THE GENERAL BEHAVIOUR AND FEEDING OF *CERIANTHUS LLOYDI* GOSSE (ANTHOZOA, COELENTERATA)

by

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Résumé

Le comportement général et la nutrition de l'Anthozoaire tubicole *Cerianthus lloydi* Gosse (Anthozoa : Coelenterata) a été étudié par plongée et télévision sous-marine. Des observations faites sur place ont démontré l'absence d'activité rythmique diurne, le Cérianthe adoptant une posture caractéristique de nutrition qui est accompagnée de mouvements tentaculaires. La nutrition de *Cerianthus lloydi* par de grosses proies s'effectue en trois temps : capture de la proie par les tentacules marginaux, transfert de la proie aux tentacules labiaux et ingestion.

L'analyse du contenu stomacal de 17 individus a révélé un régime alimentaire carnivore, la plupart des proies appartenant aux Crustacés épibenthiques et à la méiofaune. L'effet de prédation de la méiofaune a été étudié et l'importance du méiobenthos et du macrobenthos dans l'alimentation du Cérianthe est discutée. La position de *Cerianthus lloydi* dans la chaîne alimentaire est examinée.

Introduction

Cerianthus lloydi Gosse is a solitary burrowing hexacorallian (Anthozoa) inhabiting the soft sediments of many coastal areas where it is found living in a mucus tube lined with nematocysts and sediment particles.

In the course of a general survey of the benthic epifauna in a shallow bay (Firemore Bay, Loch Ewe) a small population of this anemone was encountered (Eleftheriou, 1974). Observations were made by divers and underwater TV was also used to investigate the biology and general behaviour of this anemone and other large macrofaunal species. The present contribution is based on selective information deriving from these observations which provide an insight into the natural diets and feeding behaviour of this species in its natural environment.

The habitat

The physical environment of Firemore Bay has been described by McIntyre and Eleftheriou (1968). The study area (Fig. 1) was located at the northern part of the Bay at a depth of 3m (below LW). The bottom sediment was fine well sorted sand (180-205μm)

