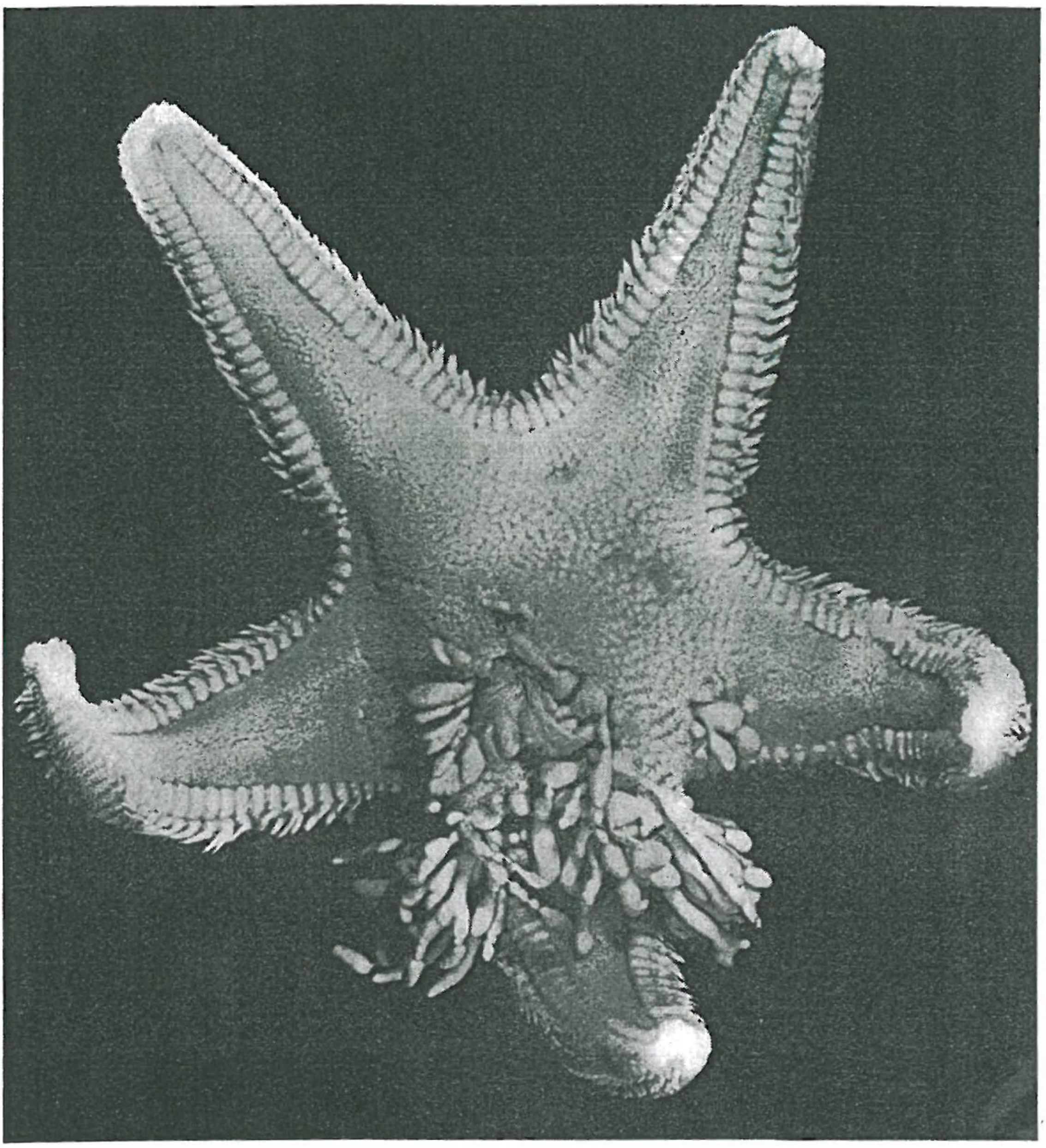


FIG. 16. Specimen of *Astropecten irregularis* with gonads protruding through body wall (cf. Fig. 15 and text). Photographed in preserved state by H. Knudsen.

early November 1960. However, a third factor obviously played a decisive role. By January 1961 the sea-star had produced so many eggs that parts of the gonads broke through the stomach wall and protruded through the mouth opening. No food was taken for at least 10 days while some of the gonadal material was disposed of through the mouth (note the reductions in weight between January and May 1961). Feeding was then gradually resumed and the animal fed at a steady rate for more than two months until early May. During the next check period only one *Nucula* was ingested, and on 7 June the animal bursted with parts of at least two gonads piercing through the body wall (Fig. 16).

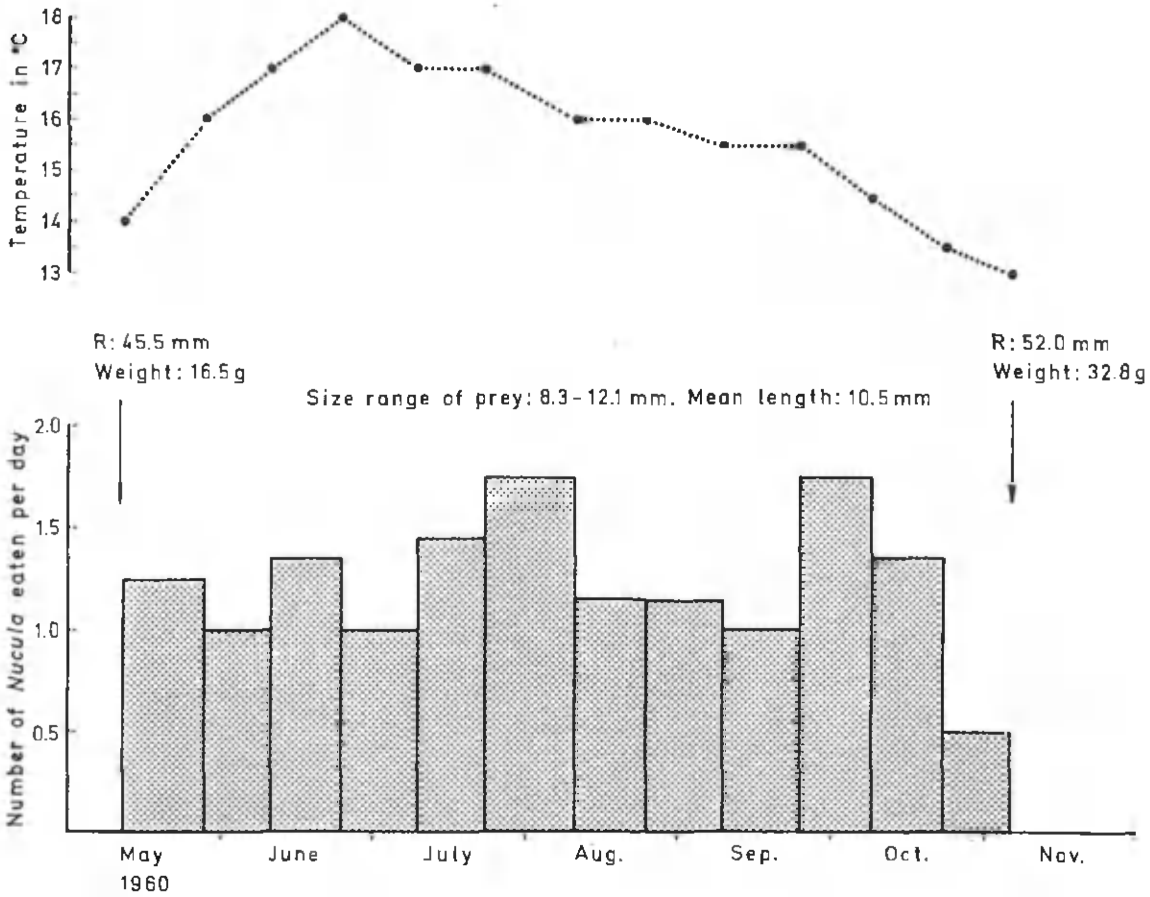


FIG. 17. Results of feeding experiment F-VI (cf. text).

