

ABUNDANCE AND FORAGING ABILITY  
OF PHYSONECT SIPHONOPHORES  
IN SUBTROPICAL OCEANIC SURFACE WATERS

A Dissertation

by

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## ABSTRACT

Abundance and Foraging Ability of Physonect Siphonophores  
in Subtropical Oceanic Surface Waters. (August 1982)

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Daytime abundances of physonect and selected caly-cophore siphonophores were tallied during SCUBA dives in the upper 15 m of subtropical oceanic surface waters off the Bahamas and in the western Gulf of Mexico. Daytime physonect densities in Bahamian surface waters during summer 1979 averaged less than 2/25,000 m<sup>3</sup>. In spring 1980, physonects averaged 5/25,000 m<sup>3</sup> in Gulf of Mexico surface waters, while in summer 1980 physonect siphonophores were rarely observed (<1/25,000 m<sup>3</sup>). In fall 1980, physonects in the Gulf averaged 30/25,000 m<sup>3</sup> and 8/25,000 m<sup>3</sup> within the surface waters of a mesoscale cyclonic circulation feature and within those of an anticyclonic feature, respectively. In winter 1981 they averaged 16 and 8 per 25,000 m<sup>3</sup> in cyclonic and anticyclonic features, respectively. Environmental correlations with the near-surface abundance patterns are discussed.

During SCUBA dives, the physonect siphonophores

Forskalia tholoides and F. edwardsi were hand-collected for shipboard foraging experiments. Large volume aquaria ( $0.2 \text{ m}^3$  and  $1.0 \text{ m}^3$ ) were used to estimate the foraging ability of these predators at prey densities similar to those of oceanic surface waters (51, 113, 226 and 452 prey  $\text{m}^{-3}$ ). Enclosure of these gelatinous planktivores in large volume aquaria did not appear to adversely affect their feeding or swimming behavior. When feeding on oceanic copepods, the number of prey ingested was proportional to prey concentration at densities at and above 200 prey  $\text{m}^{-3}$ . Based on physonect numerical abundance and prey capture rate, the foraging impact of the physonect siphonophore population in the western Gulf of Mexico is discussed.

Stochastic numerical models were also constructed to test the importance of prey behavior to prey encounter by tentaculate planktivores. The predator for these simulations was patterned as a Forskalia species. Prey swimming behaviors modeled were random directional movement in the X-Y plane and vertically in the Z direction, directed movement in the X-Y plane with a reduced probability of movement along the Z-axis, and "hop and sink" swimming behavior. Results of these simulations indicate that prey behavior may contribute to the quantitative differences in the number of prey encountered by tentaculate planktivores.

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Finally, the encouragement and support of my parents and brothers has helped make this manuscript a reality.

## DEDICATION

To my wife, Anne M. Smith, without whose patience,  
understanding and love, especially during the last few  
months of my graduate tenure, this dissertation would  
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## CHAPTER I

### INTRODUCTION

Most investigations of marine zooplankton feeding dynamics have dealt with the numerically dominant groups such as copepods, euphausiids, and thecosome pteropods (Lasker 1966; Paffenhofer 1971, 1976; Be and Gilmer 1977; Frost 1977; Mayzaud and Poulet 1978; Poulet 1978). All of these animals readily survive collection by nets. More fragile organisms such as salps, larvaceans, ctenophores and siphonophores often are physically and functionally damaged unless collected in hand-held jars using SCUBA. Consequently, basic ecological and physiological studies of soft-bodied organisms must rely on in situ observation and collection techniques (Hamner et al. 1975; Harbison and Gilmer 1976; Biggs 1977a, 1977b).

To describe the feeding dynamics of gelatinous zooplankton requires (1) a quantitative estimate of an animal's feeding ability on the kinds and concentration of food they encounter in the field and (2) estimates of population abundance. Such information will allow a direct comparison of the trophic importance of gelatinous

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This dissertation follows the format and style used in Limnology and Oceanography.

and non-gelatinous organisms in complex oceanic food webs (Steele 1974; Steele and Mullin 1977; Vinogradov and Menshutkin 1977).

Individual gelatinous herbivores process substantial volumes of water. Harbison and Gilmer (1976) recorded sulp filtration rates in excess of  $100 \text{ ml min}^{-1}$ . They calculated that, in the Sargasso Sea, one Pegea confederata aggregate 5 cm in length would probably have the feeding impact of at least 450 large calanoid copepods. Harbison and McAlister (1979) documented that these salps could filter particles as small as 4 um. Madin (1974) concluded from in situ SCUBA observations that salps feed continuously. Consequently, where salps are very numerous (e.g. California Current, Berner 1967), they rank as important consumers.