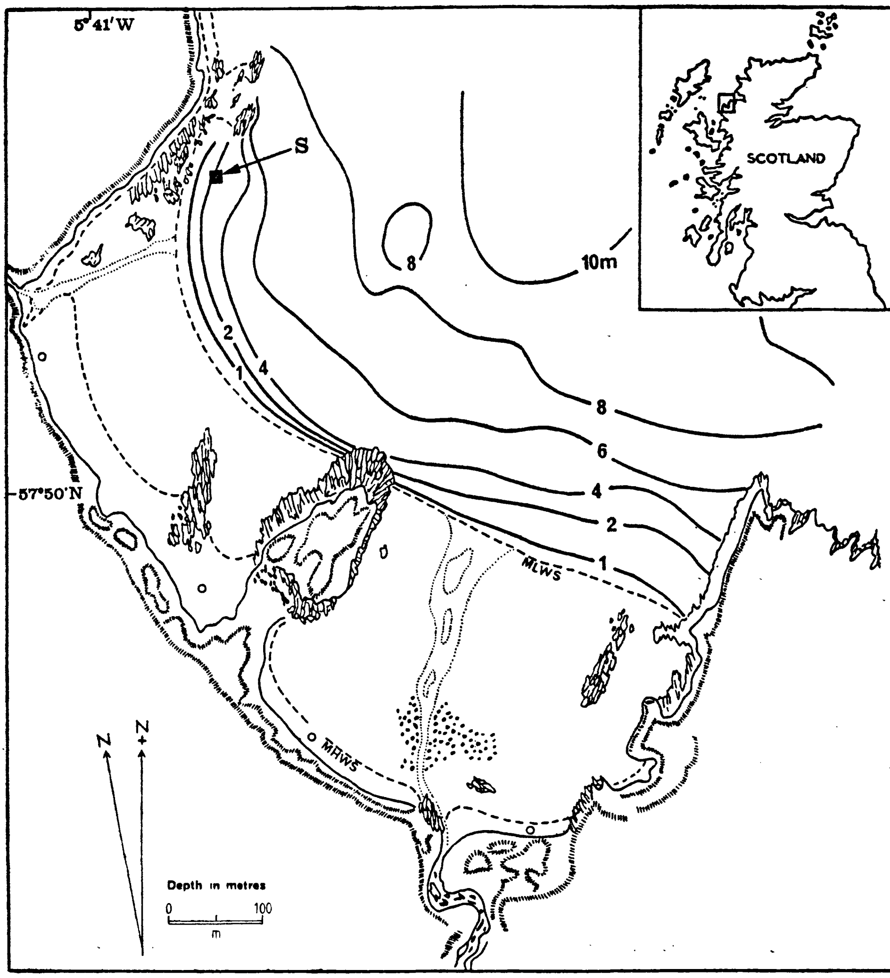

FIG. 1
Loch Ewe and position (S) of underwater station in Firemore Bay.

with a variable amount of shell fragments. A rocky promontory sheltered this part of the Bay and offered a greater environmental stability which resulted in higher production (Eleftheriou, 1979). The organic carbon content of the sediments in the area exceeded 1 000μgC g^{-1} sand and were often as high as 1 700μgC g^{-1} sand. Chlorophyll values in the sand ranged between 3.1-11.0μgChl g^{-1} sand (Eleftheriou, 1979).

The community

The associated benthic community characterized by the bivalve *Tellina fabula* included a total of 55-80 species (McIntyre and Eleftheriou, 1968). Polychaetes were the most important group accounting for at least 40 percent of the species and overall abundance. Of the polychaetes *Spio filicornis, Prionospio malmgreni, Chaetozone setosa,* *Magelona papillicornis, Aricidea minuta* were the most abundant, but important densities of amphipods such as *Bathyporeia elegans, Perioculodes longimanus* and *Megaluropus agilis* were also present. Large concentrations of hyperbenthic mysids and amphipods partly associated with the algal detrital deposits were also present in this part of the bay (Eleftheriou, 1979). The larger epifaunal species (Eleftheriou, 1974) mostly included large decapods (*Cancer pagurus, Macropipus depurator, Carcinus maenas, Pagurus bernhardus*), gastropods (*Buccinum undatum, Nassarius reticulatus*) and echinoderms (*Asterias rubens, Echinocardium cordatum, Astropecten irregularis*).

The meiofauna of Firemore Bay has been described by McIntyre and Murison (1973). Table II shows the meiofaunal groups found at the observation station and in the vicinity of *Cerianthus* tubes. The fauna was represented by a total of 14 taxa of which nematodes with densities up to 5 656 ind. $10cm^{-2}$ were the most abundant organisms. Turbellarians, gastrotrichs, ciliates and, at times, tardigrades were also present in sizeable densities. Harpacticoid copepods were present in densities up to 189 ind. $10cm^{-2}$ of which the larger *Asellopsis* sp. accounted for 50 percent of the mean abundance.

Materials and methods

The feeding behaviour of *Cerianthus* was studied by means of an underwater TV camera (Spirotechnique) with pan and tilt facilities, positioned on the sea bed and operated from a land based laboratory (Fig. 2). Monitoring the activity of selected individuals was carried out for a week and notes and video transcripts were made whenever appropriate. Extensive night observations were also carried out using infra-red lighting. These observations provided limited information on the behaviour of the animal and, partly, on the organisms which were being consumed by the anemone. Additional information on its diet was derived from the analysis of the stomach contents of anemones removed from the sediment by a diver operated suction sampler. The contents of the digestive track were flushed out using a pipette and preserved in 5 percent formalin for subsequent identification. Waste pellets excreted by a small number of captured specimens were also analysed.

To study the predation of *Cerianthus* on meiofauna, replicate cores of 2.2cm internal diameter, were taken at 2-4cm (position A) and 10-12cm (position B) from the tube in within and outwith the reach of the tentacles. The core samples which were collected on three occasions (May, October, 1979; March, 1980) were taken to a depth of 6cm. They were preserved in 5 percent formalin and analysed as decribed in McIntyre and Murison (1973).

A two way analysis of variance of the transformed data [$\log_{10}$ (number + 1)] was used to test if the observed faunal differences in the two positions attributed to predation were statistically significant. Additional samples of sediment for particle size analysis, were taken and processed according to the methods outlined in McIntyre and Murison (1973) and for organic carbon and chlorophyll were analysed as described in Steele and Baird (1968).