Fig. 17 (exp. F-VI) shows the feeding rate of another adult sea-star which was not sexed, but since it attained a weight of almost 33 grams without spawning it was in all probability a female. The animal fed at a considerably higher rate than the two equally large females feeding on *Nucula* of the same size during the same period (cf. Fig. 15). It is possible, however, that the sea-stars used in the latter experiment had a higher initial weight since they had been kept and fed in the laboratory for several months prior to the start of the experiment.

The results of the last two experiments (F-VII & F-VIII) depicted in Fig. 18 show feeding rates and growth of, in each case, two medium-sized female *Astropecten* feeding on *Spisula subtruncata* and *Nucula nitida,* respectively. It is almost certain that in terms of dry organic matter (see pp 109-110) the specimens given *Spisula* fed at a somewhat lower rate than those feeding on *Nucula* (from late December 1960 to the middle of May 1961). Note also that specimen A, after an initial period with a "normal« feeding rate and accompanying increase in weight, stopped growing and lost slightly in weight during the last ten weeks of the experiment. It is difficult to explain why this happened, but one may suspect that it had something to do with an increasing size of the *Spisula* offered in the cause of the experiment. During the first four check periods the average size

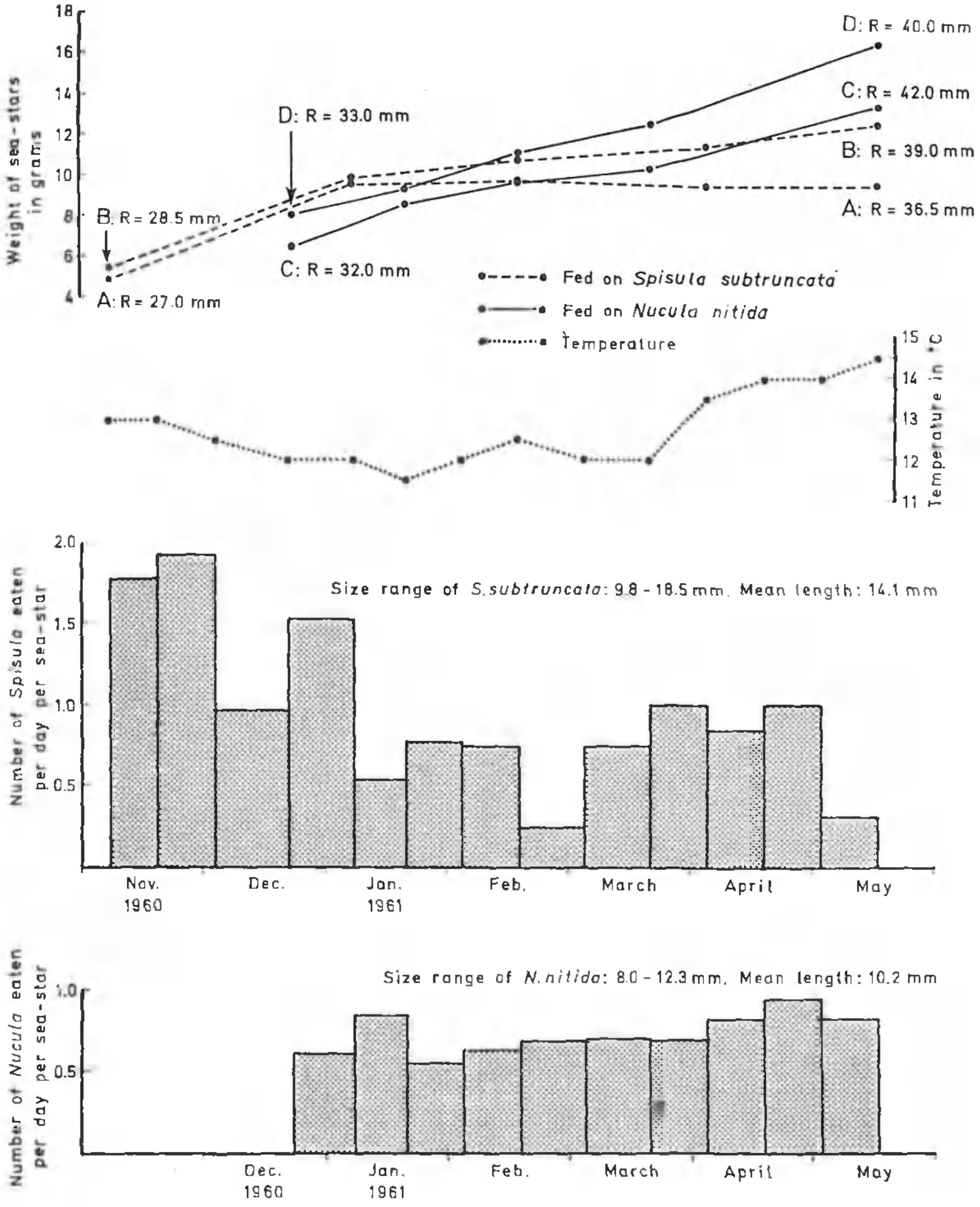


FIG. 18. Results of feeding experiments F-VII and F-VIII (cf. text).

never exceeded 14.2 mm, whereas it ranged between 14.8 and 15.8 during the last nine periods. Although the sea-stars were able to swallow the larger *Spisula*, the latter must have been more successful in their escaping attempts than smaller specimens. Individual differences in feeding behaviour may also have played a role.

What the two experiments did demonstrate, however, is that whereas an average daily consumption of about 0.75 *Nucula* with a mean length of roughly

10 mm resulted in a high growth rate, the same average consumption in numbers of *S.subtruncata* with a higher mean size (14 mm) under identical temperature conditions, i.e. during late December 1960 to the middle of May 1961, resulted in a rather modest weight increase of one specimen and a slight loss in the other. Both no doubt had to use more energy in securing their food than those feeding on *Nucula*. Considering the significantly smaller size of the latter, the results are, nevertheless, in agreement with the data obtained in experiments F-III and F-IV (Fig. 14), viz, that an *Astropecten* has to consume a higher number of *Spisula* than *Nucula* over a given period to enable it to grow at the same rate. Theoretically, specimen A in exp. F-VII could have lost some weight by spawning, as its eggs were quite ripe at the end of the experiment. It is not very likely to have happened, however, since no males were present.

Growth efficiency

When the amount of food ingested and assimilated over a given period of time and the gain in weight of the consumer are known, it is usually possible to calculate gross and net growth efficiencies under the given circumstances.

Only experiments F-VII and F-VIII yield data on which to base such calculations. Although they must be regarded as pilot experiments, it seems worth-while to include them.

The growth efficiencies were calculated on basis of the contents of dry organic matter, i.e. dry matter minus ash were determined.

Five adult *Astropecten* (R about 40 mm) kept and fed in the laboratory for about six weeks had a mean fresh weight of about 12 grams and an average content of dry organic matter corresponding to 4.7 % of their fresh weight. The average percentage for 5 somewhat larger female specimens which had been fed in the laboratory for many months and had attained an average weight of about 29 grams was 9.3 %. These specimens had converted a large part of their energy intake into eggs. On the basis of these data it is assumed that the 4 female sea-stars used in experiments F-VII and F-VIII had an initial content of dry organic matter equal to 5 % of their fresh weight and a final content corresponding to 9 %. The value of only 4.7 % for specimens fed for about six weeks is low, when compared with those given for other sea-stars (Thorson, 1957, table 1), but is really not surprising in view of the state of undernourishment of *Astropecten* in the Øresund. Furthermore, some of the values listed in Thorson's table are too high since they include ash contents. As for the 9.3 % content of dry organic matter in well fed *Astropecten*, this is not strikingly high; 12.5 % is given for the only phanorozonian sea-star, *Hippasteria phrygiana*, listed in the mentioned table.

