FEEDING RATES OF APPENDICULARIANS (OIKOPLEURA SPP.) IN COASTAL NEWFOUNDLAND WATERS: RESULTS OF IN SITU STUDIES

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FEEDING RATES OF APPENDICULARIANS (*OIKOPLEURA SPP.*) IN COASTAL NEWFOUNDLAND WATERS: RESULTS OF *IN SITU* STUDIES

by

© Deborah-Anne Steel, B.Sc. (Hons.)

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ABSTRACT

Appendicularian populations were observed in Logy Bay, Newfoundland over a two year period to quantify their feeding behavior and to elucidate their role in energy flow in a cold ocean environment. Populations were observed to fluctuate rapidly in apparent response to wind-induced changes in water mass characteristics. Very large individuals of *Oikopleura vanhoeffeni* dominated very cold waters ($< 0^{\circ}C$) while warmer waters ($> 8^{\circ}C$) were characterized by higher densities of the smaller *Oikopleura labradoriensis*.

Radioactively labelled algae were used to measure *in situ* ingestion and clearance rates of individual *Oikopleura* over a wide range of animal sizes, temperatures and ambient food concentrations. Multiple regression analysis indicated that animal body size (measured as tail length) explained 11.3% of the variance in ingestion rate and 46% of the variance in clearance rate. Temperature was not a significant variable, while the biomass concentration of phytoplankton < 2 μm explained an additional 8% of the variation in clearance rate. Animal activity, estimated from tail beat observations, explained 60% of the variation in ingestion rate for a subset of the data but was not significantly correlated with temperature, body size or ambient food concentrations. *Oikopleura* populations were estimated to clear a maximum of 2% of the water

column per day at observed densities, while literature estimates of densities for nearby Conception Bay yielded clearing estimates up to 64% per day.

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INTRODUCTION

Gelatinous Zooplankton

Gelatinous zooplankton are a heterogeneous assemblage of fragile, soft-bodied marine macroplankton which include the Hydromedusae, Scyphomedusae, Heteropoda, Pteropoda, Thaliacea (salps, doliolids and pyrosomes), Ctenophora, Siphonophora and Appendicularia (Alldredge 1984). Collectively these organisms represent different phyla and span three trophic levels yet share distinct characteristics of structure and function. Most are neutrally buoyant and the refractive index of their tissue is close to that of seawater so that they are nearly transparent (Alldredge and Madin 1982).

Gelatinous zooplankton are delicate and are often destroyed when collected in plankton nets (Hamner et al. 1975), a problem which hindered early investigations of their ecology and taxonomy. Hamner et al. (1975) noted that SCUBA divers could readily observe and capture several kinds of these zooplankton in containers without damaging them. Subsequent *in situ* studies on appendicularians (Alldredge 1976b, 1977, 1981; King 1981) and salps (Madin 1974, Mullin 1983) using SCUBA have resulted in a better understanding of the abundance and importance of these gelatinous consumers in neritic and open ocean communities.

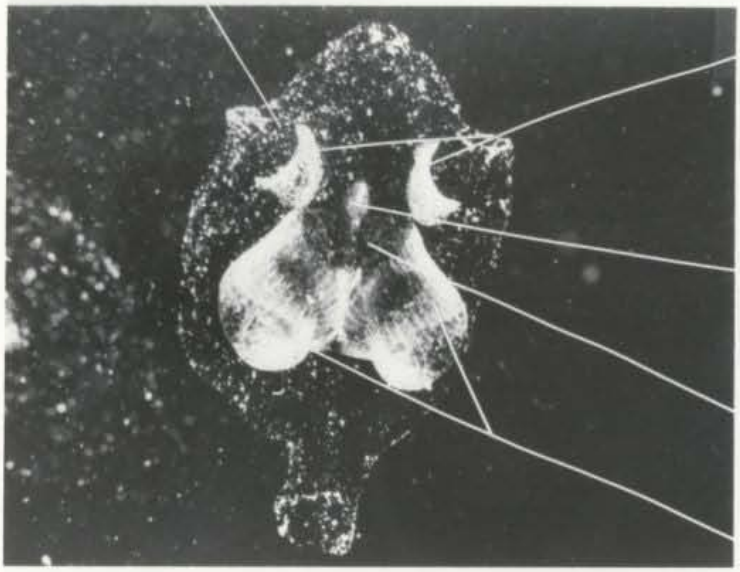
Appendicularians

The Appendicularia are a class of tadpole-like animals believed to have evolved from the larvae of bottom dwelling ascidians (Fenaux 1967). Most species of the family Oikopleuridae live within a mucous house with two sets of filters: a coarse incurrent filter which screens out large particles ($> \sim 30$ μm) and a finer inner feeding filter able to retain particles $< .1$ μm in diameter (Flood 1978,1981;Fig. 1). Hence, appendicularians are able to consume highly productive nanoplankton and bacterioplankton (Hallegraef 1981, King 1981), food sources too small for efficient consumption by setose appendage-feeding copepods (Boyd 1976).

It has been hypothesized that nanoplankton-based food chains are less efficient than those based on netplankton because the former require one or two additional trophic level transfers for energy to reach higher consumers such as fish (Ryther 1969). Appendicularians may play an important role in marine food chains by providing a more direct link between the lower and higher trophic levels. Appendicularians and their houses are an important food for a variety of fish: *Oikopleura dioica* is fed upon by larval plaice (*Pleuronectes platessa*), sandeels (*Ammodytes* spp.) (Shelbourne 1962, Ryland 1964), flounder and the planktonic larvae of both commercial and non-commercial fish in the North Sea (Last 1978).

Figure 1: Oikopleura sp. within its gelatinous house.
(photo courtesy of R. Hooper)

MUCOUS HOUSE



Members of the family Oikopleuridae have been observed to reach densities exceeding 30 animals per litre (Seki 1973), with maximum densities of 3,565 per litre in parallel surface windrows during spawning of *Oikopleura longicauda* (Alldredge 1982). The high concentrations and feeding rates of appendicularians (Paffenhofer 1976, Alldredge 1981, King 1981) imply a significant impact on phytoplankton populations (Alldredge 1981).

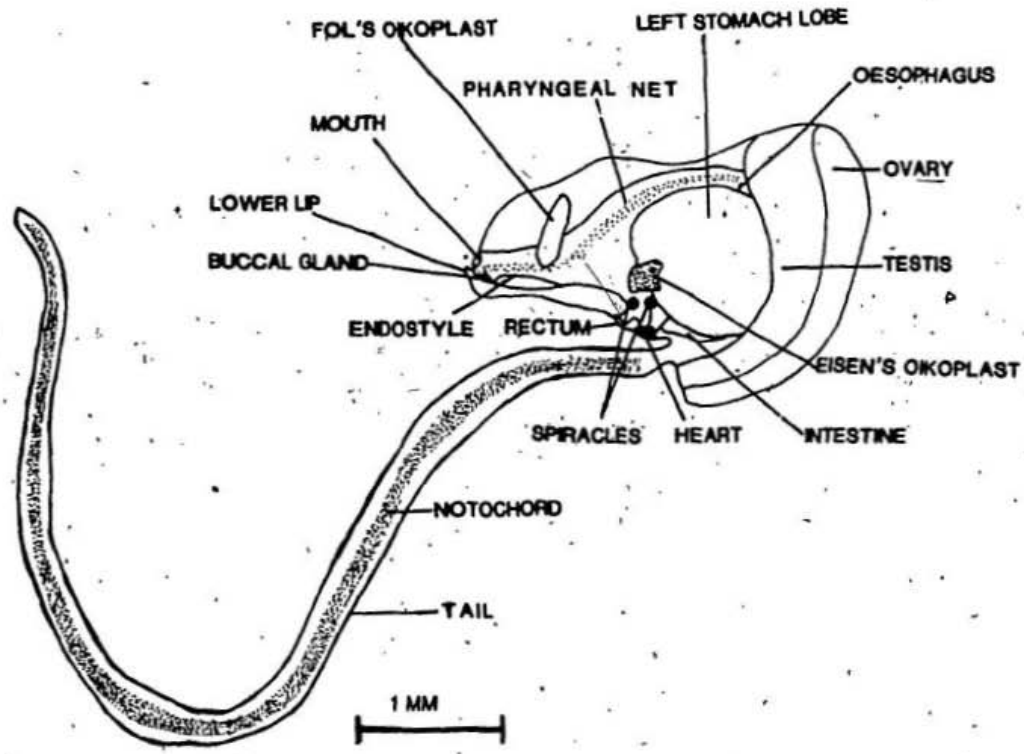
The object of the present study was to determine *in situ* clearance rates of cold-ocean appendicularians to examine both their potential feeding impact on phytoplankton their role in energy flow to higher trophic levels in coastal Newfoundland waters.

The Organism

The appendicularian body (Fig.2) consists of a trunk, which contains all major organs including the reproductive and digestive systems, and an elongate muscular tail (Alldredge 1976a). The tail is thin and flat with a notochord running longitudinally down its center (Alldredge 1976a). The digestive tract consists of a mouth, buccal glands, pharynx, oesophagus, stomach (1 or 2 lobed), intestine and a rectum which opens ventrally (Fraser 1982).

A feeding current is maintained by the sinusoidal beating of the tail, the action of which draws water and food particles into the house through the incurrent filters and internal feeding filters. The action of ciliated spiracles draws collected food particles through the mouth and into the pharynx as the animal feeds. The endostyle near the mouth secretes mucus to form a funnel-shaped pharyngeal net to which food particles adhere and which extends posteriorly

Figure 2: The larvacean body (modified from Carlisle 1979).


FOL'S OIKOPLAST
LEFT STOMACH LOBE
PHARYNGEAL NET
OESOPHAGUS
MOUTH
OVARY
LOWER LIP
BUCCAL GLAND
TESTIS
ENDOSTYLE
RECTUM
EISEN'S OIKOPLAST
SPIRACLES
HEART
INTESTINE
NOTOCHORD
TAIL
1 MM

towards the oesophagus (Jorgensen 1966). The heart is located ventrally while the large gonads are situated posteriorly.

With the exception of the dioecious *Oikopleura dioica*, appendicularians are reportedly simultaneous hermaphrodites as indicated by observations of *O. longicauda* (Alldredge 1982). Animals die soon after spawning because gamete release requires rupturing of the body wall (Alldredge 1982). Animal development is direct (Galt 1972) and juveniles build their first house within 12 to 20 hours of fertilization (Paffenhofer 1973, Fenaux 1976). Body size increases exponentially throughout most of the animal's life (King et al. 1980) and animals are sexually mature and ready to spawn within 5 to 21 days after hatching, depending upon species and temperature (Alldredge and Madin 1982). High fecundity and growth rates, a short generation time and an efficient filtering system should enable appendicularians to respond rapidly to sudden increases in food supply (Alldredge and Madin 1982).

Structure and Function of the Larvacean House

Members of the family Oikopleuridae feed within a roughly spherical mucous 'house' (Lohmann 1899) composed of proteins and mucopolysaccharides (Korner 1952, Fig. 1). The house is secreted around the animal by specialized oikoplast epithelium located on the trunk (Alldredge 1977, Fenaux 1977). This epithelium is differentiated into Fol's and Eisen's oikoplast which secrete the

feeding and incurrent filters respectively (Lohmann 1899). House size varies with species and animal size (Alldredge 1976b, 1977); Fenaux and Hirel (1972) suggested that the house volume of *Oikopleura dioica* was typically 300 x that of the trunk volume.

The house has three main functions:

1) It contains the feeding filters which are essential for feeding because movement of the tail draws water through the complex filters which concentrate phytoplankton for transport to the mouth (Alldredge 1976a). Feeding behavior has not been observed to occur outside the house (Galt 1972).

2) It serves to protect the animal from potential predators such as chaetognaths and medusae which cannot easily break through the wall of the house (Galt 1972).

3) It allows the animal to achieve neutral buoyancy. Animals without houses are forced to swim to avoid sinking, while those in houses maintain their position in the water column even when their tails are not moving (Alldredge 1976a).

During the time that an appendicularian feeds within one house, it secretes another which is carried in a collapsed form against the trunk (Fenaux 1976). A house may be discarded when it becomes clogged with particles (Alldredge 1977) or as a response to disturbance or predators (Lohmann 1909). Sensitivity to physical disturbance varies widely (Alldredge 1977, observations in this study). In most species, the escaping animal forcefully breaks through the wall of the house (Alldredge 1976b) rather than through an exit structure (Lohmann 1909). House abandonment is followed by rapid swimming towards the surface where the animal begins a series of complex cartwheel and sinusoidal motions to inflate the

new house (Galt 1972, Fenaux 1976), a process which may be completed in less than two minutes (this study).

Discarded houses are rich in carbon; houses of *O. dioica* have been observed to have as many as 40,000-50,000 living phytoplankton cells trapped on the filters and walls (Alldredge and Madin 1982). The sinking rates of houses are higher than those of individual nanoplankton cells, thus hastening the flux of surface particulate matter to deeper water (Alldredge and Madin 1982). While many houses do reach mesopelagic depths (Silver and Alldredge 1981), their slow sinking rate (about 50 m per day) and consumption by organisms in the water column makes them an important contributor to nutrient recycling in tropical surface waters (Alldredge and Madin 1982).