RESULTS

General behaviour and feeding

Continuous observations over several 24h periods by divers and underwater TV indicated the absence of any diurnal rhythmic activity. The animals were found expanded, feeding at all times during the day and night and only withdrawing into their tubes when disturbed by an external stimulus such as contact with a larger animal. Emergence and re-expansion of the disc and tentacles were slow and proportional to the intensity of the stimulus. Observations over a tidal cycle gave no evidence of a tidal feeding rhythm. Under conditions of heavy swell, *Cerianthus* exhibited a drag minimising behaviour by clumping tentacles in a semi-expanded state with the animal withdrawing progressively as velocity increased. The ultimate safety mechanism was total withdrawal into the tube whenever a threshold between 2-3 knots was reached (Eleftheriou, unpublished data).

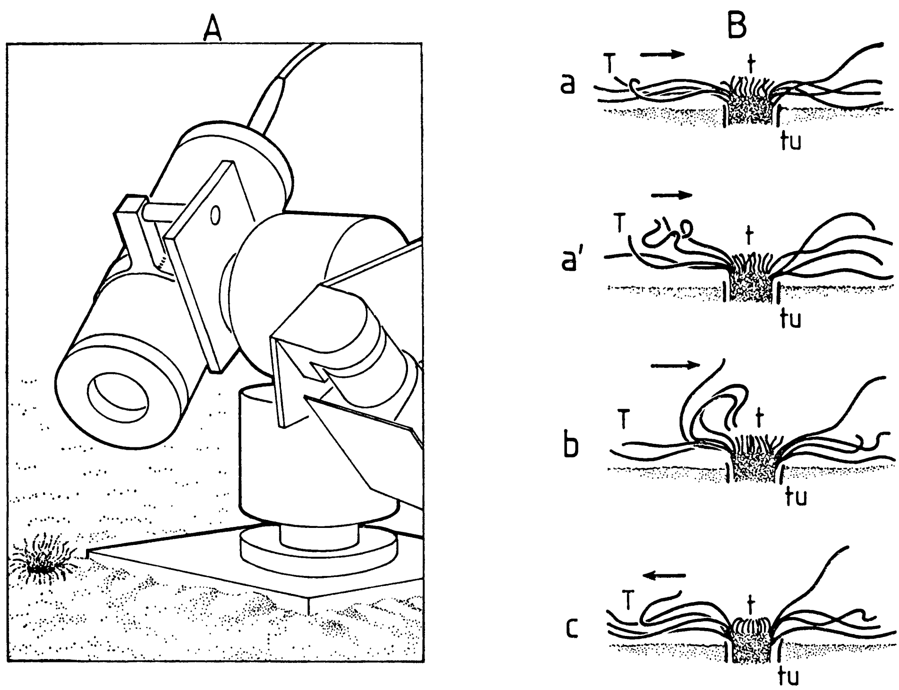

FIG. 2

A. Underwater Television camera in position.
B. Feeding phases of *C. lloydi.*

a, a'. tentacular contact with small prey and inward movement of marginal tentacles; b. prey transfer from marginal to labial tentacles; c. engulfing of prey by labial tentacles and return of marginal tentacles to expanded position (drawings made from VTR transcripts).

T = marginal tentacles; t = labial tentacles; tu = animal tube.

These and additional laboratory observations ascertained that the feeding response in *Cerianthus lloydi* in common with other Ceriantharia (Arai and Walder, 1973) consists of three phases (Fig. 2):

(i) tentacular contact during which the prey is caught by the marginal tentacles;

(ii) the prey is then transferred to the labial tentacles;

(iii) the labial tentacles engulf the prey which is then pushed into the pharynx.

These observations confirmed Gosse's (1860) laboratory findings and were very similar to the feeding response of another ceriantharian *Pachycerianthus fimbriatus* as described by Arai and Walder (1973).

The range of observations showed that feeding movements were continuous even when the tentacles and disc were not fully expanded. The marginal tentacles searched for prey at a wide angle above the sediment and frequently in close contact with it. Contact with the sediment was often followed by an inward bending of the marginal tentacles characteristic of prey transfer into the labial tentacles, which also responded indicating a feeding activity. The size of the prey determined the number of marginal tentacles involved in its capture. Capture and ingestion of the prey was not always successful and in several cases invertebrates and juvenile fish were observed to escape after a short contact with the marginal tentacles.