Alldredge's studies of larvaceans (1976, 1977, 1981) indicate that these gelatinous herbivores consume particles 6 um and smaller. Filtering rates of  $12.5 \text{ ml animal-hr}^{-1}$  have been recorded for the larvaceans Oikopleura dioica in the Gulf of California (Alldredge 1981). Since Alldredge (1981) estimated that at times nearly 40% of each cubic meter of the Gulf of California may be filtered by the O. dioica population in 24 hours, appendicularian as well as sulp grazers must exert significant grazing pressure on natural food assemblages.

Of the gelatinous carnivores, coastal cydippid and

lobate ctenophores have been studied intensively. Their ingestion rates are proportional to food concentrations over a very wide range of copepod prey densities (Miller 1970; Reeve et al. 1978; Kremer 1979). Only in the laboratory at prey densities considerably higher than those common in coastal waters (i.e.  $> 200-400 \text{ liter}^{-1}$ ) did the ingestion rates of tentaculate ctenophores level off (Rowe 1971; Reeve et al. 1978).

Several investigators (Bigelow and Sears 1939; Cronin et al. 1962; Burrell 1968; Herman et al. 1968) have reported a decrease in copepod abundance associated with a population increase in tentaculate ctenophores in the field and have hypothesized that tentaculate ctenophores may exert heavy predation pressure on zooplankton (Miller and Williams 1972). Reeve et al. (1978) have stressed, however, that ctenophores should not be considered merely wasteful "dead ends" in the food chain, but instead may perform a balancing function by (1) keeping an overabundance of copepods from decimating the phytoplankton in the water column, and (2) providing the phytoplankton with a positive growth stimulus by recycling a large amount of the ingested nitrogen.

Szyper (1978) and Feigenbaum (1979) have investigated the feeding behavior of the chaetognath Sagitta enflata. This predator consumes a variety of prey, including appendicularians and other chaetognaths in addition to

copepods. Szypor (1978) concluded that, since most of the copepods consumed were the smaller, more abundant and productive genera, the latter populations were probably little affected by Sagitta's predation. Field studies of chaetognath predation are, however, difficult because of the artifact of prey consumption by the chaetognath during collection in the cod end of zooplankton nets (Feigenbaum 1979).

The medusa Chrysaora quinquecirrha, a common coastal species known as the "sea nettle," has been studied by Clifford and Cargo (1978). They concluded that its ingestion of Artemia was linearly related to the initial brine shrimp concentration over a fairly wide range of Artemia densities. The volume foraged by Chrysaora quinquecirrha, estimated from the feeding rate/prey concentration relationship defined by Clifford and Cargo and the summertime zooplankton density in the Patuxent River estuary, was approximately 20 liters day<sup>-1</sup>.

Phillips et al.'s (1969) study of the trophic significance of jellyfish in the Mississippi Sound has shown that Chrysaora feeds on the lobate ctenophore Mnemiopsis. Cargo and Shultz (1967) have also recorded this behavior and indicate that, in the Chesapeake Bay area, Mnemiopsis leidyi is an important food organism for Chrysaora.

In a series of recent articles, Purcell (1981b,

1981c, 1981d) reported the in situ predation rates of the siphonophores Sphaeronectes gracilis, Muggiae atlantica, Rosacea cymbiformis and Rhizophysa eysenhardtii. R. eysenhardtii, a cystonect siphonophore, fed exclusively on fish larvae and consumed an average of 8.8 larvae animal-day<sup>-1</sup>. Given siphonophore and fish larvae densities, Purcell (1981b) calculated that R. eysenhardtii could consume 28% of the fish larvae per day at a study site in the Gulf of California.

In contrast to the cystonect R. eysenhardtii, the calycophore siphonophores Sphaeronectes gracilis and Muggiae atlantica consumed mainly copepods (Purcell 1980) and Rosacea cymbiformis ate primarily crab zoea (Purcell 1980, 1981c). Purcell and Kremer (in press) have estimated that S. gracilis could consume 4% of the copepod standing crop daily in their study area off Santa Catalina Island, California, but that R. cymbiformis would be unlikely to have a significant effect on the prey population in this area.