The Filtering Mechanism

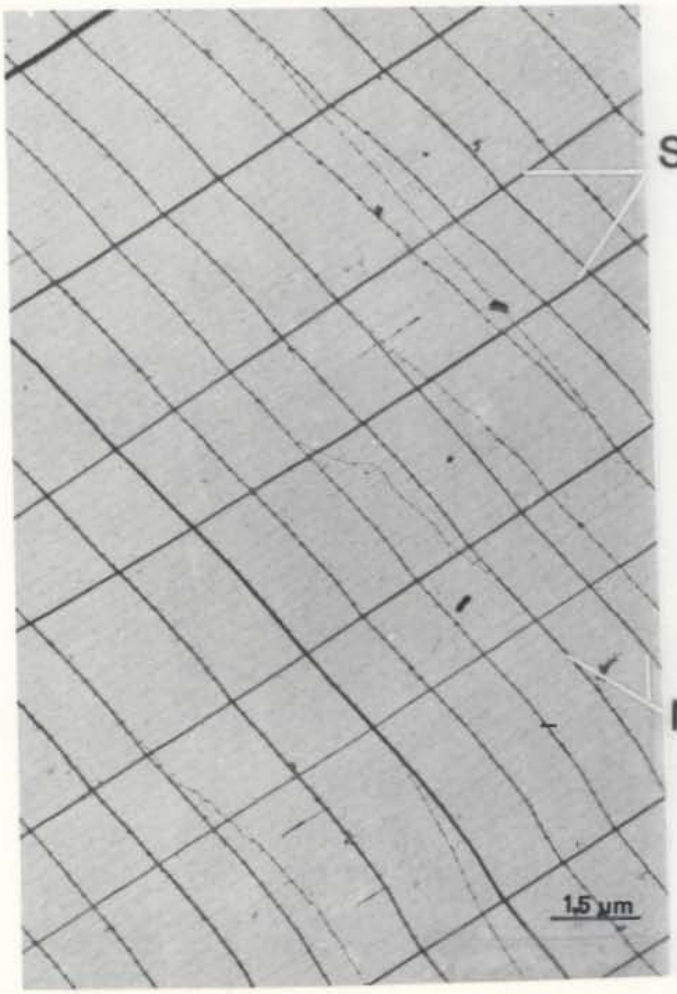
Filtration in larvaceans is a size-dependent process based on the structure of both the incurrent and feeding filters. In a study of seven species of appendicularians (Alldredge 1977), minimum pore width of the incurrent filters varied from 13 to 54 μm. Particles larger than these pore dimensions (such as most diatoms and large dinoflagellates) were trapped on the incurrent filters and did not enter the house. The incurrent filters appear to protect the feeding filter from premature clogging by large or spinous particles, enabling the house to be used longer before abandonment (Deibel et al. 1985). Transmission electron micrographs of the feeding filter of *O. dioica* (trunk lengths averaging 1.0 mm,

Alldredge 1981) revealed a mean pore size of 0.24 x 0.07 μm, enabling the animal to retain particles as small as 0.1 μm in diameter (Flood 1981). The filter consisted of a fine and regular network of filaments 0.01 to 0.04 μm thick with 90% open area (Flood 1981). King (1981) indicated that the feeding filter of *O. dioica* can retain bacteria-size particles, but at a low efficiency. Current work suggests that it is the pharyngeal mucous net which ultimately determines the retention efficiency for small particles (Jorgensen 1984; Deibel in prep.).

Oikopleura vanhoeffeni, a common species in Newfoundland waters, has one of the largest incurrent filter pore sizes reported for any oikopleurid (ca. 169 x 88 μm) and is capable of ingesting large particles such as silicoflagellates, dinoflagellates, and both unicellular and chain-forming diatoms with spines (i.e. *Chaetoceros* sp., Deibel and Turner 1985). The feeding filter of *O. vanhoeffeni* (trunk lengths from 1.5 to 2.5 mm) has mean pore dimensions of 1.04 x 0.22 μm with 91% open area (Fig. 3; Deibel et al. 1985). This large porosity permits this oikopleurid to process large volumes of water per unit time, while the pharyngeal filter net (with a smaller surface area; Fig. 2) sieves only a fraction of the water taken into the house (Jorgensen 1984) and concentrates the remaining food suspension for subsequent ingestion (Deibel et al. 1985).

Filter fiber width is important when considering the efficiency of filter feeding. Flow patterns around a fiber may be altered by the presence of neighboring fibers as well as by particle accumulation, resulting in structural changes in the filter and increased resistance to flow due to the reduction in percentage of open area (Rubenstein and Koehl 1977). Flood (1978) suggested that small rectangular meshes combined with a large percent open area delay

Figure 3: Transmission electron micrograph of feeding filter mesh showing the spatial orientation of mucous fibers (Deibel et al., 1985)


SMOOTH FIBER
NODULATED FIBER
1,5 µm

clogging of the feeding filter because particles are unlikely to enter the pores without being able to penetrate through them. Wallace and Malas (1976) have shown that rectilinear arrays of fine fibers are the most energy-efficient way for an organism to retain small particles. Transmission electron microscopy (TEM) has revealed that the fine, mucous feeding filter of *O. vanhoeffeni* is composed of three types of fibers: "smooth fibers", "nodulated fibers" and small "microfibers". Smooth and nodulated fibers measured 40 nm in diameter and microfibers were about 12 nm in diameter (Deibel et al. 1985). The ultrastructure of the feeding filter of *O. vanhoeffeni* was similar to that of smaller oikopleurids from warmer waters, although [redacted] sizes differed (Deibel et al. 1985).

The feeding filter is a complex, three-dimensional structure (Figs. 4 and 5) in the form of two curved wings connected along one edge (Alldredge 1977). The wings join at a median channel which connects to the mouth by a hollow buccal tube (Fig. 4a; Alldredge 1977). Fol (1872) stated that appendicularians directly ingest food-containing water; but, Lohmann (1899, 1909) observed that the filters concentrate food particles before water enters the mouth. Korner (1952) suggested that the feeding filter was composed of a ventral and dorsal layer of parallel tubes while Fjerdingstad (cited in Jorgensen 1966) maintained that the feeding filter of *Oikopleura* sp. consisted of three parallel membranes sandwiched to form two slit-like chambers with the intermediate membrane being porous to water (pore size of 0.8 x 1μm; Fig. 4b). These membranes are corrugated, increasing the surface area available for particle collection (Flood 1978). The corrugated folds run parallel to each other and contain thick fibres which are perpendicular to thinner fibres. Fjerdingstad proposed that particle-laden water

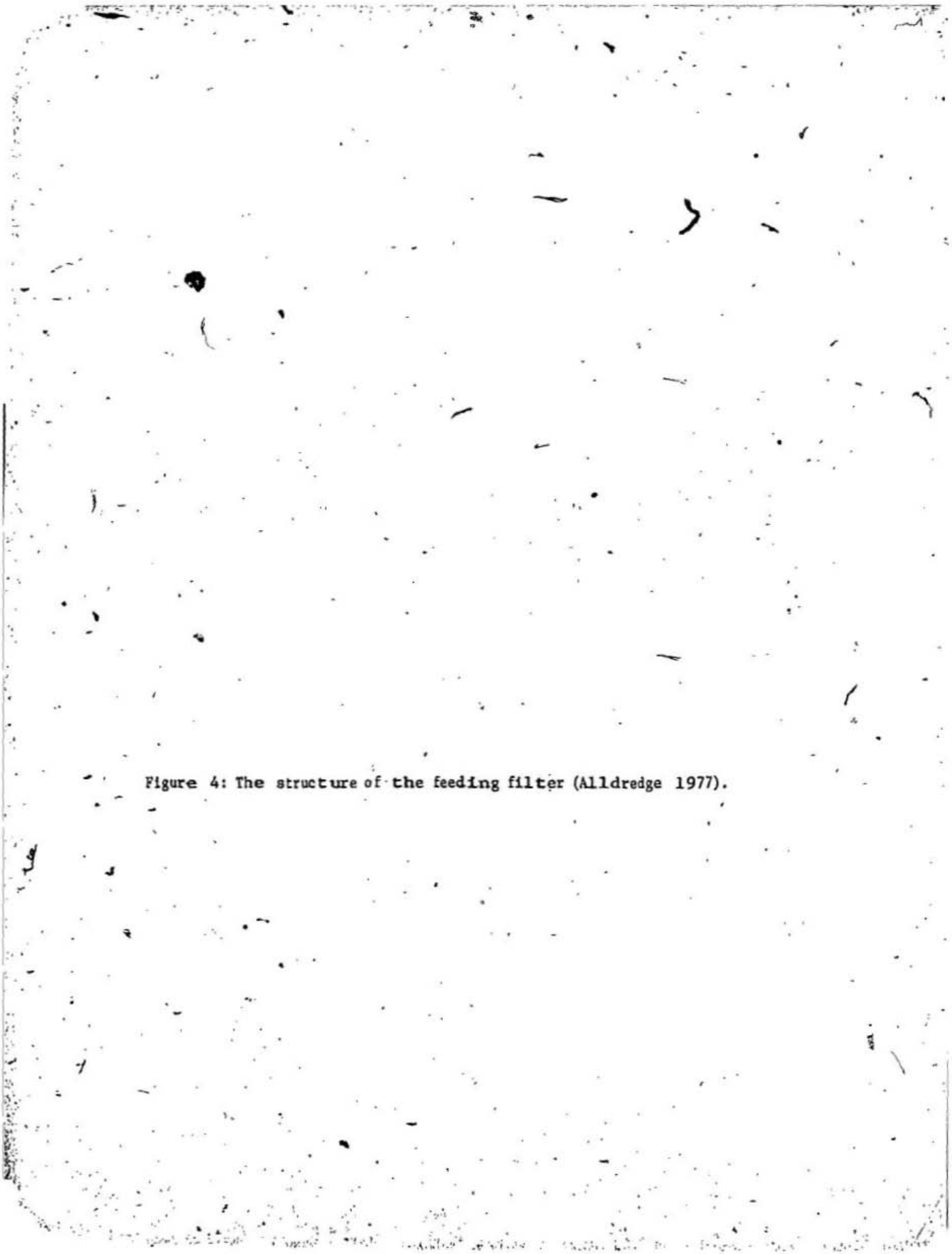
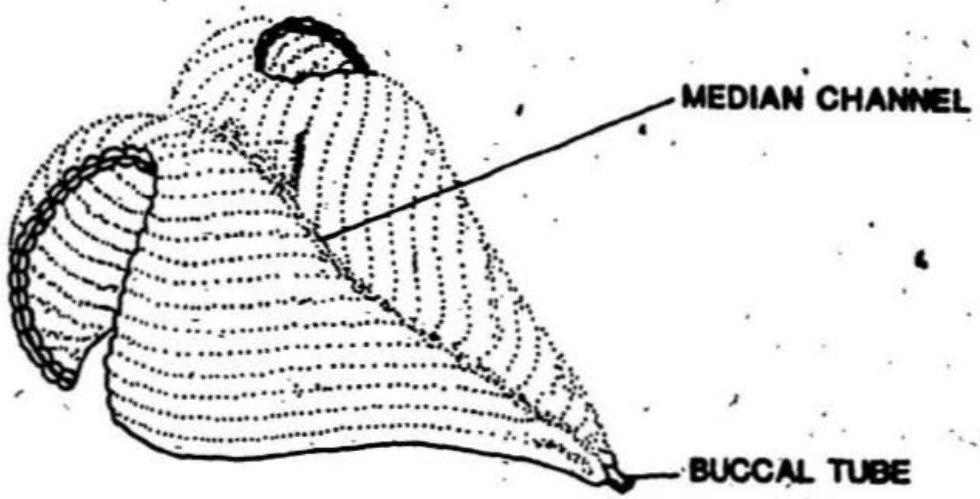
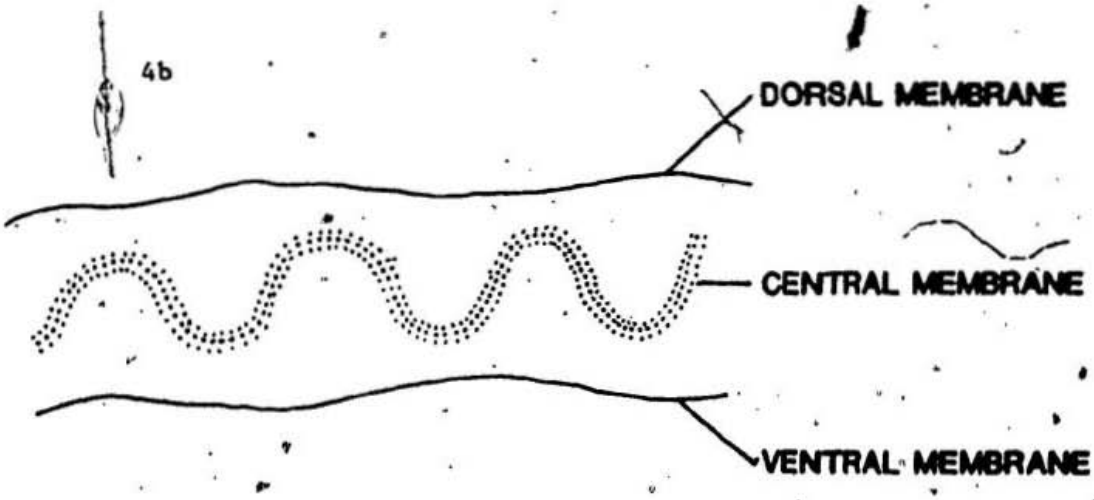


Figure 4: The structure of the feeding filter (Alldredge 1977).