In the case of *Nucula nitida*, 12 specimens were collected and analyzed in November-December 1965. The size range was 9.1 to 12.2 mm, (mean 10.2 mm), and the average content of dry organic matter was 0.0193 grams, corresponding to 5.6 % of the fresh weight (the weight of specimens opened and placed on filter paper just long enough to remove the excess water, cf. Thorson, 1957, p. 492). According to Ockelmann (personal communication) *N. nitida* seems to spawn in late winter, so the specimens analyzed may well have been ripe.

As for *Spisula subtruncata,* 20 specimens were collected and analyzed in November 1960, and 31 during the period from 14 September 1965 to 27 January 1966. The size range was 9.3-17.5 mm, mean 13.5 mm, and the average content of dry organic matter was 0.0139 grams, corresponding to 4.7 % of the fresh weight. Only 8 of the specimens were taken in September, and of these, 5 had a content of 6 to 7.7 %, indicating that they had not spawned yet, although the bulk of the population evidently spawn in early summer (K. Muus, 1966).

For both species, the values found are slightly higher than those obtained by Petersen & Jensen (1911), 5.3 % for *N. nitida* and 4 % for *S. subtruncata*, the latter determined on alcohol-preserved specimens, which always yield values somewhat lower than fresh specimens (cf. Thorson, 1957, tables 1 & 2). However, in neither case were the ash contents determined and deducted. Davis (1923), who gives a value of 5.5 % for *S. subtruncata,* also failed to deduct the ash contents, and he placed the soft parts directly on blotting paper to remove excess moisture, which easily leads to a loss of more than this prior to weighing.

In the case of experiment F-II, only the period betwen 7 November 1960 and 18 February 1961 will be considered, i.e. the period before one of the sea-stars began to loose weight. During this period the two sea-stars ingested 243 *S. subtruncata* with an average length of 13.5 mm or exactly the same as the average length of all 51 specimens analyzed for dry organic matter. Since the size distribution did not differ significantly, one may, therefore, reckon that the *Spisula* ingested represented a total amount of dry organic matter equal to 243 × 0.0139 grams, which is about 3.4 grams. We may also assume that all of it was assimilated so that gross and net growth efficiencies in the present case become identical.

On 7 November the sea-stars had R's of 27 and 28.5 mm, respectively, and a combined weight of 10.1 grams, i.e. somewhat higher than specimens just collected in the field, and thus comparable with the 5 smallest specimens analyzed in the laboratory. Hence it is assumed that the two sea-stars together contained 0.51 grams of dry organic matter, equivalent to 5 % of their fresh weight.

On 18 February the two sea-stars had R's around 35 mm and a combined weight of 20.6 grams. Since this represents weights completely out of proportion to animals of similar size just taken in the field (Øresund, Fig. 11) it is assumed that they were already full of ripe eggs, which also was the impression one got when handling them. Assuming a content of dry organic matter corresponding to 9 % this gives a figure of 1.85 grams. Consequently, the increase in dry organic matter during the mentioned period is calculated to be 1.34 grams. Relating this to the 3.4 grams assimilated, the net growth efficiency was thus about 39 %.

Turning to experiment F-VIII, the whole experimental period may be included since both sea-stars continued to grow from start to end. From 22 December 1960 to 16 May 1961 the sea-stars consumed a total of 215 *Nucula* with an average length of 10.2 mm. This corresponds well with the 12 specimens analyzed in November-December 1965, which had a similar size distribution and a mean content of dry organic matter of 0.0193 grams. This means that the 215 *Nucula* consumed must have contained about 4.2 grams. The combined fresh weight of the two sea-stars at the start of the experiment was 14.2 grams of which 0.7 grams (5 %) is estimated to have been dry organic matter. At the end the sea-stars weighed 30.3 grams of which 2.7 grams (9 %) is taken to have been dry organic matter, and in this case it was directly seen that the sea-stars were "loaded" with ripe eggs, so the amount of dry organic matter cannot have been overestimated. The increase was, therefore, about 2 grams, and when this is related to the 4.2 grams assimilated, we arrive at a net growth efficiency of about 48 %.

Strictly speaking the efficiencies found in both experiments do not pertain to growth alone since a large part of the absorbed energy went into production of eggs, but much confusion still persists concerning terminology and definitions of ecological efficiencies. However, net growth efficiencies – in the sense used here – of 30-60 % are by no means rare among marine invertebrates, of which many are much more active than *Astropecten*. Based on wet weight, Hatanaka & Kosaka (1959) found gross growth efficiencies as high as 55.5 % under the most favourable temperature conditions in a series of experiments with *Asterias amurensis* being fed on meat from shucked clams (*Venerupis japonica*). If calculated on the basis of dry organic matter their results would probably have been somewhat lower. Also based on wet weights, Fenchel (1965) found a gross growth efficiency of about 33 % for *Luidia sarsi* feeding on *Ophiura albida*. In the case of *A. amurensis*, gross and net growth efficiencies must have been more or less identical, whereas the net growth efficiency of *L. sarsi* must have been considerably higher the mentioned gross growth efficiency.

Since any ecological efficiency (sensu Odum & Odum, 1959) is greatly dependent on both physical and biotic factors, it is difficult to estimate what the net growth efficiency may be at a given time in any area where *Astropecten* occurs. Although the sea-stars living in the Øresund are undernourished, this will not by itself lead to a diminished growth efficiency, but might even have the opposite effect. On the other hand, the sea-stars are bound to spend much more energy in travelling over the bottom and in digging up prey than in the laboratory where the prey is abundant, and where each specimen swallowed may represent the same amount of organic matter as found in hundreds of the meio-fauna specimens picked up individually in nature. Furthermore, the temperature prevailing in the Øresund when such a highly preferred prey species as *S. subtruncata* settles is probably significantly below the level for optimal growth efficiency. This dependence on temperature has been well documented by Hatanaka & Kosaka (op. cit.) for *Asterias amurensis* and for many other marine invertebrates (see review by

Kinne, 1963). Off Frederikshavn, where food is much more abundant and temperature conditions much more favourable, the growth efficiency of *Astropecten* is in all probability higher than in the Øresund.

General remarks

It is not permissible to calculate the amount of food taken annually by a predator in nature on the basis of laboratory feeding rates, unless one is dealing with a highly specialized species which also in the field has easy access to an unlimited and concentrated food resource. Furthermore, all too often the physical, chemical and biotic factors cannot be duplicated in the laboratory, and it is especially easy to arrive at quite erroneous results when basing such calculations on experiments carried out over short periods only. Apart from the density factor, the type of prey used in the laboratory may also be of great importance as in the case of *Astropecten*. These and other factors have convinced me about the futility of attempting to calculate the annual food uptake of the sea-star in the field. Even if it could be done, for example, for the Hornbæk Bay, from where most information is available, the result obtained would only be valid for this area, and it would, furthermore, be subject to changes from year to year.

Sometimes one may see the feeding rate of a predator expressed as the weight of the prey eaten daily in per cent of its own living weight. Such information may help to give rough estimates concerning the differences in voracity between different predators, and this may be useful when trying to figure out how large a share competitors for the same food resource are likely to get in a given area.

In the case of *Astropecten* feeding on *N. nitida* or *S. subtruncata*, they ate anywhere between about 2 and about 16 % of their own weight daily, with the highest figure applying to the smallest sea-stars used. It is doubtful whether sea-stars of equivalent weights will ever succeed to secure as much as 16 % of their own weight daily in the field, at least not in the Øresund. This is indicated both by the available field data and by the comparatively low temperatures found in this area when their preferred food may be abundant. To use such figures to calculate annual food uptake is at any rate not permissible.