The ecological and behavioral information gathered in these and similar coastal studies has formed the basis for population models of medusae (Miller and Williams 1972; Heinle 1974; Huntley and Hobson 1978) and ctenophores (Kremer 1976) which are reasonably predictive of seasonal trends in near-shore population biomass.

Investigations of the feeding biology of oceanic

gelatinous carnivores have been largely focused on individual, rather than population, parameters (Lalli 1969; Seapy 1974; Swanberg 1974; Hamner et al. 1975; Larson 1976; Biggs 1976, 1977a). Generally, this reflects the difficulty in sampling scattered yet highly fragile open-ocean individuals with traditional nets or trawls. However, as biologists pursue alternative, in situ methods to quantify the population density of open-ocean macrogelatinous carnivores (Harbison et al. 1978; Biggs et al. 1981; Purcell 1981b), such studies of individual feeding behavior will provide the basis for open-ocean population feeding ecology simulation models.

The three chapters which follow address different aspects of siphonophore population dynamics. In Chapter II, the population abundance of physonect and large calycophoran siphonophores was estimated using a new in situ technique (Biggs et al. 1981) in the western Gulf of Mexico and in Bahamian waters.

In Chapter III, I examine the foraging ability of siphonophores of the genus Forskalia, the most common physonect in the western Gulf of Mexico study area. Unlike previous experimental studies of tentaculate carnivores, in which prey capture behavior was investigated exclusively in small containers and/or at abnormally high prey densities, this study was designed to characterize the animals' ability to forage at low ambient prey

densities.

A group of stochastic numerical models of predator-prey interaction is developed in Chapter IV to provide an estimate of prey encounter. These models contrast the encounter frequency of Forskalia feeding on three different swimming patterns of copepod prey.

The field data for this study were gathered on a number of research cruises to the Bahamas and western Gulf of Mexico. These included two cruises-of-opportunity aboard the R/V Johnson (J-080, J-084) to the Bahamas during which the feeding tanks, described in Chapter III, were tested and modified; and two short student research cruises (79-G-10, 79-G-11) and four quarterly cruises (80-G-1, 80-I-6, 80-G-11, 81-G-2) aboard the R/V Gyre or R/V Iselin into the western Gulf of Mexico. The four major research cruises into the western Gulf of Mexico occurred during March-April 1980, July 1980, October-November 1980 and February 1981, respectively, and were designed to contrast the biology and chemistry of cyclonic and anticyclonic mesoscale features in the Gulf. See Brooks and Eble (1982) for a summary of the physical characteristics of the western Gulf during these major cruises.

A list of the station positions of SCUBA dives in the Gulf of Mexico is provided in Appendix A. For comparison with the Forskalia data in Chapter III, feeding

experiments with other genera of tentaculate gelatinous carnivores which were opportunistically encountered and captured on SCUBA dives are reported in Appendix B.

Throughout this dissertation, Totton (1965) has been used as the taxonomic authority for siphonophores.

CHAPTER II  
SURFACE SIPHONOPHORE ABUNDANCE ESTIMATES  
FOR THE BAHAMAS AND THE WESTERN GULF OF MEXICO

Introduction

Typically, zooplankton abundance estimates are made using a conventional 1-m zooplankton net. Standard zooplankton nets have evolved into more sophisticated open-closing nets (e.g. open-closing BONGO nets, McGowan and Brown 1966) and some now include electronic environmental sensing packages (Wiebe et al. 1976; Sameoto et al. 1980). However, quantifying the abundance of many of the delicate representatives of the oceanic gelatinous macrozooplankton is not possible using common zooplankton sampling devices.

A standard zooplankton net tow may sample 1,000 m<sup>3</sup> of water which, in many cases in the oligotrophic environment of the open ocean, is not a large enough volume to encounter one physonect siphonophore. The morphology and spatial orientation of tentaculate gelatinous macrozooplankton and the relatively small mouth area of many nets create another problem. When relaxed, extended and fishing, siphonophores can spread their tentacles over a broad volume. It is not uncommon to observe siphonophores in situ with their tentacles extended throughout a 1/8 m<sup>3</sup>

space. Consequently, if the tow path of a net were to intersect this animal, the parts of the animal required for identification (i.e. nectophores, bracts, etc.) may not be captured. Due to the fragile nature of these animals, many fall apart as they are funnelled into the net.