4a


MEDIAN CHANNEL
BUCCAL TUBE

4b

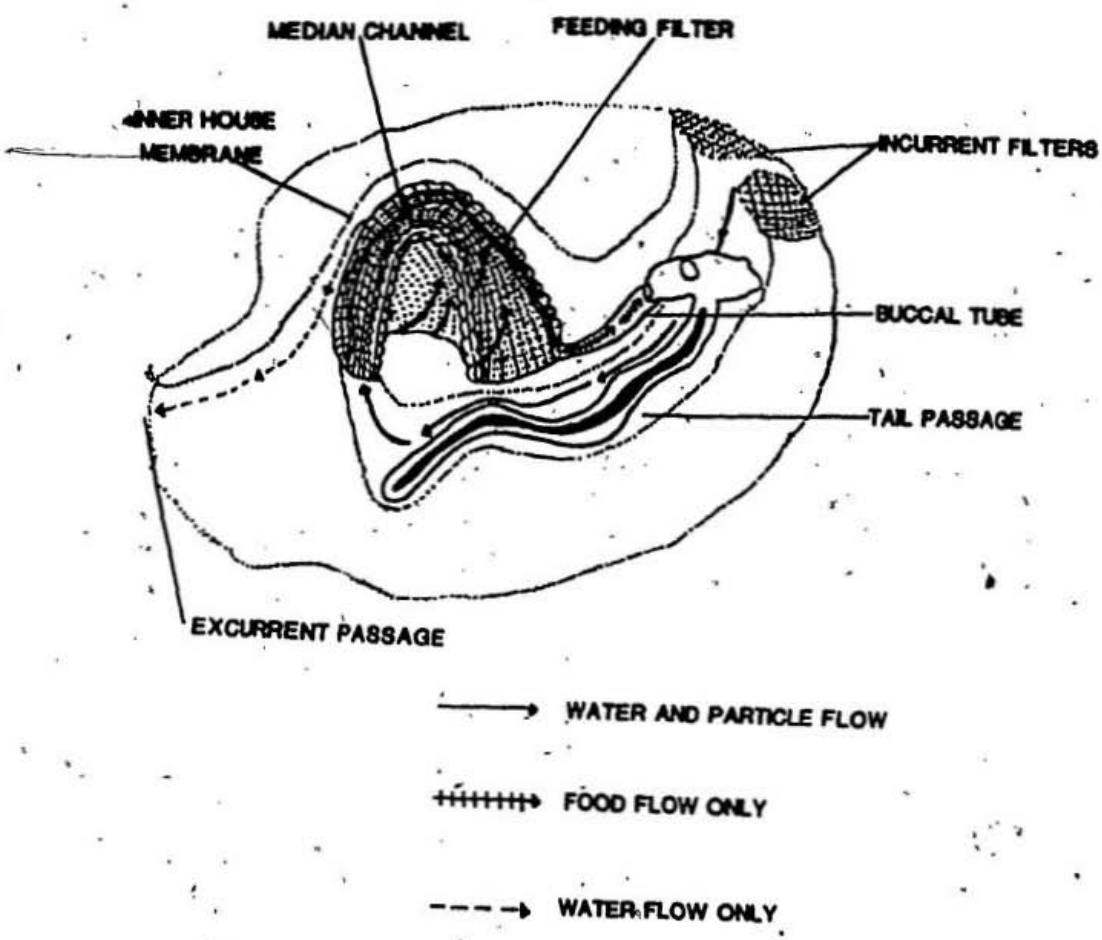

DORSAL MEMBRANE
CENTRAL MEMBRANE
VENTRAL MEMBRANE

flowing into the dorsal chamber would pass through the porous central membrane leaving all but the smallest particles trapped in the dorsal chamber.

Alldredge (1975,1977) has proposed an alternate description of food and water movement based on a two-membrane feeding filter. Particle-laden water is drawn through the incurrent filters and into the house by sinusoidal movements of the tail, which is contained within a chamber separate from the rest of the house (King 1981). This tail passage connects the incurrent filters with the base of the internal feeding filter (Alldredge 1977; Fig. 5). Water flows simultaneously up both edges of the arched wing to its apex, then down the corrugations of the filter where food particles collect on the mucous walls of the membranes. Particles are sucked into the median channel of the feeding filter and down the buccal tube to the mouth by the action of cilia in the spiracles within the appendicularian's trunks (Alldredge 1975). The animal may exhibit some particle selectivity and reject food particles by reversing the ciliary beat in response to tactile stimulation of the lower lip (Galt and Mackie 1971). Once in the mouth, food material and associated mucus are transported by the cilia of the epipharynx to the oesophagus and into the stomach (Alldredge 1977). Water that has passed through the feeding filter is retained within the inner house membrane and expelled through an excurrent opening located at the posterior end of the median channel (Alldredge 1977, King 1981; Fig. 5).

Feeding filters tend to collapse in histological solutions making it difficult to determine the exact number and arrangement of membranes (Flood 1978). Recent work with rhodamine dyes, finely powdered graphite and *Isochrysis galbana* has shown the feeding filter to be composed of three layers, functioning as

Figure 5: Schematic diagram of food and water movement through the house of Oikopleura dioica (Alldredge 1975, 1977).


MEDIAN CHANNEL
FEEDING FILTER
INNER HOUSE MEMBRANE
INCURRENT FILTERS
BUCCAL TUBE
TAIL PASSAGE
EXCURRENT PASSAGE
WATER AND PARTICLE FLOW
FOOD FLOW ONLY
WATER FLOW ONLY

a low velocity sieve. Water is forced through both the dorsal and ventral layers at a low flow rate, while the concentrated particles proceed to the mouth suspended in the bulk flow of the remaining water (Deibel, in prep.). The food particles are not "trapped" on the feeding filter, but merely concentrated by it. This highly efficient mechanism would allow the animal to maintain a high flow per unit time with reduced clogging of the filters (Deibel et al. 1985).

Feeding Rates of Gelatinous Zooplankton

The rates at which suspension feeders clear the water of suspended particles have been determined for many gelatinous zooplankton including ctenophores (Reeve 1980), salps (Harbison and Gilmer 1976, Deibel 1982, Mullin 1983, Madin and Cetta 1984, Deibel 1985a), doliolids (Deibel 1982) and appendicularians (Paffenhofer 1976, King et al. 1980, Alldredge 1981, King 1981) using a variety of techniques and over a wide range of particle concentrations. Studies of appendicularian feeding are complicated by the fact that the delicate gelatinous houses are easily destroyed by traditional zooplankton collection techniques such as plankton tows. Food particles are concentrated on both the internal and external surfaces of the house; thus particles which are not actually consumed by the animal may collect all over the external surface of the house and consequently still be removed from suspension (Alldredge 1981).

In this study, the term total clearance rate (TCR), will be used to designate the rate of labelled food collection by both the animal and the house, while animal

clearance rate (ACR), will represent the rate of collection of particles by the animal alone. Both rates will be expressed as the equivalent volume of water cleared of labelled particles per unit time. Direct comparison of feeding data is difficult because authors have employed various food suspensions and procedures at different temperatures. Furthermore, feeding studies on appendicularians have been limited to two warm water species, *O. dioica* (Paffenhoefer 1976, King et al.,1980, Alldredge 1981, King 1981) and *Stegasoma magnum* (Alldredge 1981), making it difficult to extrapolate and compare these data to cold ocean conditions.

Clearance rates for *O. dioica* have been calculated at 13.5°C in the laboratory using visual estimates of the number of appendicularians per experimental chamber and a Coulter Counter to determine the rate of decrease in the number of cells per ml of food suspension (Paffenhofer 1976). On the assumption that cell breakage and actual cell shape did not bias his cell counts (which could result in underestimation of clearing rates) Paffenhofer (1976) concluded that clearance rate was not inhibited by increased food concentrations at naturally occurring phytoplankton densities in the North Sea. His data appear not to support this conclusion, however. King (1981) fed *O. dioica* ^{3}H-labelled natural assemblages of marine bacteria under laboratory conditions and also concluded that ingestion and total clearance rates were independent of nanophytoplankton concentrations ranging from < 40 μg C/l to > 100 μg C/l.

Alldredge (1981) conducted an *in situ* warm water study whereby single appendicularians (*O. dioica* and *Stegasoma magnum*) were captured in individual containers containing ambient food concentrations and inert tracers in the form of

readily countable plastic beads. She concluded that maximum population densities of appendicularians exerted significant feeding pressure on natural food assemblages over relatively constant particulate food concentrations. Few studies have concurrently assessed both regional differences in feeding rates of appendicularian species and the complex dynamics of environmental variables affecting both grazer and food populations (King 1981). Several studies have examined the effects of temperature and food concentration on the growth and development of *O. dioica* (Paffenhofer 1976, Gorsky 1980, King 1981) but none have dealt specifically with the effects on ingestion and clearance rates, using a single technique over a wide range of these environmental parameters.

Hence, the object of this study was to determine *in situ* clearance rates of cold-ocean appendicularians using a radioactive tracer technique. Combining these rates with properties of the organisms, environmental variables and estimates of appendicularian and ambient phytoplankton densities will provide insight into both the potential feeding impact of these zooplankton in coastal Newfoundland waters and their role in energy transfer to higher trophic levels.

Methods and Materials

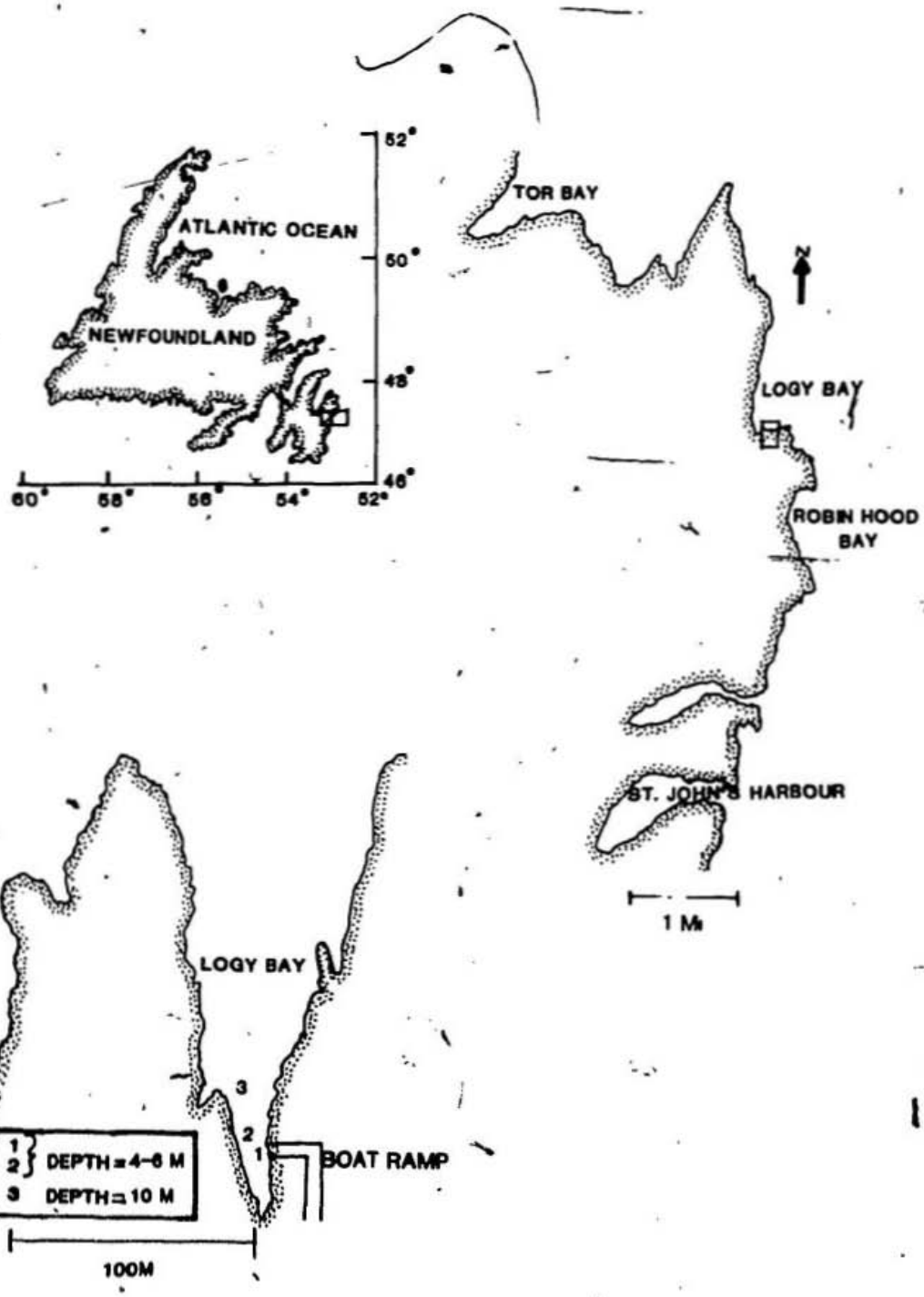
Field Methods

Study Site

In situ measurements of appendicularian feeding rates were made at Logy Bay (47° 37'N,52° 40'W) near St. John's on the Avalon Peninsula, Newfoundland (Fig. 6). Dive sites ranged in depth from 4 to 10 meters. The majority of measurements were made at site #1, with a bottom depth of ~5 meters.

Udvardy (1954) reported that coastal stations east of Newfoundland contained a mixed appendicularian fauna of both *Oikopleura vanhoeffeni* (Lohmann) and *Oikopleura labradoriensis* (Lohmann). According to Thompson and Frost (1936), *O. vanhoeffeni* is an indicator of cold water of pure arctic origin and *O. labradoriensis* is characteristic of mixed cold-temperate waters of the northern oceans. The majority of feeding experiments were made on *O. vanhoeffeni* as it was the most abundant during the sampling season, and ease of observation was facilitated by its large size and the bright red tail pigmentation.

Figure 6: Study site, Logy Bay, Newfoundland.