Another aspect also deserves some comments. The feeding rate of *Astropecten* in terms of organisms destroyed per time unit is obviously very much higher than for sea-stars of the *Asterias* type which feed on larger prey. The efficiency of energy transfer from prey to predator, i.e. the ecological efficiency as defined by Slobodkin (1960), is also very much higher, however. This is due to the well known fact that although the metabolic rate pr unit body weight of recently settled prey animals is very high, the net growth efficiency is also enormously higher than in adult animals (see e. g. Jørgensen, 1952). To put it in another way: An *Astropecten* is much less expensive to maintain than an *Asterias* since a steadily increasing percentage of the energy intake of the prey of the latter has been converted to heat during growth.

INFLUENCE OF *ASTROPECTEN* ON FAUNAL COMPOSITION

Already in an earlier paper (A. M. Christensen, 1962) it was pointed out that the selective feeding behaviour of *A. irregularis* is bound to influence the relative and absolute densities of potential prey species on bottoms where it occurs.

The information given in the preceding chapters will be used to the influence which *Astropecten* exerts on the stock of a few key species living in a typical *Venus gallina* community. Relevant information on the predation on other species may be drawn from the section on food items (p. 12) as well as the section on feeding rates in nature (p. 93).

Since a single *Astropecten* may easily swallow and digest at least 200 newly settled *Spisula subtruncata* per day, and data gathered by Thorson (unpublished) show that larvae may be present in the plankton from early May through September off Frederikshavn, each *Astropecten* may in this typical *Venus* community theoretically destroy at least 30.000 0-group specimens annually. However, apart from physical factors, as e.g. temperature, the actual number of *Spisula* destroyed per unit area must at any given time primarily depend on such factors as (1) the density of the predator itself, (2) the intensity of settling and subsequent growth rate of the clam, (3) species composition, density and size distribution of other more or less attractive prey species, (4) numbers and kinds of other predators competing for the same food, and (5) numbers of non-selective detritus feeders which "accidently" swallow newly settled specimens.

As for the first factor the following information is available. Petersen (1913) found 1, 1.5, 1.8, and 6 *A. irregularis,* respectively, at four stations in the Kattegat north of the island of Anholt, this being based on 10 to 20 samples with a 0.1 m^2 bottom sampler per station. However, judging from the subtratum data one would have expected him to have come across this species in about 15 other localities, and it is probably safe to say that only in the most suitable localities in inner Danish waters will one find more than about one specimen per 5-10 square metres. Ursin (1960) in his extensive survey of the North Sea found almost one *Astropecten* per square metre, although food conditions outside the Dogger Bank, where *Astropecten* is absent, are believed to be poorer than in the northwestern Kattegat. Admittedly, Ursin did not extend his survey into the Scottish waters of the North Sea, where the molluscan fauna is poorest (Stephen, 1933), but even in these waters as many as 5 specimens have been taken per square metre at one station (Stephen, 1923). Buchmann & Hedley (1960) found two *Astropecten* per square metre on a sandy bottom off the Northumberland coast, this being based on 65 samples with a 0.1 m^2 van Veen grab. McIntyre (1961) found 134 newly settled specimens per square metre on the Fladen Ground, but when a 1.3 mm sieve was used instead of one with a mesh size of 0.5 mm, only 4 specimens were retained and these were also juveniles (McIntyre, personal communication). No quantitative data are available for the Frederikshavn area except that Petersen (1913) found one specimen in ten samples with his 0.1 m^2 grab 6 miles southeast of Frederikshavn. However, the fact that over 400 very large specimens were taken with a seine, which was hauled aboard as soon as the fishermen discovered that it had sheared into the bottom, indicates that many were present, considering also that there almost certainly must have been many smaller specimens which were not retained due to the large mesh size of the seine. On an average one may probably assume a density of about one specimen per 5 square metres, but it may well be considerably higher in local spots. As for the Hornbæk Bay, Nicolaisen (unpublished) found only two specimens in 192 samples taken with a 0.1 m^2 Smith-McIntyre grab. Obviously many more samples would have been necessary to secure reliable data, but rough calculations based on many dredge hauls also indicate a density of about one *Astropecten* per 10 square metres. Petersen & Jensen (1911, table VI) found 3 specimens in 50 samples taken with the 0.1 m^2 grab at 20-24 metres depth off Höganäs, a locality situated only about 10 km north of the Hornbæk Bay.

With respect to the second factor, it is obvious that settling intensity of *Spisula* larvae will vary considerably throughout the settling season, The main period of settling may well be confined to a period of 6-8 weeks (cf. K. Muus, 1966), and although over 8.000, which is a very conservative estimate, may settle per square metre, the data in the paper just cited show that these may be totally exterminated within a few weeks due to predation by *Astropecten* and other predators. Assuming a density of one *Astropecten* per 10 square metres and a potential digestion of 200 spat per day, it is seen that the sea-star may be responsible for the extermination of over 1100 spat per square metre over a period of 8 weeks. This imposing figure may not necessarily be reached due to the presence of other predators (see below) and the accompanying decrease in density of the spat following immediately after the termination of settling. Off Frederikshavn, settling of *Spisula* must be so extensive and other factors so favourable that some survive the 0-group stage. Since the difference in food value of a newly settled specimen and one which has passed the meio-fauna stage is enormous, this will automatically lead to a reduction in numbers destroyed, as will the declining density. Furthermore, with the onset of winter and falling temperatures, *Astropecten,* as well as other predators, lower their feeding rate or even cease to feed at all, and next spring there will be a new population of newly settled bivalves to feed on.

The third factor mentioned may also play a considerable role, even though we know that, at least in Danish waters, *S.subtruncata* is preferred to any other bivalve prey. It is feasible, for example, that the related, fast-growing *Mactra stultorum* found in the North Sea and more southern waters may be just as attractive. In the Hornbæk Bay, however, the field data show (Table 10) that over 90 % of all prey specimens taken during the settling season of *S.subtruncata* may belong to this species. On the other hand, the data from the Frederikshavn area showed that the small opisthobranch *Retusa umbilicata* may attract the sea-star to a considerable degree, and the data from the Hornbæk Bay revealed that *Montacuta ferruginosa* and recently settled *Echinocardium* likewise attract the sea-star. None of these were present in the Hornbæk Bay in the summer of 1960, and the latter two species also generally settle later in the season than *Spisula*. Nevertheless, in other areas where *Spisula* is not wiped out within a short time or where considerable numbers settle at about the same time as some of the mentioned prey species, these may well to some degree act as "buffers". It will be recalled that the sea-star has little or no capacity for long distance perception, and it cannot "know" that it might encounter a *S. subtruncata* if it travelled a short distance further when hunting for food. In this connection it should be mentioned that Thorson (1966) credits me for stating in my 1962 paper that the water pumping rate of *Spisula* should help *Astropecten* to scent and find this bivalve much more often than a *Venus*. Actually, this statement was not made, but the mentioned factor may perhaps play a role, since a linear relationship may exist between pumping rate and metabolic rate (cf. Hamwi, 1969). That the size of alternative prey species must play a role is obvious.

The fourth factor mentioned, viz the existence of other predators feeding more or less extensively on *S. subtruncata* is in a way more important than any of the others. It is well known that many other invertebrates such as e.g. the Naticidae, *Ophiura texturata* and *Asterias rubens* feed on *S. subtruncata* (Petersen & Jensen, 1911; Hagmeier, 1930), although none of these seem to play a significant role in this respect in the Hornbæk Bay locality. Feder (personal communication) examined a large number of *O. texturata* from this area and found no bivalves in them. Naticids are not very common, although they do occur in considerable numbers in the more shallow water where *Astropecten* is absent. It is also well known that many fishes, among them notably the plaice, feed extensively on *Spisula* (Davis, 1923, p. 45). In addition it has now been discovered that newly settled specimens are preyed upon by certain turbellarians, nematodes and harpacticoid copepods (G. M. Christensen, in: Thorson, 1966). Nevertheless, although naticid gastropods are present on the Dogger Bank (Davis, 1923), the practically complete absence of *O. texturata* and *A. irregularis* may well constitute one of the reasons why this area supports a large fish population. Davis (1925) calculated for a certain patch of *S. subtruncata* that only 9 % of the mortality was due to *Natica*, whereas fishes accounted for 87 %.