For example, using BONGO open-closing paired zooplankton nets to sample the gelatinous zooplankton off Southern California, Alvarino (1967) was unable to quantify the siphonophore population because "the nectophores of a physonectes appeared in either the right or left net and in the other net the pneumatophores with the nectosoma and the siphosoma attached."

These drawbacks have not prevented investigators from using net samples to describe presence/absence relationships such as species distribution and zoogeography. Alvarino (1967, 1971) has compiled extensive lists of siphonophore occurrences in the Pacific Ocean and Pugh (1974, 1975) has looked to the distribution of siphonophores in the North Atlantic. Phillips (1972) has investigated the zoogeography of siphonophores in the Gulf of Mexico.

As a result of the inability to determine the abundance of oceanic gelatinous macrozooplanktonic species using nets and the need for healthy, intact animals for physiological experimentation, several investigators

have popularized the use of blue water SCUBA diving (Hamner 1975; Harbison et al. 1978; Biggs et al. 1981). SCUBA makes possible direct observation and in situ estimation of population abundance. Although not without disadvantages, SCUBA techniques are very useful and reliable, particularly for surface estimates, and have been used in this study to investigate siphonophore abundance in the upper 15 m of the western Gulf of Mexico and in the surface waters off the Bahamas.

#### Materials and Methods

The methodology used for SCUBA safety and population estimates has been described elsewhere (Hamner 1975; Biggs et al. 1981). Briefly, three reference grids, each measuring 5 m x 5 m, were vertically suspended, one on top of the other, beneath a Zodiac inflatable raft. These grids were constructed by suspending two weighted nylon lines from the ends of a 5-m boom extended abeam across the Zodiac. At 5 m, 10 m and 15 m depths, a horizontal nylon line was attached to the two vertical downlines, defining three vertical reference grids. All lines used were white and could be easily seen by the divers (Fig. 1). All abundance estimates were made in the upper 15 m and consequently were within the mixed layer.

Three SCUBA divers tethered off the back of the

Fig. 1. Underwater photo of three 5 m x 5 m grids arranged below surface raft. (Photographed by R. R. Bidigare.)



Zodiac, so that one diver viewed each grid. The divers would observe and count the number of physonects and large calycophores which drifted through the grids during the course of a dive. A fourth diver functioned as the safety man. Each dive was divided into four consecutive 5-minute counting intervals resulting in a total dive time of 20 minutes. To increase the volume of water searched, the Zodiac operator slowly motored the raft through the water so that the water flow was 90° to the plane of the grids. The motoring rate was monitored by the Zodiac operator who would record the time period required for a marker to drift from the stern of the Zodiac to a float trailing 10 m behind at various times during a 20-minute dive. The lines defining the grid were of small diameter (5 mm), thereby reducing the drag of the grid arrangement and keeping the shape of the reference grids from being distorted as they were pulled through the water.

Biggs (1977a) has described the salient morphological features and swimming-fishing posture of siphonophores which allow in situ generic identification. Divers recorded sightings of siphonophores on either underwater tape recorders (Sound Wave Systems, Costa Mesa, CA) or underwater writing slates.

To investigate temporal differences in siphonophore abundance, grid dives were scheduled twice daily, once

in the early morning and then in the late afternoon. Ideally, the divers would enter the water as soon as there was enough light for a safe morning dive and wait until the last hour of useful light in the afternoon before beginning their evening dive.

By using the three vertically arrayed reference grids and dividing the dive into four consecutive 5-minute counting intervals, the technique allows for the determination of vertical patchiness on a scale of meters and horizontal patchiness on a scale of tens-of-meters or tens-of-minutes (Biggs et al. 1981).

### Results

Bahamas--The data were gathered on six dives in an area of the subtropical ocean during June of 1979. Fig. 2 displays the location which was southeast of Grand Bahama Island and west of Great Abaco Island, seaward of the 1,000 m isobath. The initial three dives (010, 011, 012) were made in the morning of three consecutive days. On the next three days, dives were conducted in the evening (013, 014, 015). Table 1 displays the motoring rates, volume searched and standardized abundance estimates for each dive. All abundance estimates have been standardized to 25,000 m<sup>3</sup>; an average of 22,000 m<sup>3</sup> was viewed on the six Bahamian dives.