ATLANTIC OCEAN
NEWFOUNDLAND
52°
50°
48°
46°
60°
58°
56°
54°
52°
TOR BAY
N
LOGY BAY
ROBIN HOOD BAY
ST. JOHN'S HARBOUR
1 M
LOGY BAY
3
2
1
BOAT RAMP
1
2
DEPTH = 4-6 M
3
DEPTH = 10 M
100M

Design and Manipulation of the Experimental Chambers

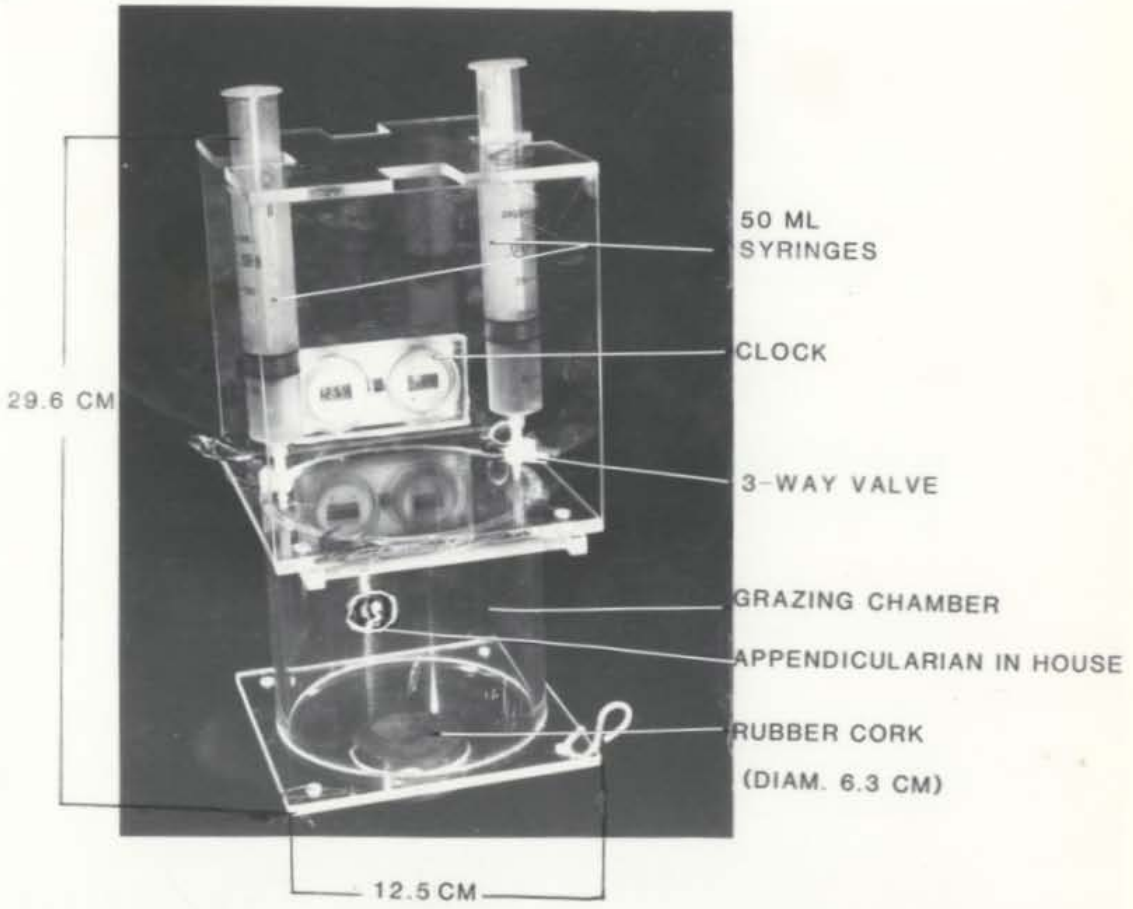
Feeding experiments were conducted in plexiglass chambers (Fig. 7) similar in design to those of Alldredge (1981). The chambers were of two sizes with diameters of 11.7 and 13.7 cm and volumes of one and two liters respectively. Two clocks in a watertight case were attached to the interior wall of the upper part of each chamber to facilitate *in situ* timing of the feeding period and observations of animal activity. A three-way valve permitted attachment of a 5 ml syringe for delivery of the radioactive food suspension to the feeding chamber. Following addition of the food suspension, the two 50 ml syringes were alternately filled to effect mixing inside the chamber. Rubber stoppers completely sealed the chambers during the feeding experiments.

Preparation and Maintenance of Algal Food Suspension

Scenedesmus quadricauda (MUN stock algal culture #008) was selected for the *in situ* feeding studies because the cells have an average diameter of 4 μm, which is within the ingestible size range of appendicularians (Alldredge 1981), and grow well in culture as unicells without clumping. The cells have a high efficiency of radioactive label incorporation and did not leach radioactivity to the seawater during the *in situ* incubation as demonstrated by comparison of whole water and filtered samples.

Unialgal cultures were grown in stoppered 500 ml glass flasks containing Bold's Basal medium (Stein 1973) which produced carbon-limited growth, thereby

Figure 7: Experimental feeding chamber.


50 ML
SYRINGES
CLOCK
29.6 CM
3-WAY VALVE
GRAZING CHAMBER
APPENDICULARIAN IN HOUSE
RUBBER CORK
(DIAM. 6.3 CM)
12.5 CM

enhancing radiocarbon uptake. The cultures were maintained on a shaker table (to maintain unicellular growth) on a 12:12 photoperiod under cool white fluorescent illumination at 25°C.

For radioisotope labelling, algal culture in stationary growth phase (~4 x 10^6 cells/ml) was drawn into a 50 ml plastic syringe and purged of inorganic carbon by acidification to pH 3.5 with 0.1N HCL (Holtby and Knoechel 1981). Air was drawn into the syringe which was then shaken gently to promote release of dissolved carbon dioxide. This process was repeated six times and then the medium in the syringe was restored to its initial pH of 10.0-11.0 by adding 0.1N NaOH. Either 20 or 200 μCi of dissolved $NaH^{14}CO_3$ were added and the syringe was placed on a shaker table and maintained under the same light and temperature regime as the unlabelled algal cultures. Isotope incorporation ranged from 90-95% as determined by comparison of radioactivity of acidified and non-acidified subsamples.

Field Procedures

Feeding Trials

For each feeding trial, a SCUBA diver gently captured a single animal in its house in an open feeding chamber (Fig. 7) which was then stoppered and brought near the surface. Shore personnel then handed the diver a 5 ml syringe containing

1-2 mls of the labelled food suspension. The diver added the food through the three way valve and alternately filled the two 50 ml syringes to effect mixing within the feeding chamber. The chambers were suspended near the bottom for the designated incubation time. If the animal jettisoned its house, the feeding trial was aborted. Feeding periods ranged from 5 to 20 minutes although most were for only 10 minutes. Alldredge (1981) noted that fecal pellets were produced in a minimum of 8 minutes in laboratory feeding studies on *O. dioica* at 25°C. Similar studies on *O. vanhoeffeni* at temperatures equivalent to those encountered in this study (ca. -1.0° C), indicate that fecal pellet production takes longer at colder temperatures (Deibel, pers. comm.). Thus a 10 minute feeding period should avoid loss of ingested ^{14}C tracer in fecal pellets.

The experimental chamber was hauled to the surface by shore personnel at the end of the feeding period and placed in a plexiglass holder on the wharf. Feeding in the chamber was terminated by gently prodding the animal from its house with a 5 ml automatic pipette with an enlarged bore (approx. 0.8 cm). The animal and house were then collected separately with the pipette and placed into pre-weighed scintillation vials. A 4 ml water sample was taken from the grazing chamber to determine the radioactivity of the food suspension in the chamber. Hence, after each feeding trial, three sample vials were collected: the animal and associated fluid drawn up into the pipette with the animal; the house and accompanying fluid in the pipette; and the 4 ml food sample. Acid Lugol's iodine was used to preserve the samples because this preservative has been found to minimize loss of radioactivity from zooplankton fed ^{14}C labelled algae (Holtby and Knoechel 1981).

Animal Activity Observations

The possible effects of capture and enclosure of the animal in the grazing chamber were evaluated by monitoring animal activity prior to and during the feeding interval. Animal activity was determined by the number of sinusoidal beats of the tail per minute using the clocks affixed to the chambers. A nonparametric multiple comparisons test (n=34) indicated no significant differences ($p > 0.05$) in animal activity before and after enclosure within the chamber, and before and after addition of the algal suspension ($p > 0.05$). *In situ* observations indicated a high degree of variation in activity level between animals and for a single animal over time. Movement of the tail drives the water into the house through the filters, thus variation in activity would be expected to affect feeding rates. Hence, from March to July 1983, animal activity was qualitatively ranked as being; very slow(1), slow(2), medium(3), fast(4) and very fast(5) for future correlation with feeding rates.

Zooplankton Collection

Zooplankton were collected from oblique and horizontal hauls using a 30.0 x 30.5 cm, 125 μm mesh Nitex net, and preserved with ethanol for laboratory analysis. Collections were not performed on sampling days when appendicularians were extremely rare (i.e. $\leq 1/m^3$), a situation which also hampered experimental work. Temperature readings and water samples were taken at depths at which animals were collected. The water samples were preserved with Lugol's iodine for subsequent determination of ambient phytoplankton biomass and of background radioactivity.

Laboratory Methods

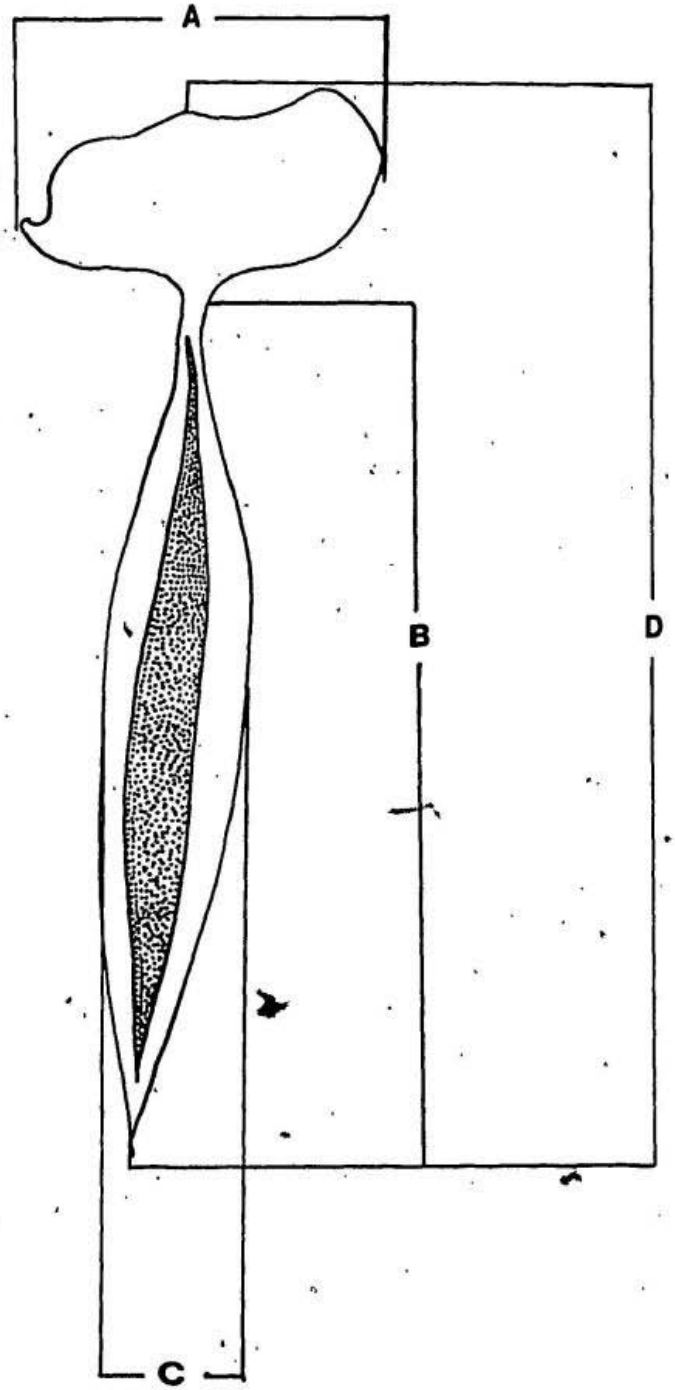
Sample Processing

In the laboratory, each capped scintillation vial was weighed to the nearest tenth of a gram to obtain the fluid volume. These fluid volumes for both the animals and their houses were used to evaluate variability in the radioactive counts of the labelled food suspension, and used in subsequent feeding rate calculations (see page 38). Animals were removed from the vials and the vial containing the remaining fluid was weighed. Animal dimensions (Fig. 8) were

measured to the nearest 0.01 mm using a Bausch-Lomb projection microscope and Zeiss MOP-3 digitizer, then were placed on unipore polycarbonate membranes (Bio-Rad laboratories) and weighed (wet) to the nearest 0.1μg using a Cahn-21 electro-balance. Animals and membrane filters were then placed in loosely capped vials, dried for a minimum of 24 hours at 60°C and re-weighed. Prior to determination of radioactivity, animals were moistened with 1 ml of distilled water and 1 ml of Protosol (New England Nuclear) and left to dissolve overnight because tissue digestion increases the counting efficiency of the low energy ^{14}C particles. Sodium thiosulphate (20%) was added (0.02 mls/vial of fluid) to decolorize the liquid samples because the colouring effect of the Lugol's preservative decreased the detection efficiency of the spectrometer (Wang et al. 1975).

Ten mls of Aquassure liquid scintillation solution (New England Nuclear) were added as fluor to all vials except the one containing the digested animal, to which 10 mls of PCS (Phase Combining System, Amersham) and 5 mls of OCS (Organic Counting Scintillation Solution, Amersham) were added. To minimize sample chemoluminescence, all samples were kept in the dark for at least 24 hours prior to determination of radioactivity in a Beckman LS-3150T Liquid Scintillation Spectrometer adjusted to count ^{14}C. Counts per minute (cpm) were determined for ten minutes or 1% precision, and corrections for counting efficiency and quenching were made using the external standards ratio method calibrated by internal standardization with ^{14}C labeled toluene (Wang et al. 1975). Counting efficiency was highest during trials three to five of repetitive sample counts, hence an average cpm value from these trials was used in

Figure 8: Body measurements of appendicularian specimens.
(lengths in mm as: A= trunk, B= tail, C= tail width,
D= total length).


A
B
C
D

subsequent clearance rate calculations.