Finally, with reference to the fifth factor, Thorson (1966) calls attention to the "accidental" predation by a number of non-selective detritus feeders. Based on data published by Blegvad (1914) he reckons that the adult population of *Echinocardium cordatum* in the Kattegat may destroy at least 224 young bivalves, out of which close to 200 may be *S. subtruncata*, per square metre within 4 weeks.

With all the above information at hand, there is no reason to wonder why the large majority of *S. subtruncata* are destroyed soon after settling, and that only very few specimens reach an age of more than two years. There is more reason to ask why it has not been exterminated long ago. As we have seen, this may in fact be the case in local areas as in the Hornbæk Bay, where even very heavy settling is insufficient to establish an adult population. Only in shallow water (8-12 metres), where *Astropecten* is absent, does this occur, although I do not wish to imply that this is the only reason why this is so.

At any rate, the reason why the species has not been exterminated must be its high growth rate, early maturity and high reproductive rate (cf. Davis, 1925; Thorson, 1957). As amply stated by Slobodkin et al. (1967), high loss rates must be matched by the latter factor as a species will be eliminated altogether from a habitat if this balance cannot be made.

V.gallina is known to have a slow growth rate (Ansell, 1960b) and a late maturity (see also Thorson, 1957). Consequently, if it was preyed upon to the same extent as *S.subtruncata,* it would in all probability not be able to survive. It has now been shown that although it may occur in the stomachs of *Astropecten* in considerable numbers, very few are in reality eaten, and it is evident that any other predator, which does not mastigate its prey, is also unable to digest *Venus* before it succumbs due to lack of oxygen. Likewise it can be taken for granted that even newly settled specimens will pass through the alimentary tract of non-selective detritus feeders quite unharmed. Apart from this, it is common knowledge that *Venus* is not taken to any great extent by fishes, presumably because of its rather thick shells. *Natica* may feed on it, as shown by Ansell (1960a), but according to Ziegelmeier (1954) it will only rarely do so in the presence of other bivalves which, in contrast to *Venus,* have smooth shells. The fact that Davis (1923) found numerous empty valves of *Venus* on the Dogger Bank, but states nothing about finding bore-holes in them, points in the same direction. Furthermore, it will take much longer time for a *Natica* to drill a hole through the thick shell of a *Venus* than e.g. that of a *S.subtruncata.*

It is precisely for all these reasons that *V.gallina* usually attains a life length considerably longer than that of *S.subtruncata.*

Most of what has been said about predation on *Venus* also applies to other bivalves with thick shells and a pronounced ability to withstand anaerobic conditions for a long time. In the present case it is notably *Corbula* and juvenile *Cyprina* which are protected in the same way, although the former species and possibly also *Cyprina* are more often eaten by naticids than *Venus.*

As we have seen, *Mya truncata* is highly attractive to *Astropecten.* However, the larvae settle at a time at which the temperature is at a level at which the feeding rate of *Astropecten* (and other predators) is reduced. This gives the clam a chance to grow significantly before *Astropecten* becomes really voracious, and when this happens, other attractive bivalves may be settling in addition to such apparently attractive prey as e.g. *Pectinaria koreni.*

To my knowledge, no predator has up to now been known to feed extensively on newly settled sea-urchins. It is, therefore, of considerable interest that *Astropecten* seems to play a role in controlling the rate of survival of recently settled *Echinocardium cordatum*. Usually, a *Venus gallina* community is defined as containing a certain set of species ± *E. cordatum* (cf. Thorson, 1957, p. 508), and it would seem worthwhile to investigate whether the absence or low density of this sea-urchin shows any correlation with the density of *Astropecten*. Again, however, the newly settled prey may in some years be more or less "protected" if another species ranking as high or higher on the preference list is present in large numbers during the settling season and while the sea-urchins are still small enough to be attractive to *Astropecten*. In the Øresund, *Montacuta ferruginosa* may well act as a "buffer" organism in certain years (cf. Table 10, last column). It should be stressed, however, that since *Astropecten* by no means will switch from one prey species to another which becomes more abundant, unless the latter is as attractive as the former, it does not moderate competition and induce stability in the community as implied for predators in general by Elton (1927, p. 122).

Based on laboratory studies on *Pisaster ochraceus*, Landenberger (1968) discussed this idea. He concluded that if the rather pronounced preference displayed in the laboratory also exists in the field, as all available evidence indicates, the model does not fit in this particular case. Referring to other species in which a strong preference for certain prey is known to pertain, Landenberger questions whether the hypothesis is generally valid, and with this point of view I certainly agree. Although it is clear that one cannot entirely dismiss the idea of Elton (1927) and the similar ones inherent in the theoretical discussions by MacArthur (1955) and Connell & Orias (1964), it is indeed questionable whether stability in fact in all cases and in all communities requires that predators display a tendency to switch from one alternative prey to another which has become more abundant. If *Astropecten*, for example, did not prefer prey species such as *S. subtruncata*, which can tolerate a high predatory loss rate, other more sensitive species might in fact be in danger of being exterminated.

Another sea-star, *Acanthaster planci*, however, feeds almost exclusively on stony corals which – in contrast to *S. subtruncata* – cannot sustain heavy predation. Since this sea-star has undergone a spectacular population increase in many areas of the Pacific Ocean, the result has been that huge reef areas have been completely decimated for living corals (Chesher, 1969). In this case, the chance for maintaining community stability would obviously have been greatly enhanced if the sea-star did not so tenaciously "hunt" for just one type of prey.

The physical, chemical and biological factors influencing community structure are numerous as the review by Thorson (1966), which deals mainly with biotic factors, clearly reveals. Among these factors, the influence of *Astropecten* constitutes only one part of a large puzzle. However, as emphasized by Petersen (1913), if one is to gain a complete insight concerning trophic as well as other relationships within a community, it is necessary to acquire as much knowledge