Once the prey had been in contact with the labial tentacles and before its disappearance into the pharynx, it remained surrounded by the labial tentacles for a period of time which was proportional to the size of the prey. Tiffon (1975) showed that this corresponded to a phase of extracellular and extracorporeal digestion carried out by hydrolases secreted by the labial tentacles.

Food

Identification of the macroscopic prey organisms by direct TV observations indicated a diet consisting of small crustaceans, both benthic and planktonic (in particular mysids, decapods and amphipods) and planktonic larvae of macrofaunal species. Algal fragments and detritus were rejected. Under laboratory conditions, *Cerianthus* was observed to capture and ingest amphipods such as *Bathyporeia elegans, Dexamine spinosa* and *Gammarus locusta* and, occasionally, plaice juveniles up to 2cm length. Animals accepted only live or freshly killed food such as fish and crustaceans, rejecting similar deep-frozen food. *Cerianthus* fed *ad libitum* on *Marinogammarus marinus* consumed up to 0.5g total wet weight. Satiety was reached after three hours and it was followed by partial withdrawal of the animal.

The natural diet of 37 individuals was investigated by examination of the stomach contents and, occasionally, the waste pellets. Twenty animals had empty stomachs; the contents of the remainder is shown in Table I. This confirmed the *in situ* observed predation on macrofaunal itinerant crustaceans and indicated that *Cerianthus* also feeds

TABLE I

Stomach contents analysis of a population sample (N = 37) of *Cerianthus lloydi* (Animals with empty stomachs not included)

Food items	Number of individual anemone																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cypris larvae	3	—	8	—	3	21	—	7	—	4	—	9	—	—	—	—	—
Amphipoda (frags.)	2	1	1	—	—	—	4	—	2	1	1	—	3	1	+	2	2
Harpacticoida	3	1	2	2	10	15	2	8	6	—	5	5	9	7	4	—	—
Calanoidea	—	—	—	—	—	—	—	—	2	—	1	—	3	—	2	5	—
Copepod nauplii	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2
Cirripedia (exuviae)	—	—	—	1	1	—	—	—	—	—	—	—	—	—	1	—	—
Caridea (juvs)	—	—	—	—	—	—	—	2	—	1	—	—	—	1	—	3	—
Decapoda (juvs)	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1
Ostracoda	—	—	—	—	—	—	—	2	—	1	—	—	2	—	1	—	1
Mysidacea	—	—	—	—	—	—	4	—	5	+	—	—	—	3	—	3	4
Polychaeta (setae)	—	—	—	—	—	—	—	+	—	—	+	+	—	—	—	—	—
Pisces (juvs)	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—
Diatoms/algae	—	—	—	—	+	—	—	+	—	—	—	—	—	+	—	—	—
Unident. material	+	+	—	+	—	—	—	+	—	+	+	—	—	—	+	+	—

actively on meiofaunal organisms of which the harpacticoid copepods were the most important single group. In many instances, a quantity of unidentified organic matter was also found in the stomach contents; possibly the remains of soft bodied macro-and meiofaunal organisms such as turbellarians, gastrotrichs, nemerteans etc. Sand particles were present in the stomach contents but their role if any

TABLE II

Density of meiofaunal groups in three sampling times and in two different positions (A = 2-4cm; B = 10-12cm) in relation to anemone tube (numbers per $10cm^2$)

	May 1979		October 1979		March 1980	
	A	B	A	B	A	B
Nematoda	5 656	3 570	3 878	3 643	4 572	3 380
Harpacticoida interstitial	182	32	189	66	5	124
Harpacticoida benthic	171	16	53	45	92	45
Nauplii	1 200	63	79	142	221	110
Turbellaria	110	184	381	113	105	213
Gastrotricha	526	337	1 176	231	350	734
Tardigrada	905	26	37	13	—	11
Oligochaeta	3	—	—	—	—	—
Polychaeta	24	5	5	5	—	—
Bivalvia (juvs)	5	—	—	—	—	—
Ostracoda	18	—	—	—	—	—
Halacarida	8	—	—	—	—	—
Ciliata	179	237	347	434	642	342
TOTAL	8 987	4 470	6 145	4 692	5 987	4 959

in the nutrition of the animal is not clear. Ellehauge (1978) also observed the presence of sand grains in empty stomachs of species of *Edwardsia*.