Phytoplankton Biomass Measurement

Water samples collected at the sample sites were analyzed to determine the available biomass and size spectrum of ambient phytoplankton. Replicate 10 ml water samples were settled onto slides using 5.08 cm tall settling columns (Knoechel and Kalff 1976). Cells greater than 2 μm diameter were counted at 480 X magnification over a 1 cm by 150 μm wide transect using a Leitz Diavert phase contrast microscope. Cell sizes were determined using an eyepiece micrometer. After the initial transect was counted, one-fifth of this area was scanned for cells less than 2 μm in diameter. Three additional transects were also scanned for larger, rare cells (e.g. diatoms), followed by a full slide count of the largest colonies and dinoflagellates. Phytoplankton volume was calculated from formulae for simple geometric solids, converted to wet weight biomass using a specific gravity of 1.0, and then summarized in categories corresponding to cells with maximum dimensions of < 2 μm, 2-5 μm, 5-10 μm, 10-30 μm, greater than 30 μm and cylinders greater than 30 μm.

Zooplankton Samples

Zooplankton were enumerated under a dissecting microscope into the major

groups present during the study: copepods, nauplii, fish larvae, gastropods, amphipods, pteropods, euphausiids, decapod larvae, siphonophores, medusae and oikopleurids (*Fritillaria* sp., and *Oikopleura* spp.). Densities were calculated assuming 100% net collection efficiency and no predation after capture. Cumulative feeding rates were calculated using size-dependent regression equations (see Results) and the size-abundance distribution of *Oikopleura* spp. populations per sampling day. The number of appendicularians per cubic meter in each size class was multiplied by the mean feeding rate of that size class and then summed to obtain the total population feeding volume. Population feeding rates were expressed as a percentage of unit water column swept clear on a daily basis. For example, a population feeding rate of 100% would indicate that the appendicularian population in one cubic meter of water was clearing the food particles from one cubic meter of water each day.

Rate Calculations

Clearance rates were calculated using background-corrected disintegrations per minute (DPM) for the animal, house and food suspension. Count per minute (cpm) data from the spectrometer were converted to disintegrations per minute (dpm) as follows:

$$DPM = \frac{CPM - B}{E} \qquad \text{Eq. 1}$$

where CPM is the measured radioactivity of the sample in counts per minute, B is

the background CPM and E is the standard counting efficiency of the sample and fluor solution determined by internal standardization (refer to "Sample Processing" above).

Net food dpm/ml (Eq. 2, 3 and 4) was determined as the mean value for the 4 ml food water and the water collected with the animal (after removal of the animal) in order to reduce sampling error. The ratio of food dpm/ml to animal fluid dpm/ml should be 1.0 if the added food suspension was homogeneously distributed within the experimental chamber. Examination of this ratio revealed large deviations from 1.0 in several instances (range 0.6 to 2.0). Very high and low values for this ratio were presumed due to heterogeneous distribution of food in the feeding chamber; only those feeding trials with ratios in the range from 0.9 to 1.1 were included in the final data analysis, thereby reducing variance due to sampling error.

Animal clearance rates (ACR) were calculated as:

$$\text{ACR (ml/d)} = \frac{\text{animal dpm}}{\text{net food dpm/ml}} \times \frac{\text{1440 min/day}}{\text{incubation time (min)}} \quad \text{Eq. 2}$$

Net house dpm was calculated as:

$$\text{Net house dpm} = (\text{house + fluid dpm}) - (\text{mls fluid x food dpm/ml}) \quad \text{Eq. 3}$$

Net house dpm thus represents the residual activity dpms due to particle collection on or in the animal houses after correcting for the activity of the food in the water that was unavoidably collected along with the house.

Total clearance rates (TCR) were calculated as:

$$\text{TCR (ml/d)} = \frac{\text{animal dpm + net house dpm}}{\text{net food dpm/ml}} \times \frac{\text{1440 min/day}}{\text{incubation time (min)}} \quad \text{Eq. 4}$$

Inherent in the assumption of extrapolating the calculated feeding rates to a daily value is that there is no diurnal variation, a factor which has not been examined in previous studies.

In the analysis of feeding rates as a function of tail length, some observations had unusually high or negative dpm values on the houses, and were not included in the final data analysis for the following reasons: negative net house dpms reflected probable heterogeneous distribution of the food suspension in the chamber because the fluid correction value in Equation 3 was greater than the total observed radioactivity; very high dpms on houses might have resulted when the animal was near the three-way valve during injection of the algal suspension resulting in immediate coverage of the house with labelled algae.

RESULTS

Plankton Populations

Oikopleurids were often noted to appear and disappear quickly following a sudden and sustained change in wind direction which caused variable water temperatures (Buggeln 1980) and alteration of water masses within Logy Bay. *Oikopleura* spp. were observed by divers in late November 1982, but not from December 1982 thru February 1983. Populations were present in March but were absent for the month of April, reappearing again from May to late July 1983. In January 1984, red-tailed oikopleurids were present at $< 1/m^3$, but ice conditions precluded regular sampling procedures. Populations reappeared in April then disappeared from late May to late June, with sporadic occurrences in July.

The density of appendicularian populations at the sample sites was variable on a seasonal and even daily basis (Table 1). For example, in Logy Bay gut on May 13, 1984, density was 2 animals/m^3, which increased dramatically to 53/m^3 on May 15 (Table 1) accompanied by a temperature change from -1.5 to 1.0°C. Mahoney (1981) observed that appendicularian densities went from 5-30 /m^3 to >30 m^3 and then back down to 0.1-5 /m^3 in Logy Bay during a three day period in May 1980, accompanied by a temperature change from 3.0 to 3.5°C.

Oikopleurid densities ranged from 0 to 93/m^3 in the present study. In July 1983, animal density calculated from net hauls ranged from 25-93/m^3, while in

Table 1 Density of net zooplankton (number/m^3) at Logy Bay sampling site.

	1983			1984									
	JULY			MAY				JUNE			JULY		
TAXON	07	08	13	13	15	18	20	25	31	27	05	18	24
COPEPODS	153	176	760	107	342	530	454	590	1420	22	6	250	70
NAUPLII	3	7	45	0	0	0	0	0	0	0	0	0	0
FISH LARVAE	0	1	0	0	1	1	2	0	0	0	0	3	0
GASTROPODS	18	0	19	20	11	42	4	9	23	1	0	0	1
AMPHIPODS	37	8	1	1	3	3	0	1	1	0	0	1	0
PTEROPODS	1	0	2	1	15	2	6	5	0	0	0	0	0
EUPHAUSIIDS	0	0	14	2	1	1	2	1	0	0	0	11	1
DECAPOD LARVAE	0	0	0	2	1	2	0	0	0	0	0	0	0
SIPHONOPHORES AND MEDUSAE	0	0	0	0	16	9	2	11	9	1	0	0	2
OIKOPLEURIDS:													
FRITILLARIA spp.	0	0	0	0	24	7	13	18	19	11	0	0	0
OIKOPLEURA spp.	93	25	25	2	53	5	18	38	15	9	2	0	5

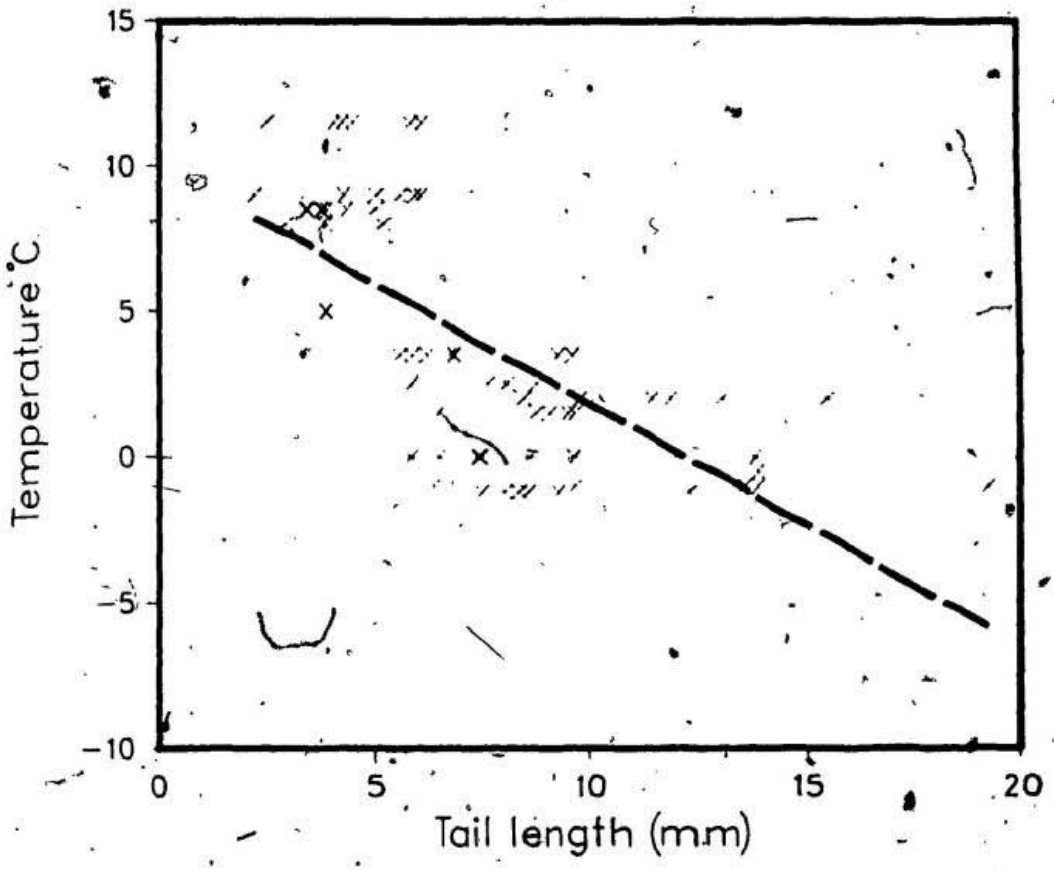
July 1984 the range was much lower, from 0-5/m^3 (Table 1). Mahoney (1981) also found sporadic fluctuations in oikopleurid abundances Logy Bay; in May 1980, animals ranged from 5 to > 30/m^3, while in late July densities dropped to 0-5 /m^3. Davis (1982) noted oikopleurid density varied from 9.8 to 448/m^3 from early July to mid-August in Conception Bay, Newfoundland, and Mahoney (1981) recorded densities of > 2000/m^3 for the same area.

Vertical plankton hauls were made in two coastal bays in July 1983 to determine if oikopleurids were present in deeper waters when they were absent from warmer surface waters during summer months. Vertical hauls were made from 10 to 70 m in 10 m depth increments. Oikopleurids were absent from 0 to 40 m at water temperatures ranging from 12.5°C (surface) down to 2.5°C. Tows to 50, 60 and 70 m (temperatures of 1.5°C, 0.0°C and -0.5°C respectively) produced appendicularian populations of increasing density, with the greatest abundance at 70 m. Essenberg (1922) noted that increases in appendicularian numbers during summer months were related to the upwelling of cold waters. Vertical haul results tend to support her suggestion that populations dwell in deeper, colder waters during the summer months when surface temperatures increase.

In the current study, animal size (tail length) was strongly correlated with temperature ($r = -0.738$), reflecting a restricted size range at any given temperature (Fig. 9). Below 2.0°C, appendicularians were large (maximum 19.0 mm tail length) with red tail colouration as opposed to smaller colourless forms (maximum 8.0 mm tail length) at warmer temperatures (8.0 to 11.5°C). The distribution of the temperature data was discontinous, with only one observation

Figure 9: The relationship between animal tail length (mm) and temperature (°C), ($r = -0.738$).

Figure 9



between 4.0 and 8.0°C. The relationship between tail length and temperature may reflect a species shift; *Oikopleura vanhoeffeni* has been described as having a red tail colouration and occurring at temperatures ranging from -1.7 to 11.7°C while *O. labradoriensis* has been found at temperatures from -1.3 to 20.1°C and has not been described as having a coloured tail (Forneris 1957). There is disagreement among workers regarding the significance of tail colouration as a taxonomic characteristic (Mahoney 1981); however, the pattern of luminescent inclusions and arrangement of subchordal cells suggest that the red-tailed specimens are *O. vanhoeffeni* (Deibel pers.comm).

Phytoplankton populations in Logy Bay were similarily variable with typically a two-fold or greater variation in total phytoplankton concentration on subsequent sampling days (Table 2). For example, total concentration approximately doubled from 106 mg wet weight/m^3 on July 13, 1983 to 202 mg wet weight/m^3 on the 14th of July. Temperature was not significantly correlated with phytoplankton biomass ($p > 0.05$) over the entire sampling period.