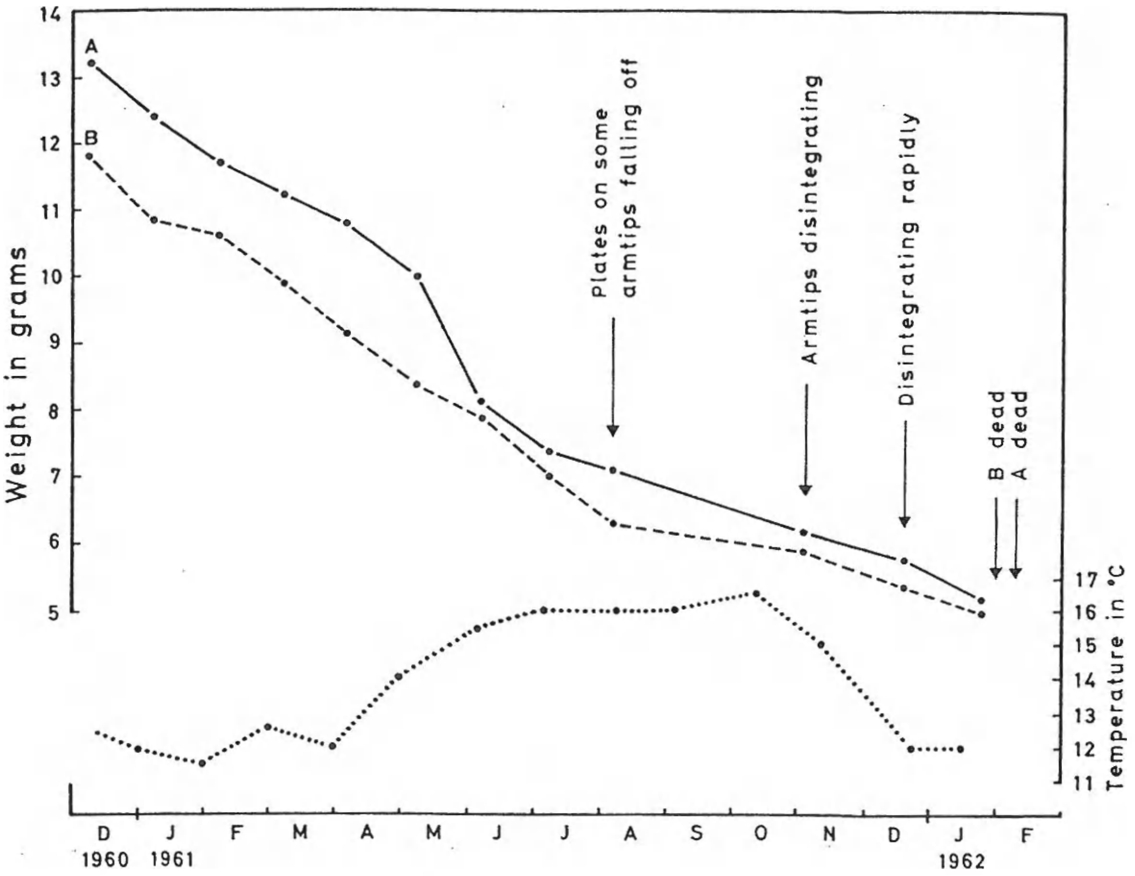


FIG. 19. Results of starvation experiment (cf. text).

as we possibly can about every organism normally occurring in it. Recent studies by Paine (1969a & b), based largely on another sea-star, *Pisaster ochraceus*, also show how important this is. Many interactions between *Astropecten* and its potential prey species are similar to those between *Pisaster* and the prey of this species. Based on present knowledge there is in fact good reasons to regard *A. irregularis* as a "keystone species" as defined by Paine.

Among other invertebrate predators inhabiting *Venus*-communities, members of the Naticidae are usually regarded as the most important. Contrary to *Natica*, however, whose density fluctuates with the density of suitable prey (Hagmeier, 1930; Picard, 1930; and others), *Astropecten* seems unaffected by this factor. Laboratory experiments and observations have shown that it may survive for many months without food at a temperature range considerably higher than that in nature. Fig. 19 shows the results of an experiment where two specimens were kept without food until they died, after more than one year. Since *Astropecten* has a long life span, it will always be present to take advantage of spatfalls of the prey it prefers.

FEEDING BEHAVIOUR IN OTHER *ASTROPECTEN* SPECIES

The genus *Astropecten* is far richer in species than any other sea-star genus. Döderlein (1917) records over a hundred species, and although a systematic revision may reduce the number of valid species, this will not invalidate the above statement. The genus is represented in nearly all boreal, subtropical and tropical waters, with most species occurring in the tropics. The large majority inhabit more or less sandy substrates, but may occur on mud bottoms in some cases, as for example *A.javanicus* (Bedford, 1900). Another species, *A.spinolosus* is nearly always found on bottoms covered with a dense growth of algae, *Zostera,* or *Posidonia,* but has been found on a clean stone bottom (Zavodnik, 1960, 1967; Picard, 1965). Ludwig (1897) writes about *A.auranciacus* that it is most common on sandy or muddy ("schlammigen") bottoms, but may occasionally be found on detritus or coral debris substrates. Tortonese (1943-48) also found it on different substrates, including *Zostera* bottoms. *A.johnstoni* may likewise be found on different kinds of substrate (Picard, 1965). Concerning 493 specimens of *A. californicus* caught off San Pedro, Fisher (1911) writes that the bottom was sand together with shells, shale, cobbles, pebbles, or sand alone; less frequently mud or sandy mud.

Although few quantitative investigations are available, it is well known that many tropical species may be extremely abundant in very shallow water. Dr. Heegaard (personal communication) estimates that several species may occur in densities of 5-10 specimens per square metre in certain coastal waters of Java. MacNae & Kalk (1952) state that *A.granulatus* may reach a density of 5 per square metre at Inhaca Island, Mocambique. *A.javanicus* is abundant in Malaccan waters (Bedford, 1900) and the same is true for *A.michaelsoni* off the coast of Ghana (Bassindale, 1961). UNESCO fellows from tropical countries have also informed me that they know of beaches where *Astropecten* spp. occurs in similar numbers as those indicated by Dr. Heegaard. Outside the tropics, densities are seemingly lower, except in restricted spots or areas.

Ghelardi & North (1958) report that *A.californicus,* within a narrow strip along the slope of the La Jolla canyon, reaches an average density of 4 per square metre, and the late Conrad Limbaugh informed me (1958) that he had observed densities exceeding 10 per square metre, although this was definitely an exception to the rule. Turner (personal communication), states that station records for the Canyon de las Encinas survey (see Turner et al. 1964) indicate that 4 to 8 *A.californicus* were present in the approximately 40 square metres of bottom surveyed. In a similar survey about 10 miles further to the south one to eight *A.armatus* were observed during dives over an area of about 30 square metres, but in other areas densities of one specimen per square metre were occassionally recorded. Hildebrand (1954) states that *A.antillensis* is excessively abundant on the shrimp grounds in the western part of the Gulf of Mexico, and data supplied by McNulty et al. (1962) indicate that *A. duplicatus* may reach a density of about one specimen per 8 square metres in the Biscayne Bay area, Florida. Gray et al. (1968) show a photograph covering 4 square metres of bottom off the North Carolina coast. From this it is apparent that at least 6 specimens of *A. americanus* may be present per square metre. The same authors state that *A. articulatus* probably is the most common sea-star in North Carolina waters.

Ludwig (1897) states about the Mediterranean species *A. auranciacus* "Wo die Art vorkommt scheint sie fast immer in grosser Menge das ganze Jahr hindurch aufzutreten". This agrees well with the more recent studies of Zavodnik (1960), who states that it is very common in some places and that it is, for example, the most common echinoderm off Krk and Baska on the island of Krk. Another Mediterranean species, *A. bispinosus,* may be represented with one specimen per square metre off the French coast (Massé, 1966). Vaissiére & Fredj (1963) state that it is very abundant at a station off the coast of Algeria, and this is also the case in the Tunisian Gulf (Bruun, 1940). The findings of three specimens in one sample taken in the Gulf of Salerno with the 0.2 m² Petersen grab (Spärck, 1931), also indicates that it may occur in high densities in many areas.

On this background it is of considerable interest to see whether the feeding behaviour of other *Astropecten* species is similar to that of *A. irregularis.* Two aspects seem to be especially important to discuss, viz whether all species are selective feeders, and if they are, whether they show preference for the same kind of prey as *A. irregularis.*

Concerning the first point there are a few statements in the literature, but before discussing these it is worth recalling that Kisch (1958) stated that *A. irregularis* picks up whatever it comes across (see p. 30).

Using somewhat similar arguments, Wells et al. (1961) state that *A. articulatus* is a non-selective predator. These authors found no less than 91 species represented in the stomachs of 124 sea-stars, but among the 17 bivalve species present, there were apparently none belonging to easily accessible, fast-growing species. This reminds one of the situation where *A. irregularis* lives in a locality where the preferred prey species are absent or scarce with the result that a large number of different prey species are taken in small numbers (Table 9). A closer analysis of the data reveals, however, that over 30 % of the prey specimens found in *A. articulatus* belonged to a single species, the tectibranch *Acteocina candei* which, according to Abbott (1954), probably is identical with *Retusa canaliculata* and thus belongs to a genus which also seems to be attractive to *A. irregularis.* It occurred in 57 of the 124 sea-stars. *Natica pusilla* occurred in 89 of the sea-stars and made up about 24 % of all the prey specimens. The fact that it apparently was more widespread in the collecting area and that the numbers found probably represent at least 4-5 days consumption should be pointed out. Furthermore, members of this genus may also occur in significant numbers in *A. irregularis* when really attractive bivalve prey species are absent or scarce (Tables 5, 6 & 9).