Effect on meiofauna

Having ascertained that *Cerianthus* does feed on meiofauna, an attempt was made to assess the possible effect that predation may have on the meiofaunal community living in the proximity of the anemone.

Table II and Figure 3 show the group composition and density of the meiofauna taken on different sampling occasions and at two positions A and B in relation to the *Cerianthus* tube. Analysis of these data showed that there were no significant differences in the total fauna between the two positions and sampling occasions. Nevertheless group analysis showed that significant differences ($p<0.05$) in the abundance of nematodes and gastrotrichs existed between the two positions, the higher numbers occurring near the tube within reach of the tentacles (position A). A similar trend was exhibited by tardigrades and ciliates which were more abundant nearer rather than further away from the area of influence of the anemone .

DISCUSSION

The observations provide conclusive evidence that *C. lloydi* is lacking an activity rhythm. Ellehauge (1978) described an absence of an activity rhythm in edwardsiid anemones, while La Touche (1978) made similar observations in the feather star *Antedon bifida*. Retraction of the animal into its tube was mainly due to accidental contact with larger animals (mostly crabs and fish), strong wave action and food consumption reaching satiation level. The latter however could not be investigated *in situ* and the high threshold of satiation which was observed in the laboratory would be unlikely to occur in nature.

The feeding behaviour of *Cerianthus* as observed under a wide range of hydrodynamic conditions showed a great degree of adaptation to the prevailing conditions which is a combination of drag minimising and maximising feeding efficiency. Under conditions of heavy swell clumping of the tentacles in an upright position to catch horizontally drifting animals was observed. This alternated with a bending of the column and horizontal flexing of the tentacles in calm conditions in such a way as to increase the hunting area enabling the anemone to catch food items which fell from above or, were moved vertically in the water/sediment boundary layer. Koehl (1977) described how the mechanical responses of *Metridium senile* and *Anthopleura xanthogrammatica* to different current regimes can be related to the manner in which the anemones harvest food from flowing water. The former bend over in currents and suspension feed through their oral discs whereas the latter remained upright in the surge and catch mussels which fell on their oral discs.

Arai and Walder (1973) showed that ingestion in Ceriantharia is chemically controlled, activated by arginine. Moreover the same authors found that mechanical stimulation of the marginal tentacles leads to a transfer response but without excluding the possibility of a chemical stimulation.

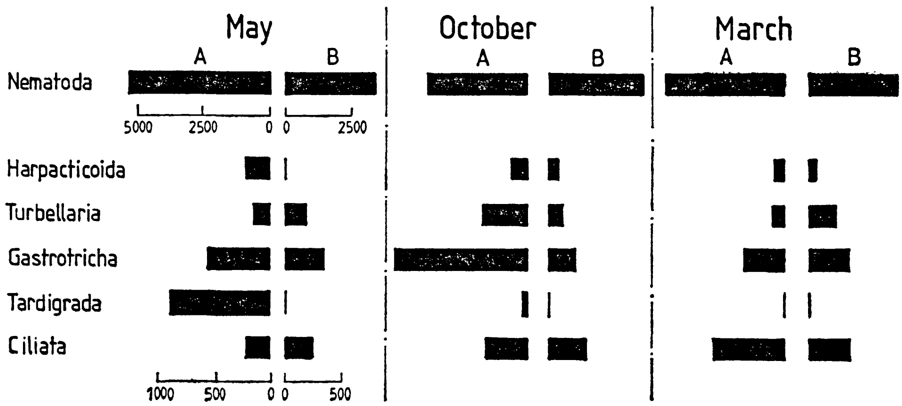

FIG. 3

Seasonal abundance and distribution of main meiofaunal groups in two positions (A = 2-4cm; B = 10-12cm) in relation to anemone tube (numbers per $10cm^2$ and 6cm depth).