Analysis of Feeding Rates

Relationships between feeding rates, parameters of the organism, and environmental variables were examined using multiple regression analysis (Statistical Package for the Social Sciences, Nie 1983) on the VAX 1170 system at Memorial University. The relationship between individual feeding rates and body lengths is a power function which was linearized by log transformation of the data

Table 2 : Daily summary of temperature, phytoplankton concentrations by size class (μm), mean daily clearance rates (ml/hr) and mean tail lengths (mm). (cyl= cylinder; ACR= animal clearance rate; TCR= total clearance rate; cyl= cylinder; TL= tail length)

PHYTOPLANKTON CONCENTRATIONS (mg/m^3)

DATE	< 2	2-5	5-10	>30	cyl>30	total	°C	ACR	TCR	TL
1983										
22-03	3.9	60.9	27.6	0.0	0.0	92.4	- 1.2	8.2	71.4	8.3
25-03	7.3	382.2	255.1	0.0	0.0	624.6	0.0	13.0	32.5	7.3
31-03	3.2	7.8	28.9	0.0	0.0	108.6	-1.2	1.8	75.9	10.4
16-05	4.5	73.1	28.9	0.8	0.0	107.4	3.5	15.7	32.2	5.9
18-05	5.4	8.6	19.3	14.1	78.2	203.2	1.5	4.6	12.3	8.7
19-05	5.0	52.5	15.6	12.0	50.2	135.3	3.5	35.6	90.1	11.6
21-05	4.6	52.7	11.9	3.9	9.5	82.6	2.5	17.0	26.3	7.6
07-06	4.1	65.3	25.2	0.0	4.3	137.7	3.5	1.1	15.5	7.4
07-07	4.4	56.9	21.5	0.8	4.9	88.6	8.0	9.2	22.8	3.9
08-07	5.4	68.1	25.2	0.0	1140.0	1238.8	8.5	3.3	16.0	3.9
13-07	2.0	72.1	25.2	1.8	5.2	106.3	9.0	8.2	11.1	4.6
14-07	8.3	133.9	60.1	0.0	0.0	202.3	9.0	3.0	8.1	5.3
20-07	5.0	96.3	41.5	1.1	3.8	147.7	11.0	no Oikopleura spp		
30-07	4.4	26.8	23.0	0.0	0.0	54.3	8.0	"	"	"
05-08	15.0	27.7	22.3	15.7	0.0	80.6	12.0	"	"	"
09-08	10.0	51.2	17.1	0.0	0.0	78.3	11.0	"	"	"
17-08	5.9	55.5	11.1	0.0	0.0	72.5	9.0	"	"	"
07-09	4.2	38.4	12.8	0.0	0.0	55.3	10.0	"	"	"
14-10	10.5	49.6	19.3	0.0	0.0	84.8	5.0	"	"	"
1984										
08-04	7.1	49.2	43.0	0.0	50.1	149.4	-0.5	<1/m^3		
25-04	8.9	56.0	35.6	1.1	189.4	289.1	0.5	<1/m^3		
01-05	8.6	50.1	32.6	3.9	39.5	134.7	-1.0	<1/m^3		
09-05	10.3	43.0	14.1	3.4	119.1	189.9	-1.0	4.3	67.9	12.3
13-05	10.6	50.9	37.1	11.9	103.0	213.6	-1.5	4.2	14.0	13.9
15-05	12.7	49.5	53.4	3.9	268.9	388.4	-1.0	2.0	54.8	19.2
18-05	15.7	48.9	35.5	0.9	247.9	349.0	0.0	6.6	13.3	9.9
25-05	7.5	11.9	11.9	6.7	21.6	283.3	0.5	<1/m^3		
31-05	20.3	57.9	16.3	0.0	0.0	94.5	3.0	no Oikopleura spp		
10-06	9.1	27.7	11.9	0.0	0.0	48.7	2.0	"	"	"
15-06	3.5	24.9	26.7	0.0	0.0	55.1	3.5	"	"	"
27-06	7.8	33.7	14.8	0.0	29.7	86.0	5.5	"	"	"
05-07	8.2	34.5	16.3	0.0	0.0	59.0	5.0	2.4	10.1	3.8
18-07	10.8	47.4	17.1	0.0	0.0	75.3	10.0	no Oikopleura spp		
24-07	9.8	53.4	14.8	2.8	0.0	80.8	11.5	4.1	8.5	4.5

for entry into the multiple regression models (Knoechel and Holtby 1985). Residual and scatter plots for both animal clearance and total clearance rate models were examined to determine underlying trends in the data and relationship strengths (Hartwig and Dearing 1979).

Animal Clearance Rates

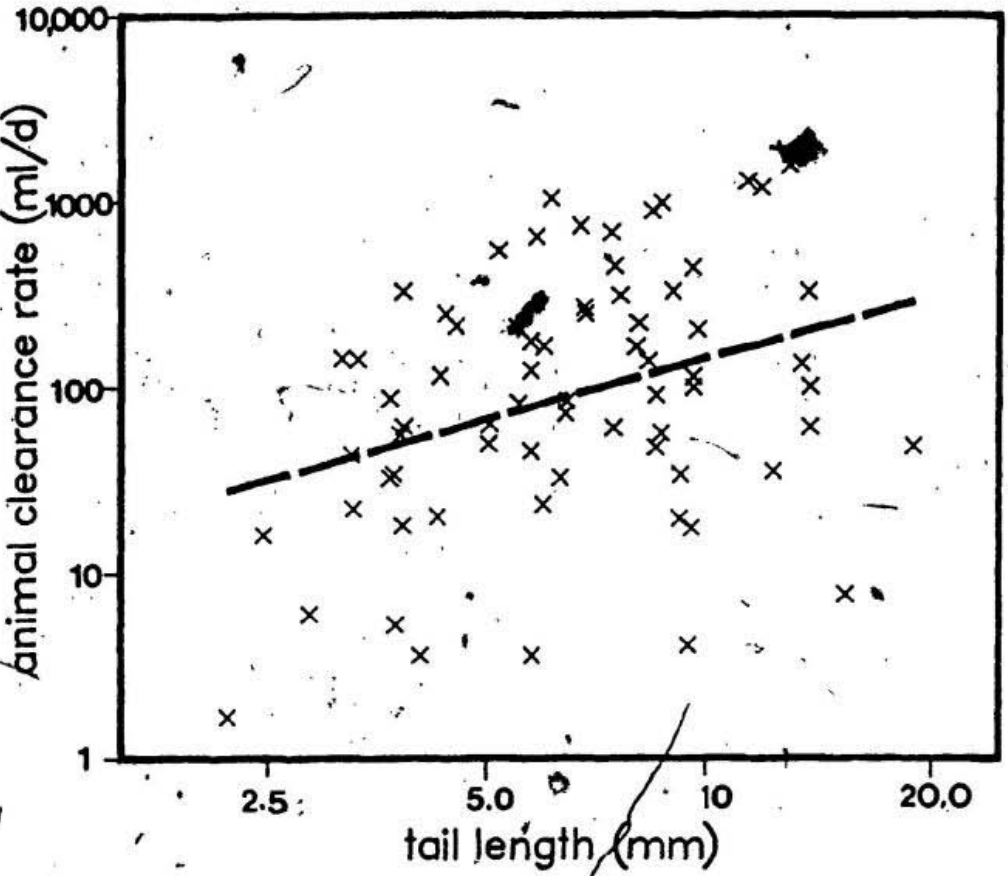
Individual *in situ* animal clearance rates ranged from a minimum of 2 ml/animal/d to a maximum of 1560 ml/animal/d for animals ranging from 2 to 13 mm in tail length over a three-four fold variation in ambient food concentration (Table 2). The relationship between log animal clearance rate and log tail length was highly significant ($p < 0.005$) but explained only 11.3% of the overall variance (Fig.10). Inclusion of temperature and phytoplankton biomass concentrations (mg wet weight/m^3) in the multiple regression model did not significantly increase explained variance and examination of regression residuals versus temperature and phytoplankton concentrations revealed no obvious non-linear patterns. The regression equation for animal clearance rate presented as a power function was:

$$ACR = 11.736\ L^{1.086} \qquad \text{Eq. 5}$$

where ACR is the individual animal clearance rate (ml/d) and L is the tail length in mm. The exponent is the slope of the log:log regression (Fig.10) and the

Figure 10: The relationship between animal clearance rate (ml/animal/d) and tail length (mm) for Oikopleura spp.; Log Y = 1.068 + 1.086 log X; r^2 = 0.113).

Figure 10


10,000
1000
100
10
1
animal clearance rate (ml/d)
2.5
5.0
10
20.0
tail length (mm)

coefficient is the antilog of the Y-intercept and is the predicted animal clearance rate of a 1 mm individual (because log 1=0). The observed coefficient of 11.736 is nearly identical to that of 11.7 noted for cladocerans feeding on similar-sized food particles in fresh water (Knoechel and Holtby 1986).

Total Clearance Rates

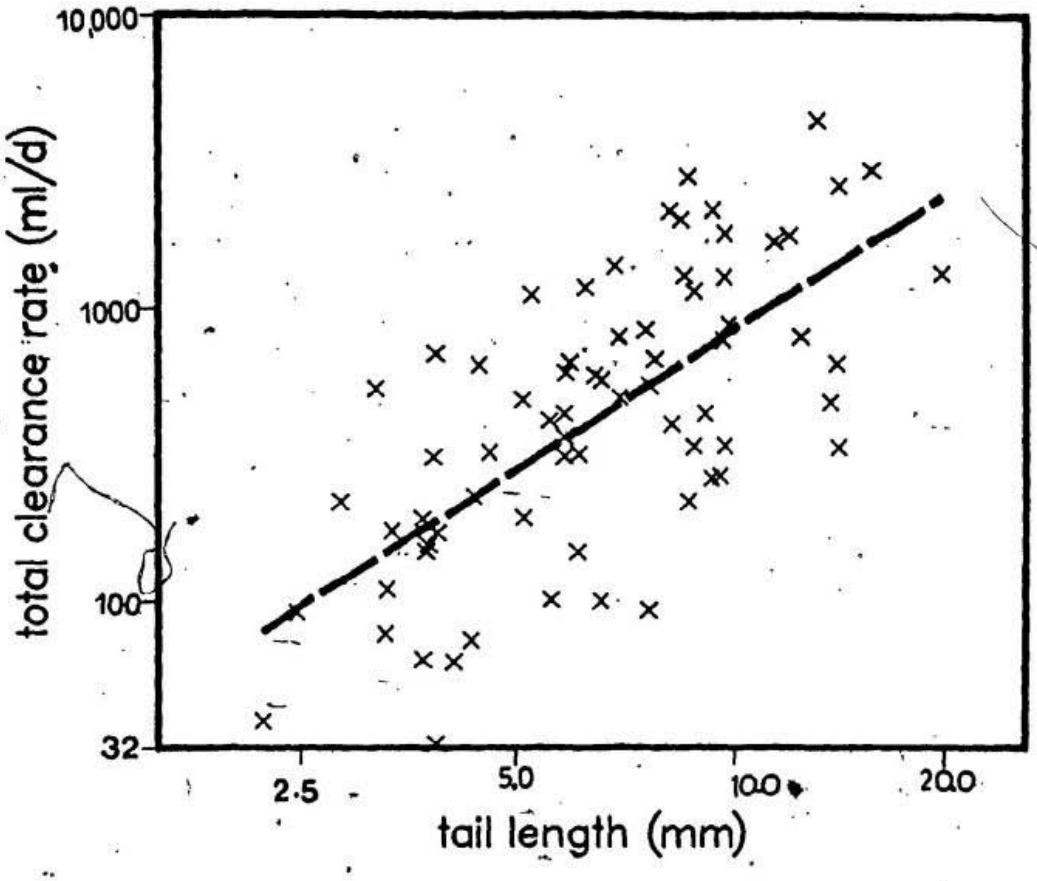
Observed *in situ* total clearance rates ranged from a minimum of 38 ml/animal/d to a maximum of 4382 ml/animal/d over the same range of animal sizes and ambient food conditions and were strongly correlated with tail length (r^2= 0.460, Fig.11). Total clearance rate was negatively correlated with temperature (r= -0.592, $p < 0.005$);however, multiple regression suggested that this trend resulted from the previously noted inverse correlation between temperature and animal length because temperature was not a significant factor in the multiple regression once tail length had entered the model. The power equation was:

$$TCR = 22.608\ L^{1.578} \qquad \text{Eq. 6}$$

with TCR in ml/d and L representing tail length in mm. The biomass of the < 2 μm phytoplankton category also entered in the regression model as a significant variable ($p < 0.002$) and resulted in a final explained variance of 54%.

Figure 11: The relationship between total clearance rate (ml/animal/d) and tail length (mm) for Oikopleura spp.; Log Y = 1.354 + 1.58 log X (r^2 = 0.460).

Figure 11


10,000
1000
100
32
total clearance rate (ml/d)
2.5
5.0
10.0
20.0
tail length (mm)

The power equation was:

$$TCR = 32.880\ L^{1.719} * 10^{-0.044(\text{phytoplankton } 0\text{-}2\ \mu m)} \quad \text{Eq. 7}$$

Visual inspection of residual plots of log total clearance rate and log tail length versus all other phytoplankton categories and temperature revealed no obvious non-linear patterns in the data.

Animal Activity and Feeding Rates

Animal activity, in terms of the number of tail beats per minute, was observed to vary greatly between animals both within and between sampling days. Tail beat frequency was highest at warmer temperatures (i.e. $> 9.0^{\circ}C$), but was very inconsistent over time. Counts were made on a few animals of the actual number of tail beats each minute for the entire feeding period within the chamber. The results showed that animal activity was highly unpredictable from one minute to the next; even animals outside of the chambers were observed to cease movement for as long as 3 minutes, often followed by tail beat activity too rapid to count accurately. However, contrary to Alldredge (1976), the amplitude of the sinusoidal waves varied also; animals would abruptly halt tail activity and then sometimes slowly restart with shallow wave pulses, which gradually increased in height until a relatively constant pattern was established.

Qualitative activity rankings (refer to Methods) were determined at

temperatures between -1.2 and 9.0°C and over a range of total phytoplankton biomass concentrations from 82.6 to 1238.8 mg/m^3. Animal tail lengths ranged from 2.21 mm to an unusually large animal of 15.40 mm, with the majority being less than 9.0 mm. Activity ranking explained 60% of the variation in animal clearance rate (Fig.12) when added as an interval variable to the stepwise multiple regression model (Kim and Kohout 1975). The significant inclusion of log tail length in the multiple regression model resulted in a final explained variance of 76.4% (n=25, $p < 0.02$). Recent laboratory and *in situ O. vanhoeffeni* feeding studies using latex beads have also revealed erratic and unpredictable tail undulations subsequently reflected in variable feeding rates (Deibel, pers. comm). Phytoplankton biomass categories and temperature did not contribute significantly to explaining further variation in animal clearance rate and residual plots revealed no additional trends in the data.

The animal clearance rate model incorporating activity and tail length was:

$$ACR = 0.240\ L^{1.342} * 10^{(0.451A)} \qquad \text{Eq. 8}$$

where ACR represents animal clearance rate (ml/d), L represents tail length in mm, and A, the qualitative activity ranking on a scale from 1 to 5.