Hulings & Hemlay (1963) who studied the feeding habits of the same sea-star disagree with Wells et al. (op. cit.) in stating that there seems to be a certain amount of selective feeding. They found that the opisthobranch *Odostomia impressa* dominated the stomach contents one year, whereas the prosobranch *Bittium cerithoides* was the most abundant form found a year later. From these two studies one might conclude, as done by Hulings & Hemlay, that *A. articulatus* prefers small gastropods, although this apparent preference could be due to an absence or scarcity of suitable bivalve prey. As implied in this discussion, I am fairly convinced that Wells et al. (op. cit.) are in error in stating that it is a non-selective feeder, and it is certainly not warranted to state that this evidently applies equally well to other species of *Astropecten* inhabiting sand.

There are other species, which apparently prefer gastropods. Among them is *A. granulatus* from Moçambique, which almost exclusively feeds on the myriads of tiny *Assiminea* sp. that litter the surface of sand flats in the very shallow water where it lives (MacNae & Kalk, 1962). Another less abundant species, *A. acanthifera*, found in the same area feeds on several topshells but also on bivalves such as *Circe pectinata*. MacNae & Kalk give no information on number of sea-stars investigated, nor is it clear whether the two species are intermingled on the flats, or whether there is any difference between their habitats. If not, there appears to be a distinct difference in food choice. It is worth noting that the authors state that although several bivalves are present, none are really common. Considering that they regard pyramidellids as frequent, when there are 5-7 per square metre, one may take it for granted that the sea-stars could not possibly secure sufficient food amongst the bivalves present which, furthermore, seem to include mainly two species of *Tellina, Cultellus pellucidus* [?] and *Solenomya*, i.e. species which are more or less protected against predation by *Astropecten*, depending to some extent on size.

Another example showing the influence of the fauna present on food uptake is also very illustrating. MacGinitie & MacGinitie (1949) state that *A. armatus* feeds on snails, but not on sand dollars. Conrad Limbaugh informed me, however, that the species does in fact feed on the sand dollar *Dendraster excentricus* on sandy bottoms near La Jolla, but admitted that he had never observed it further north, where the MacGinities had made their observations. Later I also learned that it had been seen feeding on the pennatulid *Renilla koellikeri*. Hopkins & Crozier (1966) also state that it feeds on the mentioned three prey types and on dead fish. A recent paper by Fager (1968) throws considerable light on the inherent controversy, however. It is apparent that the sea-star in the La Jolla region, where Hopkins & Crozier as well as Fager made their studies, is living in a community made up of a surprisingly small number of species. Of special interest in the present connection is that the naticid snail *Polinices recluzianus* was observed to feed on such unusual prey as hermit crabs, a fact which Fager believes is due to a scarcity of bivalves in the area. Hence even if *A. armatus* might possess a preference for certain bivalves, it would never be observed in this community. Two species of *Nassarius* are present as potential prey, but Fager explicitly states that medium-sized snails easily escape even when held on the oral surface of the sea-star until a good grip should have been obtained. Although the observations of Fager, and others diving with him, leave no doubt that *A. armatus* feeds extensively on *Dendraster* and to a somewhat lesser extent on *Renilla* in the La Jolla region, it should be pointed out that they did not make any microscopic observations on stomach contents in the laboratory, and it is, therefore, possible that they would have found juvenile gastropods, and possibly also bivalves, if this had been done. Fager indicates this himself, and the mentioned observations of the MacGinities also show that the sea-star probably prefers molluscan food, when this is available. The fact that *A. armatus* often is observed on the sand surface in daylight hours (see also al Reese, 1966, p. 164) is probably also an indication of food shortage.

Hartman (1956) classifies *A. californicus* as a detritus feeder, although many were caught in traps baited with dead fish. Limbaugh informed me that he found its food to consist mainly of small gastropods. Furthermore, Hopkins & Crozier (1966) state that its food probably consists of polychaetes, molluscs and ophiuroids. This has been confirmed by Dr. W. Austin (unpublished) who found that the molluscs dominated the food contents in 21 specimens investigated.

Massé (1966) studied the food uptake of five species living in the Mediterranean and found that four of them, viz *A. spinulosus*, *A. irregularis* var. *pentacanthus*, *A. auranciacus*, and *A. bispinosus* all are selective feeders, showing a preference for molluscan food, but as in the case of *A. irregularis*, other prey may also be found in them (for *A. auranciacus* see also Tortonese, 1943-48). With the exception of the first mentioned species, which seeks its prey among gastropods and other animals living on algae or sea grasses, the others apparently prefer bivalves to gastropods. The fifth species, *A. johnstoni*, is reported to be a non-selective feeder, which at all times of the year engulfs bottom substrate, in which may be found a foraminiferan (*Rotalia beccaria*), ostracods, amphipods, mysids, tiny polychaetes, and – very rarely – juvenile bivalves. Since Eichelbaum (1909) got the impression that *A. irregularii* swallows considerable amounts of detritus, and Hartman (1956) erroneously classified *A. californicus* as a detritus feeder, it is natural to ask whether the conclusions drawn by Massé concerning *A. johnstoni* could be incorrect. The question cannot be answered at present, but since the swallowed substrate seems to be rather rich with respect to content of small animals it seems feasible that the sea-star at least is a *selective* detritus feeder. It is also to be expected that it is capable of picking up prey in the same manner as other *Astropecten* species do. Recently, however, Ferguson (1969) stated without further comments: "A more direct approach is used by some species of *Astropecten* which completely engorge themselves with detritus". As no American species, apart from *A. californicus*, has been reported to feed on detritus it would be of considerable interest to know which species Ferguson is referring to and under which circumstances (i.e. type of substrate and fauna present) the sea-stars were caught.

Perhaps some *Astropecten* species do resort to detritus feeding under certain circumstances.

Massé (1966) also states that the "caecums digestifs" are much larger in *A.johnstoni* than in other *Astropecten* species. If this refers only to the pyloric caeca, as it appears to do, one cannot use this phenomenon as a criterion for a different mode of feeding. However, if the Tiedemann's pouches situated beneath the pyloric caeca are enlarged it becomes a different matter, since this seems to be characteristic of particle feeders (Anderson, 1960).

On the background of our present knowledge concerning digestion and assimilation of ingested food in *Astropecten* as well as other asteroids (Anderson, 1966) it is not likely that digestive juices are released freely into the stomach lumen as suggested by Massé. Hence any digestible matter in swallowed ditritus must still be brought in direct contact with the stomach lining to be digested and absorbed.

Several hundred specimens of *A.cingulatus* collected in Argentine waters were examined by Carcelles & Parodiz (1938) and Carcelles (1944). Judging from their data, this species feeds almost exclusively on mulluscs, among which opisthobranchs and bivalves dominate, whereas prosobranchs play a minor role. Foraminiferans and *Balanus improvisus* were the only non-molluscan prey present in their material.

The food of the tropical species *A.javanicus* seems to consist principally of small bivalves according to Bedford (1900), who collected his material in Singapore-Malaccan waters. Sladen (1879) found a large bivalve in two specimens of *A.formosus*, so this species may also feed primarily on molluscs. *A.africanus* appears to feed on bivalves (Cherbonnier, 1966), but further studies are needed in this case too.

During the 5th Thai-Danish expedition, 37 *Astropecten velitaris* were taken in a single trawl haul at 7 metres depth on 23 January 1966 off the Thailand coast in the northeastern part of the Malaccan Strait. These sea-stars – with R's ranging between 8.5 and 23 mm – were kindly placed at my disposal and analysed for stomach contents.

Of a total of 545 prey specimens found, 346 were bivalves. The remaining specimens comprised 101 prosobranchs, 29 tectibranchs, 58 crustaceans (harpacticids, ostracods, cumaceans, tanaids, isopods, amphipods, and decapods), 6 polychaetes, 1 sipunculid, 1 foraminiferan, and 2 juvenile *Astropecten*. In addition a few fish scales, fish eggs, prosobranch egg capsules and inorganic nodules were also present. The bivalves were not identified, but about half of them belonged to two or three species of Veneridae and 41 belonged to the Corbulidae.