The examination of the consumed food organisms suggested that *Cerianthus* preyed upon animals of a differing range of sizes. The degree of predation on any prey item and predation rate depended on prey availability (Table I, II; Fig. 3), mostly of itinerant benthic, planktonic and hyperbenthic crustaceans which were common in the area and which consequently appeared frequently in the diet of the anemone. In the laboratory, Gosse (1860) observed *Cerianthus* feeding on entomostracan crustaceans and Blegvad (1914) reported the presence of crustacean remains in the stomach of the species. Ellehauge (1978) found copepods in the stomach and concluded that *C. lloydi* is a carnivore preying upon animals from the plankton and the meiofauna. As the trophic role of meiofauna in marine ecosystems is insufficiently known, the predation of *Cerianthus* upon meiofauna organisms is of particular interest. The ability of some macrobenthic species to prey on meiofauna has been confirmed by many authors (Gerlach *et al.*, 1976; Bell and Coull, 1978; Reise, 1979; Scherer and Reise, 1981). However, in most cases, the overall predation pressure placed on the meiofauna is only moderate and the meiofauna is second rate prey. Bell and Coull (1978) showed that shrimp predation is capable of regulating meiofauna but it had yet to be shown that shrimps significantly alter meiofaunal abundance in the natural environment. Reise (1979) concluded that the permanent meiofauna of the Wadden Sea was only locally and temporarily "grazed down" by macrofauna.

The higher densities of meiofauna in the immediate vicinity of the anemone is of particular interest. Initially these differences (Table II) in meiofaunal densities were thought to be result of seasonal variation. However, samplings at different times of the year showed a recurrent pattern which indicated that a factor or factors were in operation promoting higher meiofaunal densities there. Examination of the particle size and organic content of the sediments between the two positions did not reveal any important differences (Table III). Speculating, it is suggested that an enrichment of the sediment with digestible wastes and dissolved organic components stimulated a bacterial growth near the tube aperture where nematodes, gastrotrichs, tardigrades and copepods were attracted and multiplied. The rate of predation on these meiofaunal populations could not be assessed and it seems that the removal of a fraction of these organisms was amply compensated by their population expansion. This process of stimulating growth of these organisms which were subsequently used as food is in a loose way reminiscent of Hylleberg's (1975) gardening concept suggested for *Abarenicola pacifica.*

These large concentrations of diatom feeding meiofauna groups (copepods, nematodes, etc.) grazing on the microflora were probably responsible for the lower chlorophyll values recorded from the vicinity of the tube (Table III).

TABLE III

Particle size, organic carbon and chlorophyll content of the sediments at the observation station (March, 1980)

Position A Fraction (cm)	Md Ø units	OC µg g^{-1} sed.	Chl µg g^{-1} sed.
0-2	2.49	2 310	3.67
2-4	2.56	2 380	3.60
4-6	2.46	2 390	4.39
Position B Fraction (cm)			
0-2	2.57	2 180	7.07
2-4	2.50	2 280	4.38
4-6	2.34	2 300	5.38

Tentacular contact with the sediment particles was an unselective way of preying upon meiofauna but probably also on microfauna. Tiffon and Daireaux (1974), Tiffon (1976) and Tiffon and Boutibonnes (1976) showed that *C. lloydi* captures and phagocytoses fine detrital particles and bacteria. Furthermore Tiffon (1976) and Tiffon and Daireaux (1974) demonstrated the ability of *C. lloydi* to extract organic substances in solution. Schlichter (1975, 1978) demonstrated the ability of *Anemonia sulcata* to take up glucose and aminoacids at concentrations found in natural water. It could be suggested that microorganisms and soluble organic substances which cannot be detected by the standard stomach contents analysis, play an important part in the diet of *C. lloydi.* Reiswig (1971) showed the importance of small organic particles and bacteria in the diet of reef demosponges and Tiffon and Daireaux (1974) suggested that these particles and micro-organisms may be important in the diet of many alcyonarians and zoantharians.