A similar analysis of total clearance rates for the activity data set revealed that log tail length explained 63% of the variation (Fig.13), and the statistically significant inclusion of activity ranking to the regression model resulted in a final explained variance of 72% ($p < 0.02$). Activity ranking thus did not explain as large a proportion of variance in total clearance rate as it did for animal clearance

Figure 12: The relationship between relative activity level (1-5) and animal clearance rate (ml/animal/d) for Oikopleura spp.; (n = 25, r^2 = 0.600).

Figure 12

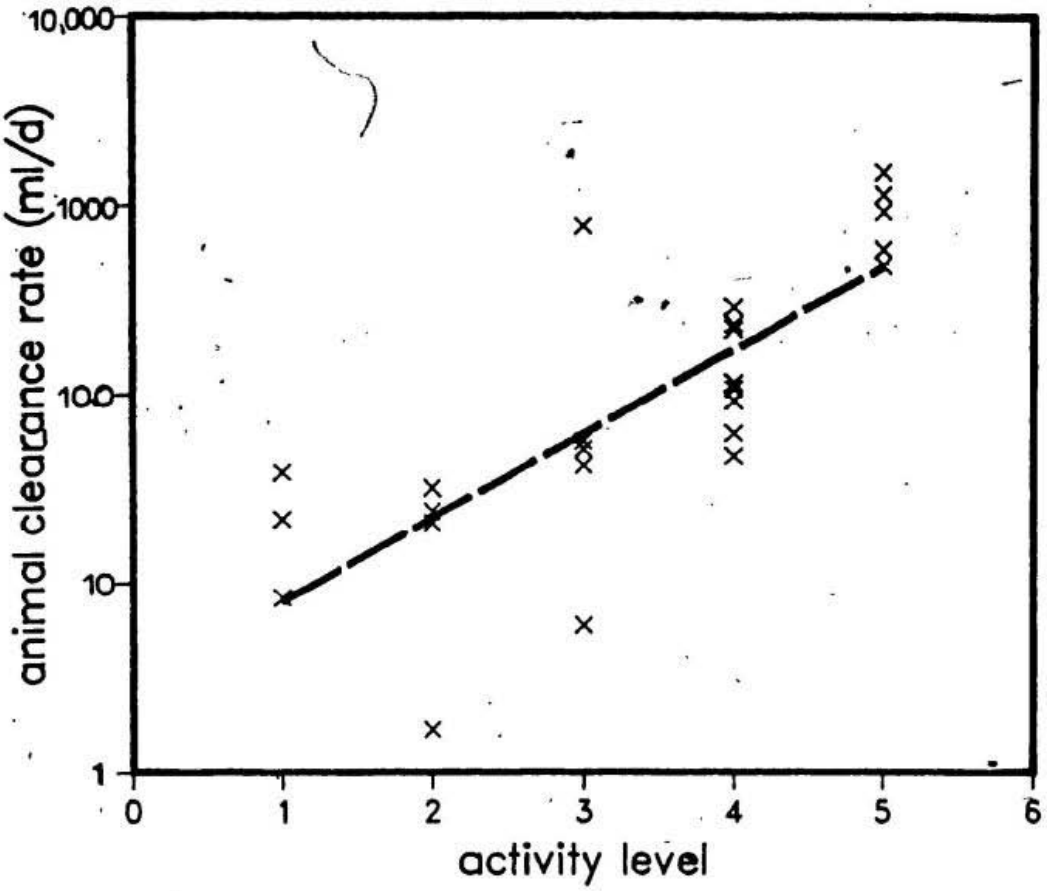
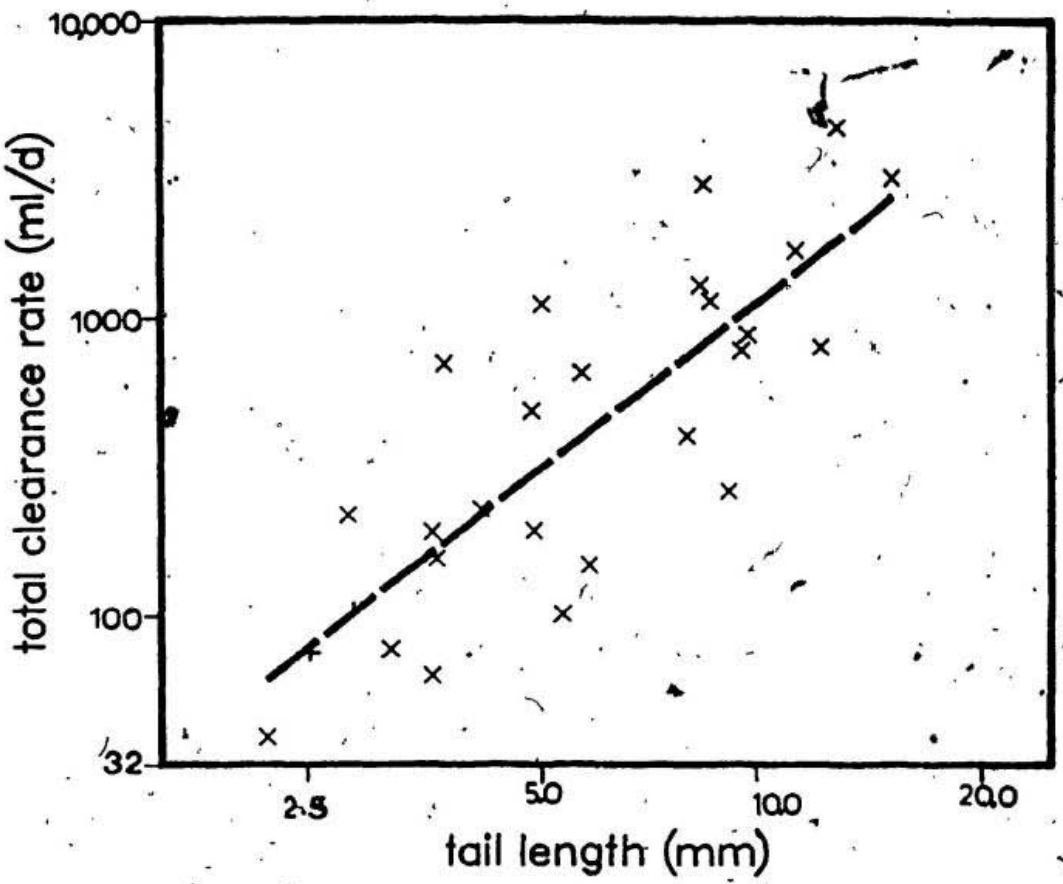

10,000
1000
100
10
1
animal clearance rate (ml/d)
0
1
2
3
4
5
6
activity level

Figure 13: The relationship between total clearance rate (ml/animal/d) and tail length (mm) for the activity data subset ; ($n = 25$, $r^2 = 0.630$).

Figure 13


10,000
1000
100
32
total clearance rate (ml/d)
2.5
5.0
10.0
20.0
tail length (mm)

rate. A stronger correlation with animal clearance rate than with total clearance rate might be expected because activity of the tail drives the water through the feeding filters, whereas the external surface of the house can clear particles passively regardless of tail movement. Addition of temperature and phytoplankton biomass categories did not significantly increase the amount of explained variation and residual plots showed no further trends in the data. The total clearance rate model incorporating tail length and activity was:

$$TCR = 4.772L^{1.956} * 10^{(0.126A)} \qquad \text{Eq. 9}$$

where TCR represents total clearance rate (ml/d).

An attempt was made to quantify activity level more precisely by counting the actual tailbeats/minute for two consecutive minutes following addition of the labelled food to the feeding chamber. Average tail beats per minute were, unexpectedly, not significantly correlated with either animal or total clearance rates ($r = -0.022$ and $r = 0.010$ respectively, $n = 34$). Nevertheless, the actual tail beat counts did support the qualitative observation that tail beat activity varied considerably from one minute to the next. The lack of correlation suggests that the two minute observation period was not indicative of average tail activity over the full 10 minute feeding period. On one sampling day (May 18, 1984), tailbeats per minute were recorded for 5 animals over the entire 10 minute feeding period. Comparison of the average tail beats per minute for the first two minutes with the average for the entire feeding period indicated errors of from 0.9 to 92.7% with a mean error of 33.2% (Table 3). The coefficients of variation for tail beats per minute of individual animals ranged from 9 to 112% (Table 3). This

Table 3: Tail lengths (TL), tail beat counts, mean count, coefficient of variation (c.v.), mean count of first two minutes and errors of the two minute mean expressed as a percentage of the ten minute mean

TL (mm)	MINUTE 1	2	3	4	5	6	7	8	9	10	MEAN	c.v.	2 MIN. MEAN	% ERROR
8.7	103	97	109	104	107	100	80	90	110	109	100.9	9.0	100.0	0.9
8.3	63	64	56	72	48	27	64	66	76	70	60.6	23.0	63.5	4.8
10.5	00	02	26	23	17	00	08	34	25	02	13.7	93.0	1.0	92.7
10.7	15	53	00	00	07	27	07	37	40	78	23.1	112.0	34.0	47.2
13.7	35	69	58	63	88	53	59	86	67	75	65.3	24.0	52.0	20.4

confirmed the suspicion that a two minute observational period was inadequate to characterize activity during the 10 minute feeding trial.

In both qualitative and quantitative analyses, activity was not significantly correlated with the environmental parameters measured in this study. Jorgensen (1984) and Madin and Cetta (1984) suggest that variation in animal behavior may be due to inherent, genetically determined capacities of water processing structures. Collection of quantitative tail beat data for various sized animals over longer time periods is required before their theory can be properly evaluated.

Population Feeding Rates

The impact of a population of suspension feeders on natural food densities must necessarily depend both upon the rates at which the individuals clear the water of suspended particles and on the size composition and abundance of the population (Jorgensen 1984). These latter parameters were combined to calculate population feeding rates expressed as a percentage of the water column swept clear on a daily basis (refer to Methods). Estimates were made for several dates to reflect the full range of animal densities and sizes encountered during the study (Table 4). A maximum of only 2.09% of the water column was estimated to be cleared of particles. The estimated impact due to animal clearance alone was lower, with a maximum value of 0.39%. Thus feeding impact was approximately three to five fold greater due to particle removal by both the animal and the house than by the animal alone.

Table 4: Size-abundance distribution of oikopleurids and estimated population clearance rates expressed as equivalent percentage of the water column cleared of particles per day.

DATE	TAIL SIZE CLASS (MM)	#/M^3	TOTAL CLEARANCE (%/DAY)	ANIMAL CLEARANCE (%/DAY)
07-07-83	1-2	12.68		
	2-3	50.73	0.76	0.34
	3-4	29.59		
13-05-84	6-7	2.00	0.09	0.02
15-05-84	1-2	6.00		
	2-3	7.26		
	3-4	5.56		
	4-5	6.84		
	5-6	5.98		
	6-7	5.13		
	7-8	2.14		
	8-9	2.14	2.09	0.39
	9-10	2.56		
	10-11	0.85		
	11-12	0.42		
	12-13	3.85		
	13-14	0.42		
	14-15	0.85		
18-05-84	1-2	3.00		
	2-3	0.43	0.049	0.014
	4-5	0.85		

DISCUSSION

Plankton populations

Logy Bay is an oceanographically dynamic area as indicated by the variable zooplankton and phytoplankton populations encountered during the two year study period (Tables 1, 2), suggesting an unstable and unpredictable species assemblage. The observed total phytoplankton biomass varied two to three fold over the sampling period. Oikopleurid densities were highly variable, with observed densities ranging from 0-93/m^3. Appendicularians were observed in Logy Bay as early as March and April in 1983, but did not appear until late April 1984 at densities below 1/m^3. These seasonal fluctuations may be due in part to variations in the strength and movement of the Labrador Current. The inshore presence of Labrador Current water is the result of upwelling of deep offshore water (Mahoney and Buggeln 1983) in conjunction with local wind, tide and current patterns (Essenberg 1926). Distributional patterns of *O. vanhoeffeni* suggested that the Labrador Current differed in strength from year to year as it flowed along the east coast of Newfoundland (Thompson and Frost 1936). Kendaris (1980) conducted a six month study of the physical and biological environment in Logy Bay and concluded that the water masses in the bay

consisted of a warmer surface layer (lower salinity) of combined coastal and Labrador Current water with a bottom layer of pure, cold Labrador Current water. The thickness of the surface layer is strongly influenced by wind speed and direction, especially in the summer when surface water temperature rises and the layer becomes less dense (Steele 1975). Strong offshore winds can move this warmer layer offshore with the result that it is replaced by the colder bottom layer of Labrador Current water. Onshore winds have the reverse effect of thickening the warmer mixed surface layer in coastal locations while the colder bottom layer is offshore.

Movement of these two water masses within Logy Bay coincides with the appearance and disappearance of oikopleurid taxa. Studies by Thompson and Frost (1936) and Udvardy (1954) revealed that the density and distribution of oikopleurid taxa and size class was reflective of the movement of the Labrador Current. Observations from this study suggest that the larger oikopleurids were restricted to colder water masses as water temperature was correlated with both the abundance and size distribution of *Oikopleura* spp. At temperatures below 0°C, the oikopleurid density was low and animals were generally large (tail lengths from 8 to 20 mm, Table 2) with red tail pigmentation characteristic of *O. vanhoeffeni*. At temperatures between 8.0 and 9.0°C oikopleurids reached higher densities although animals were considerably smaller (< 4 mm tail lengths, Table 2) and lacked the red pigmentation. Stratified vertical haul data from two coastal bays in late July indicated that the oikopleurids were present in deep, cold water when they were absent from the warm surface layer. At intermediate water temperatures small colourless individuals and large red-tailed specimens were

sometimes present on the same sampling day. The red pigmentation of the tail of *O. vanhoeffeni* appears only in the mature animal and thus the small colourless animals could have been juveniles of either species, *O. vanhoeffeni* or *O. labradoriensis* (Deibel pers. comm.).