This prey composition does not differ from what one may find in a collection of other species of *Astropecten,* including *A. irregularis,* taken in a single locality. The same applies to the size of the prey since 88 % of the specimens were of meiofauna size, with the large majority being less than one mm long. The above information embodies, as far as I know, our present knowledge on food uptake within the genus.

Concerning feeding in other species of Astropectinidae. Sokolova (1957) found that *Psilaster pectinata,* collected at more than 2000 metres depth in the Bering Sea, contained almost exclusively 1-4 mm long bivalves and scaphopods in their stomachs. Furthermore, on the basis of very convincing evidence, she states that the sea-star must be a selective feeder, which not only selects molluscan food, but makes a choice between the bivalves present. The closely related *P. andromeda* also appears to feed mainly on bivalves, whereas diatoms, foraminiferans, echinoderms and crustaceans are taken in much lower numbers (Petersen, 1893; Grieg, 1902; Eichelbaum, 1909). The fact that *Cardium* spp. dominated among the bivalves found in the North Sea material examined by Eichelbaum (op.cit.) suggests that this sea-star may be as selective in its feeding habits as its relative, and that it chooses bivalves with the same characteristics as those preferred by *A. irregularis.* No other species have been investigated, but a single specimen of *Dytaster spinosus,* collected at a depth of 4800 metres in the Indian Ocean, was found with a partly engulfed fish bone which still had some meat attached to it (Bruun & Wolff, 1961). This shows that the species is a scavenger, and one may suspect that it will prove to be at least a facultative predator. The suggestion given by Clark (1963) that the antarctic species *Bathybiaster loripes obesus* may feed on settling detritus is only based on the assumption that the spinelets present in fascioles separating the marginal plates may move detritus from the dorsal to the oral side.

DISCUSSION

The results of the present investigation have clearly shown that *A. irregularis* is properly characterized as a selective feeder, which prefers juvenile specimens of certain bivalves with a low resistance to anaerobic conditions. However, information derived purely from stomach investigations indicates that it may also accept certain other prey types, which are susceptible to immediate digestion once they are swallowed. Among these are notably the following: *Retusa umbilicata* and newly settled *Echinocardium cordatum* and *Pectinaria koreni.* Many other types of prey may be found in specimens collected in the field, but laboratory experiments have shown, at least in the case of bivalves, that feeding on non-attractive prey leads to a highly significant reduction in feeding rate. It is also shown that although some potential prey species occur sparingly in the stomachs, they may well be attractive to the sea-star. Apart from a possible low density the reason for this may either be that the prey is situated too deep in the substrate or that it possesses an effective escape response, both of which are factors whose influence often depend on size.

In spite of what has just been summarized, one must also accept the fact that *A. irregularis* in a sense is a highly adaptive animal. Otherwise it would not occur on bottoms other than those where it was assured of sufficient and attractive food. Although it is regarded as a sand-bottom species, it may be found on anything from gravel to mud bottoms and occur in localities where attractive prey species are rather rare.

From all available accounts it seems safe to conclude that all species of *Astropecten,* with the possible exception of *A. johnstoni,* are selective feeders, which primarily feed on molluscs. Whether apparent differences in choice of molluscan food, i.e. whether some species prefer gastropods to bivalves for example, are real cannot be determined on the basis of our present knowledge. The reasons for this are mainly that information concerning presence and density of potential prey species at the times when collections were made, is either lacking or insufficient, and/or that the necessary laboratory experiments have not been carried out. It is also unfortunate that most investigators seem to have failed to examine the stomachs carefully enough under a dissection microscope. This is quite clear in most cases, and in other cases it is indicated by the size range of the prey specimens found and a conspicuously low average stomach content. It is therefore to be expected that very tiny prey, as for example newly settled bivalves, to a large extent has been overlooked.

The best data available are those on *A. bispinosus* studied by Massé (1966), and they do not in any way differ from those obtained in the present study with respect to choice of prey.

Just as *A. irregularis* at least some of the other species may be found on quite varying kinds of substrates. They may also often contain undesirable prey specimens in their stomachs, and one extreme case may be mentioned. In the neighbourhood of Corsica, Pérès & Picard (1957) found 46 *Corbula gibba,* 10 *Venus gallina* and one each of six other prey species in an unknown number of *A. aurantiacus.* Judging from the accompanying data, there was not a single attractive species present in the collecting area. The mentioned bivalves seem to survive in the stomachs of Mediterranean *Astropecten* spp. for just about as long as they do in *A. irregularis* in Danish waters (Massé, 1966). The consequences for the sea-star must be a reduced food uptake, slow growth and a reduced reproductive rate, provided that the community remains unchanged in species composition for a significant time.

One of the more important implications of the adaptability of *Astropecten* with respect to its food spectrum is, however, that in contrast to e.g. certain naticids, it will always be able to survive even if settling of first rate prey species should fail for one or more years. In this connection it is worth noting that the specimen which lived for $9^1/_2$ years, probably only died because it had accidentally been left in standing water at room temperature (about 21°C) for four days. Since field temperatures are much lower than in the laboratory, it is, therefore, not unreasonable to assume that *Astropecten* may reach a considerably higher age in nature.

What this discussion is leading up to is whether other species of *Astropecten* may have the same effect on community structure as *A. irregularis.* In those cases where they occur in communities parallel to the *Venus gallina* community, there seems little reason to doubt that this is the case, and that they may play a similar role in other communities seems at least feasible.

At the present stage, however, the available data do not permit one to make too many generalizations. An interesting aspect is the fact that the genus is most abundant in subtropical and tropical waters, especially in the Indo-Pacific area. In these waters, and even in some waters outside the tropics, one may find sediment bottoms inhabited by a large number of species, each of which only occurs in very low densities (see Thorson, 1966 for references). Under such circumstances any *Astropecten* species present must feed on a large number of prey species, but this does not necessarily mean that they have to be non-selective feeders. They may show a preference for molluscs and, as *A. irregularis,* they may also primarily be attracted by those with the least resistance to anaerobic conditions. On the other hand, we also know that a fair number of *Astropecten* species live in very shallow water on sandy beaches or sand flats, which may become "dry" at low tides. Depending on the degree of wave action, the number of animals adapted to this kind of milieu is known to be low, whether it is in the tropics or not. So far, the only information available concerning *Astropecten* living under these conditions stems from MacNae & Kalk (1962), who found that tiny gastropods constituted the main food. In more exposed localities, the sea-star may feed, for example, on small specimens of *Donax* spp., a genus known to have a wide geographical distribution (Morton, 1964), and which apparently is unable to withstand anaerobic conditions for very long. The latter assumption is based on the findings by Massé (1966) and the first on the fact that *A. irregularis* feeds on *Donax* on sand flats off the Dutch coast (see p. 59), where there probably is little else for it to feed on. What may speak against this hypothesis is that tropical species of *Donax* apparently dig into the substrate much faster than boreal species (Ansell & Trevallion, 1969), which by no means are slow burrowers. It is possible, however, that they do not retreat upon contact with *Astropecten,* but simply close their valves.

Finally, attention is called to the recent paper by Mauzey et al. (1968). These authors studied the feeding biology of 18 sea-stars in their natural habitats through all seasons of the year. For many of the species, laboratory studies were also undertaken and the results related to field data. As also found in the case of *Astropecten,* the data obtained show how the relative abundance of potential prey species, regional differences in prey composition, and annual variations of the fauna may influence the diet of many sea-stars, which in the laboratory exhibit a more or less distinct preference for certain prey organisms. Another highly needed set of data is given concerning the number of specimens observed feeding in relation to all specimens observed during the diving trips. It is unfortunate that no members of the Astropectinidae occur in the Puget Sound region, where these studies were carried out.

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