Siphonophores were rare in Bahamian surface waters

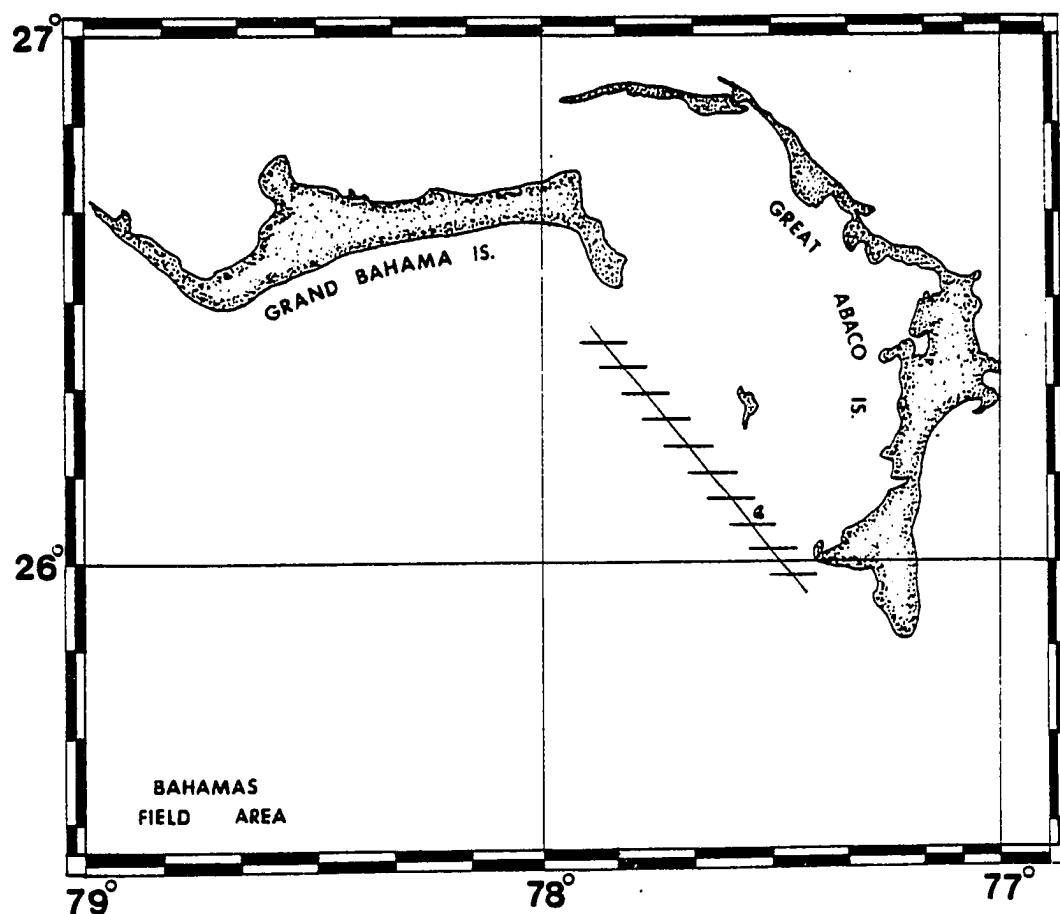


Fig. 2 Field area in the Bahamas where the research dives were carried out (indicated by cross-hatched area).

Table 1. Volume searched per dive and calculated abundance estimates (individuals per 25,000 m<sup>3</sup>) for physonect and calycoptile siphonophores during research cruise J-080 (July 1979) in the upper 15 m off the Bahamas.

TAMU Dive No. 1	Motoring Rate (m/min.) <sup>2</sup>	Volume Searched (m <sup>3</sup> )	Time of Day <sup>1</sup>	Siphonophores	Physonects	Calycoptiles
010	11.5 ± 1.1 (n=10)	17,250	A.M.	1	1	9
011	14.2 ± 1.3 (n=14)	21,300	A.M.	0	0	2
012	12.2 ± 0.7 (n=8)	18,300	A.M.	0	0	0
013	14.2	21,300	P.M.	0	0	2
014	21.1 ± 2.3 (n=22)	31,650	P.M.	1	1	1
015	14.6 ± 1.4 (n=9)	21,900	P.M.	16	—	97

<sup>1</sup> For the time of the dive, see Appendix A.

<sup>2</sup> n-value in parenthesis indicates number of times motoring rate was determined during 20-minute SCUBA grid dive.

with the exception of dive 015. On this dive, both physonect and calycophore siphonophores were relatively abundant. Examination of Fig. 3 indicates that these animals were primarily found in the upper grid (0-5 m depth).