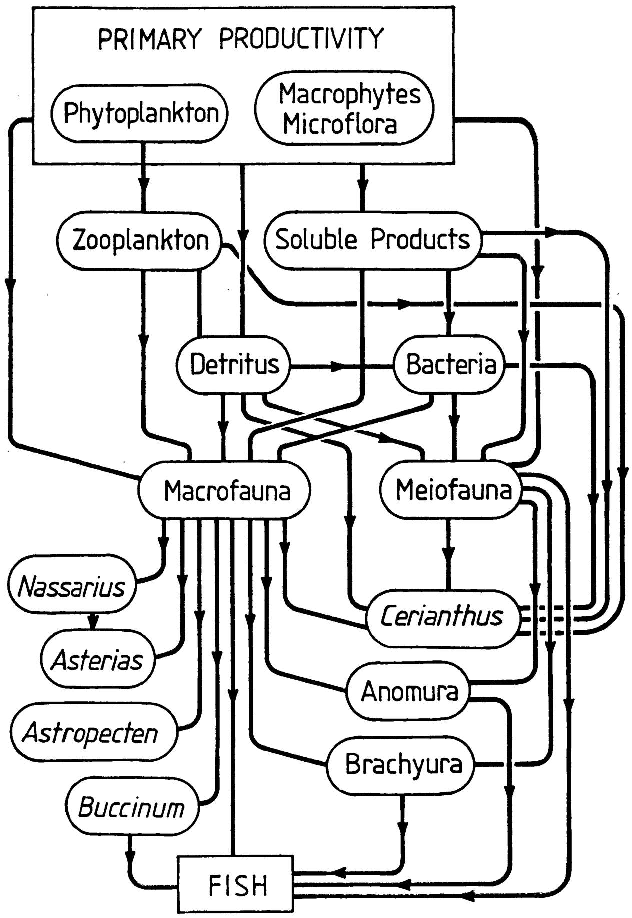

FIG. 4
Principal links in food chain of a shallow sandy bay (Firemore Bay).

There is no evidence of predation by vertebrate and invertebrate species on *C. lloydi* whose position in the food chain appears to be one of a wide spectrum predator (Fig. 4). In view of the recent evidence concerning the exploitation of other links in the food chain including bacteria and soluble organic substances it is suggested that *C. lloydi* is an opportunistic omnivorous feeder, performing an alternative deposit and suspension feeding similar to the feeding strategies observed in the polychaete *Lanice conchilega* (Buhr and Winter, 1977). Deposit feeding has been observed in the anthozoan *Sagartia troglodytes* (Riemann-Zurneck, 1969 and Pérès, 1966) classified the Ceriantharia as benthic detritus feeders.

The exploitation of several food sources by alternative feeding is of special importance, especially when the amount of food is limited. Thus it appears that alternative and continuous feeding is essential to *C. lloydi* in order to meet its energy requirements. However quantification of the feeding relationships is essential and further work is required before we fully understand the position of *C. lloydi* in the benthic food chain.

Summary

The general behaviour and feeding of the tube dwelling coelenterate *Cerianthus lloydi* was investigated *in situ* in a shallow sandy bay by means of Underwater Television. Continuous field and laboratory observations failed to show the existence of any diurnal rhythmic activity, the animal remaining expanded and feeding actively on a continuous basis. Observations on the sequence in tentacular movements in capturing and ingesting the prey were also made.

Analysis of the stomach content of 17 individuals revealed a carnivorous diet consisting of epibenthic invertebrates mostly crustaceans as well as smaller components such as meiofaunal organisms from the sediments surrounding the anemone tube. Predation effect on the abundant meiofaunal community is examined and the importance of the meiofaunal organisms in the diet of *Cerianthus* and other species is reviewed. The position of *Cerianthus* in a benthic food chain is briefly discussed.

REFERENCES

ARAI, M.N. and WALDER, G.L., 1973. — The feeding response of *Pachycerianthus fimbriatus* (Ceriantharia). *Comp. Biochem. Physiol. Part A, Comp. Physiol.* 44 (4), *pp.* 1085-1092.

BELL, S.S. and COULL, B.C., 1978. — Field evidence that shrimp predation regulates meiofauna. *Oecologia,* 35, *pp.* 141-148.

BLEGVAD, H., 1914. — Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. *Rep. Dan. biol. Stn,* 22, *pp.* 43-78.

BUHR, K.J. and WINTER, J.E., 1977. — Distribution and maintenance of a *Lanice conchilega* association in the Weser Estuary (FRG), with special reference to the suspension-feeding behaviour of *Lanice conchilega. In:* Biology of benthic organisms. B.F. Keegan, P. O'Ceidigh and P.J.S. Boaden (eds.), 11th European Symposium on Marine Biology, Galway, Oct. 1976, *pp.* 101-113.