In summary, wind and current patterns influence the distribution of two distinct water masses in Logy Bay and of their respective oikopleurid populations. Better characterization of these water masses and their correlation with the oikopleurid taxa would require more detailed salinity and temperature data than are currently available.

Feeding Rates of Oikopleura spp.

Appendicularians collect food both on the feeding filters and on the outside of the houses which may serve as a carbon rich food source for other zooplankters (Alldredge 1975, 1981). Most authors (e.g. Paffenhofer 1976, King 1981, Alldredge 1981) therefore determine total clearance rates when discussing the potential impact of appendicularian feeding rates on resident phytoplankton populations. Techniques for estimating feeding rates that focus on changes in particle concentration in the water (Paffenhofer 1976) are limited to measuring only total clearance, whereas techniques involving tracer particles (such as those employed by King 1981) can potentially separate the two processes by examination of material actually cleared by the animal as opposed to that collected by the house alone.

Animal Clearance Rates

Feeding rates of zooplankton in general have usually been related to size (length or weight), temperature and food concentration. The experiments by King (1981) were the first to measure actual ingestion rates in appendicularians, specifically *O. dioica*, and his experiments were restricted to a single temperature. The *in situ* measurements in the current study are the first detailed observations for cold ocean appendicularians. Animal clearance rates of from 1.7 to 1560 ml/animal/d were observed over a range of ambient food concentrations and temperatures. Log tail length explained 11.3% of the variation with neither temperature nor ambient food concentration entering the multiple regression equation as significant factors. This relationship was expressed (Eq.5) as:

$$ACR = 11.736\ L^{1.086}$$

with animal clearance rate in ml/animal/d and L representing tail length in mm. Temperature effects were difficult to evaluate in the current study because of the high correlation between temperature and body size. Despite the fact that temperatures ranged from -1.2 to 11.5°C, there was actually a much narrower range of temperatures associated with animals of any particular size. King's (1981) rate measurements were on much smaller animals than in the current study, and were conducted at a single temperature (14.0°C) in the laboratory. A

very high correlation ($r^2 = 0.94$) between body size and ingestion rate was observed:

$$I = 69.416\ T^{3.083} \qquad \text{Eq. 10}$$

with ingestion rate in ml/animal/d and T representing trunk length in mm (tail lengths are approximately two-three times trunk lengths). He similarily did not observe any significant influence of various phytoplankton concentrations.

Eq. 10 predicts that an animal with a tail length of 3.68 mm (equivalent trunk length of 0.93 mm) would ingest 55.5 ml/animal/d which is quite close to the value of 69.4 ml/animal/d predicted by Eq. 5 of my study. The largest oikopleurid in King's (1981) study was barely the minimum size encountered in the present study making it difficult to use his equation for comparative purposes with larger animals. However, extrapolating King's model would predict an animal cleaance rate of 800 ml/animal/d for a 9.0 mm animal (trunk length approx. 2.2 mm), as compared to a prediction of 127.5 in the current study (Eq. 5).

It is also notable that King's (1981) experiment showed ingestion rate to be a cubic function of length, whereas the exponent was only 1.086 in the current study. The slope of a least squares linear regression is dependent both on the underlying functional relationship and on the strength of the correlation (Ricker 1973). Ricker (1973) recommends that geometric mean regression (GMR) be used to show the functional relationship. Although few authors have employed GMR to compare relationships between feeding rates and body size, the slope of the

GMR can be readily calculated as the least squares regression slope divided by the correlation coefficient, thereby allowing one to remove the influence of the strength of the correlation (Ricker 1973). When this is done for the present study, the slope increases from 1.08 to 3.21 similar to that of King (Table 5).

Total Clearance Rates

Total clearance rates, which include the collection of particles on the exterior of the house as well as particles in the feeding filter that have not yet been ingested, were observed to be two to three times animal clearance rates in the present study. In comparison, King (1981) estimated that the total clearance rate of *O. dioica* for bacterioplankton suspended in filtered seawater was 1.2 times the ingestion rate. One would expect the ratio to be higher in my study because the large-sized oikopleurids had correspondingly larger houses and hence larger surface areas available for particle collection.

The observed total clearance rates at various temperatures ranged considerably from as low as 38 to 4382 ml/animal/d and were strongly correlated with tail length ($r^2 = 0.46$). The biomass of the < 2 μm phytoplankton category did enter as a significant variable and increased explained variance to 54% ($p < 0.002$). The coefficient was negative (Eq. 7) indicating that an increase in biomass of this phytoplankton size category had an inhibiting effect on total clearance rate, an effect which has not been noted by other researchers.

There were large differences in correlation strength noted between the

Table 6: Comparison of clearance rate:length regression slopes calculated by least squares regression (LSR) and by geometric mean regression (GMR) and comparison of correlation coefficients (r) between the present and other studies

SPECIES AND REFERENCE	TECHNIQUE	SLOPE				r	
		LSR		GMR			
		TCR	ACR	TCR	ACR	TCR	ACR
O. dioica (Paffenhofer 1976)	cell counts Coulter Counter	1.19	---	3.06	---	0.98	---
O. dioica (Alldredge 1981)	latex beads as in situ tracers	1.63	---	2.45	---	0.68	----
O. dioica (King 1981)	labelled bacteria as tracer	2.80	3.08	3.85	3.19	0.73	0.97
Oikopleura spp. (Steel)	labelled algae as in situ tracer	1.58	1.08	2.33	3.21	0.68	0.34

various clearance rate studies (Table 5). Correlation coefficients between body size and clearance rate range from a high of 0.98 to a low of 0.66 and it appears that much of this variation results from the length of time over which the experiments were conducted. Correlations were highest for measurements taken on a single day or over consecutive series of days. Alldredge's (1981) regression model for *O. dioica* combined four days of data with a fairly weak correlation of 0.66 relating clearance rate and body size. However, if her results are examined on a daily basis, correlations between body length and clearance rate tend to increase (range 0.53-0.99, Table 6). It can also be noted that her size range of animals was fairly restricted (0.5 to 1.2 mm trunk lengths) and that her maximum trunk length was approximately the minimum encountered in this study. Only Alldredge's (1981) data for *Stegasoma magnum* cover a size range of animals comparable to that encountered in my study. She measured *in situ* total clearance rates of from 15 to 1700 ml/animal/d for *S. magnum* with trunk lengths of 2-4 mm (equivalent tail lengths in the current study of from 8 - 12 mm). Her reported correlations were very strong (0.84, 0.93, 0.93) but decreased dramatically to 0.27 when I combined the data for the three day period (Table 6). Conversely, selecting data from the current study for two dates with similar environmental conditions (May 19 and 21, 1983) produced a much higher correlation between clearance rate and tail length (r= 0.90) than for the entire study period (r= 0.68, n=22, Table 6). Obviously, caution must be exhibited when examining clearance rates on a daily basis, and then extrapolating these measurements over longer time periods. Correlation strengths do weaken as experiments are conducted over longer periods suggesting that variations in the

environment may affect behavioral patterns over time.

Animal Activity and Feeding Rates

Logically, animal clearance rates must be correlated with tail beat rate because it is the movement of the tail which draws the flow of food-containing water into the house and through the feeding filters. Activity levels do vary between animals (Alldredge 1981, King 1981) but this has not previously been examined as a potential source of variation in feeding rates. In the current study, animal activity varied considerably among animals both within and between sampling days. The inclusion of the qualitative activity rankings (see Methods) in a regression model explained 60% of the variation in animal clearance rate and with the addition of tail length, (the only other significant variable) the final explained variance was 76.4% ($p < 0.002$, $n=25$). A similar analysis of total clearance rates revealed that log tail length explained 63% of the variation and the significant addition of activity ranking resulted in a final explained variance of 72%. The qualitative activity data suggest that the frequency of tail movement has a greater effect on animal clearance rate than on total clearance rate. Laboratory observations of *O. vanhoffeni* feeding on *Isochrysis* revealed that this oikopleurid may even temporarily detach the buccal tube from the mouth during cessation of tail activity, thus halting ingestion altogether (Deibel, pers. comm.). This observation suggests an explanation for the highly variable tail beat counts noted for the animals observed for the full 10 minute feeding period (Table 3)

Table 6: Comparison of strength of correlations of total clearance rate (ml/animal/d) and body length (mm) over different time periods of various authors

SOURCE	SPECIES	DAYS	N	r
Alldredge (1981)	O. dioica	1 (July 9)	9	0.53
		1 (July 12)	8	0.99
		1 (July 14)	4	0.82
		1 (July 20)	7	0.67
		4(above days combined)	28	0.66
Alldredge (1981)	S. magnum	1 (July 22)	8	0.84
		1 (July 23)	7	0.93
		1 (July 26)	7	0.93
		3(above days combined)	22	0,27
King (1981)	O. dioica	?	> 100	0.73
Steel (this study)	Oikopleura spp.	2(May 19,21 1983)	10	0.90
		22(entire study)	70	0.68

wherein the two most variable animals sporadically ceased tail activity altogether for periods exceeding one minute.

Other authors have also noted irregularities in tail beat behavior of *O. dioica*. Bone and Mackie (1975) attached electrodes to the tails of tethered *O. dioica* (still in their houses) and noted that the swimming behavior consisted of short bursts of tail movement alternating with periods of inactivity. Both the amplitude and frequency of the tail movements were variable as were the lengths of the bursts of activity and the interburst periods (Bone and Mackie 1975). Alldredge (1976) noted intermittent suspension of tail beat of warm water appendicularians feeding on natural particles in seawater, with intervals of inactivity ranging from one to 60 seconds and with no apparent patterns in the timing of tail beat suspension. Animals were noted to be active from 0-100% of the observational period although no actual times were given. However, these irregularities in animal behavior were apparently not observed in Alldredge's (1981) subsequent warm water *in situ* feeding studies. The possible effects of the concentration of available food particles on feeding rates still has yet to be properly investigated, especially in the cold ocean environment. The density of particles in seawater may alter the collection abilities of the filters of appendicularian houses. Rubenstein and Koehl (1977) suggested that a buildup of particles on the filters results in structural changes to the filters which alters their collection abilities as well as their resistance to flow. Perhaps oikopleurids can 'sense' particle buildup on their filters and attempt to adapt to changes in flow rate by altering tail beat activity. To examine the effects of particle density on feeding rates, one could conduct feeding experiments on animals in newly inflated,

particle-free houses, and then compare the rates and activity levels to those of animals in houses which were of various ages with differing levels of particle buildup. In my study, the condition of the houses likely varied among experimental animals.

Potential Impact of Appendicularian Feeding

In the current study, the impact of oikopleurid feeding on plankton populations ranged up to 2.09% of the water column cleared per day at a density of 53 animals/m^3. These results suggest that the feeding rate impact in coastal Newfoundland waters would be minimal unless resident food population growth rates were extremely low. Greater maximum densities of oikopleurids have been observed in Newfoundland coastal waters, however, ranging from 448/m^3 (Davis 1982, Mahoney and Buggeln 1983) to greater than 2000/m^3 (Mahoney 1981). Predictions of total clearance rates for these higher densities (using Eq.6), using tail lengths typical of the period in question range from 3 to 64% cleared per day, values comparable to those estimated in warmer ocean regions (e.g. Alldredge 1984).

Gelatinous zooplankton have been estimated to consume typically less than 10% of their food populations per day (reviewed in Alldredge 1984), in agreement with the impact estimates obtained in this study. However, the effect of this clearance rate on phytoplankton biomass is difficult to predict unless the phytoplankton growth rate is also known. Investigators have examined the effects of appendicularian feeding on the population dynamics of their food stocks using

mathematical models in combination with growth rate calculations based on both lab and field data (Alldredge 1984). King et al. (1980) used laboratory experiments to predict daily clearance rates by populations of *O. dioica* feeding on bacterioplankton in a Controlled Ecosystem Populations Experiment (CEPEX) in Saanich Inlet, B.C. Clearance rates ranged from 5 to 100% at oikopleurid densities of 100-1000/m^3. They concluded that appendicularians and other zooplankton combined could only consume all bacterioplankton production when bacteria were growing their slowest (1 doubling per day) and zooplankton grazing was highest (60 to 70% of the water column per day). However, they suggested that dense patches of appendicularians, combined with other grazer populations could lead to temporary depletion of food particles.

Studies in the Gulf of California by Alldredge (1981) were the first attempts to measure feeding rates, population sizes and ambient food concentrations *in situ*. Her experiments produced daily total clearance rates of 1.3-3.7% for *O. dioica* at densities of between 205 and 4587/m^3 and *S. magnum* populations of 11 to 63 animals/m^3 cleared from 5.4 to 13.4% per day (Alldredge 1981). *In situ* measurements of the rate of increase of particulate organic carbon (POC) in the absence of grazers suggested that only at their maximum population densities could the appendicularians halt the growth of their food supply. However, Alldredge (1981) cautioned about the difficulty of estimating feeding impacts which are dynamic and time dependent from population and food biomass measurements, which are static. Currents, upwelling, seasonal changes in nutrients and other environmental variables might all result in unpredictable fluctuations and patchiness in both the abundance of the food source and of the

consumers.

Feeding by appendicularians may affect not only their food organisms, but also the biology of other resident zooplankton. Many species of gelatinous zooplankton have high intrinsic rates of population increase, allowing them to reach high population densities rapidly when food resources increase (Alldredge 1984). Under favorable environmental conditions, appendicularians have reduced generation times, allowing these zooplankters to outgrow other planktonic consumers at high food densities (Alldredge 1984).

Directions For Future Research

Detailed studies of plankton food biomass and growth rates are needed for comparison with appendicularian feeding rates to assess more accurately the feeding impact of these abundant gelatinous zooplankton in the cold ocean environment. Detailed studies should also examine the morphology of the incurrent and feeding filters of both *O. vanhoeffeni* and *O. labradoriensis* which appears to be different from that of warm water oikopleurids. The phenomenon of variable animal activity and its effect on feeding should also be addressed. Such studies would increase our understanding of the biology of these organisms and their ecological role in the cold ocean waters of Newfoundland.

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