ELEFTHERIOU, A., 1974. — The epifauna of a plaice nursery ground. *Int. Counc. Explor. Sea CM* 1974/K:24, 4 *pp.*

ELEFTHERIOU, A., 1979. — The ecology and biology of the shallow water hyperbenthos in a sandy bay. Ph. D. Thesis, Aberdeen University, 241 *pp.*

ELLEHAUGE, J.O., 1978. — On the ecology of *Edwardsia longicornis* and *E. danica* (Anthozoa, Actiniaria). *Biokon Rep.* (7), *pp.* 13-40.

GERLACH, S.A., EKSTROM, D.K. and ECKARDT, P.B., 1976. — Filter feeding in the hermit crab, *Pagurus bernhardus. Oecologia,* 24, *pp.* 257-264.

GOSSE, P.H., 1860. — Actinologia Brittanica. A History of the British Sea-Anemones and Corals. London, 358 *pp.*

HYLLEBERG, J., 1975. — Selective feeding of *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia,* 14, *pp.* 113-137.

KOEHL, M.A.R., 1977. — Effects of sea anemones on the flow forces they encounter. *J. exp. Biol.* 69, *pp.* 87-106.

LA TOUCHE, R.W., 1978. — The feeding behaviour of the featherstar *Antedon bifida* (Echinodermata : Crinoidea). *J. mar. biol. Asss. UK,* 58, *pp.* 877-890.

MCINTYRE, A.D. and ELEFTHERIOU, A., 1968. — The bottom fauna of a flatfish nursery ground. *J. mar. biol. Ass. UK.* 48, *pp.* 113-142.

MCINTYRE, A.D. and MURISON, D.J., 1973. — The meiofauna of a flatfish nursery ground. *J. mar. biol. Ass. UK.* 53, *pp.* 93-118.

PÉRÈS, J.M., 1966. — La vie dans l'océan. Editions du Seuil, Paris, 190 *pp.*

REISE, K., 1979. — Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. *Helgol. wiss. Meeres.* 32, *pp.* 453-465.

REISWIG, H.M., 1971. — Particle feeding in natural populations of three marine demosponges. *Biol. Bull. Mar. biol. Lab., Woods Hole,* 141, *pp.* 568-591.

RIEMANN-ZURNECK, K., 1969. — *Sagartia troglodytes* (Anthozoa). Biologie und Morphologie einer schickbewohnenden Aktinie. *Veroff. Inst. Meeresforsch. Bremerh.* 12, *pp.* 169-230.

SCHERER, B. and REISE, K., 1981. — Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kieler Meeres.* 5, *pp.* 490-500.

SCHLICHTER, D., 1975. — Die Bedeutung in Meerwasser geloster Glucose für die Ernahrung von *Anemonia sulcata* (Coelenterata : Anthozoa). *Mar. Biol.* 29, *pp.* 283-293.

SCHLICHTER, D., 1978. — On the ability of *Anemonia sulcata* (Coelenterata : Anthozoa) to absorb charged and neutral aminoacids simultaneously. *Mar. Biol.* 45, *pp.* 97-104.

STEELE, J.H. and BAIRD, J.E., 1968. — Production ecology of a sandy beach. *Limnol. Oceanogr.* 13, *pp.* 14-25.

TIFFON, Y., 1975. — Hydrolases dans l'ectoderme de *C. lloydi, C. membranaceous,* et *Metridium senile :* mise en évidence d'une digestion extracellulaire et extracorporelle. *J. exp. mar. Biol. Ecol.* 18, *pp.* 243-254.

TIFFON, Y., 1976. — Nutrition expérimentale chez les Cérianthaires, *In:* Coelenterate Ecology and Behaviour, Mackie, G.O. (ed.), Plenum Press, New York, *pp.* 147-153.

TIFFON, Y. and BOUTIBONNES, P., 1976. — Nutrition particulaire expérimentale de l'anthozoaire *Cerianthus lloydi. C.R. Acad. Sci., Paris* (*ser. D*), 282, *pp.* 1629-1632.

TIFFON, Y. and DAIREAUX, M., 1974. — Phagocytose et pinocytose par l'ectoderme et l'endoderme de *Cerianthus lloydi* Gosse. *J. exp. mar. Biol. Ecol.* 16 (2), *pp.* 155-166.