Gulf of Mexico, Spring 1980--Five grid dives were completed. Three other dives were cut short because of the appearance of one or more sharks. On this cruise, the ship transected both a cyclonic and an anticyclonic mesoscale feature. Two of the successful grid dives were located in the cyclonic feature (031, 032), one in the anticyclonic region (030), and two in the open Gulf of Mexico outside the influence of either physical feature (028, 029). Dives 031 and 032 occurred within 15 hours of each other at a biological sampling station, marked by a parachute drogue, in the cyclonic feature. The other three dives occurred at different geographical locations (Fig. 4).

To provide objectivity in determining whether or not a particular dive station was within a cyclone, anticyclone, or outside either feature, I defined a cyclonic station as one where the 13°C isotherm was above 300 m. Conversely, when the 14°C isotherm was below 300 m, the station was described as anticyclonic. Water temperatures at 300 m generally ranged between 13-14°C in areas which were obviously outside the

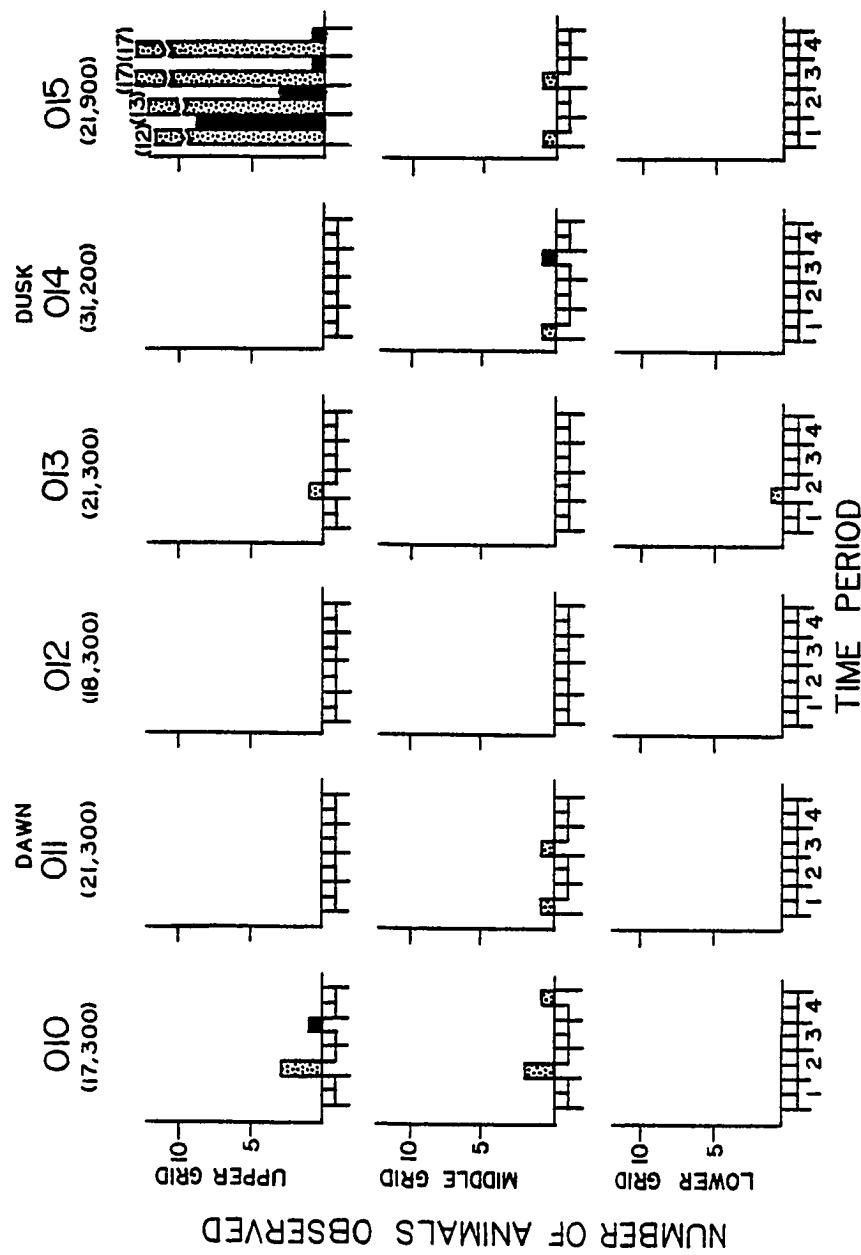
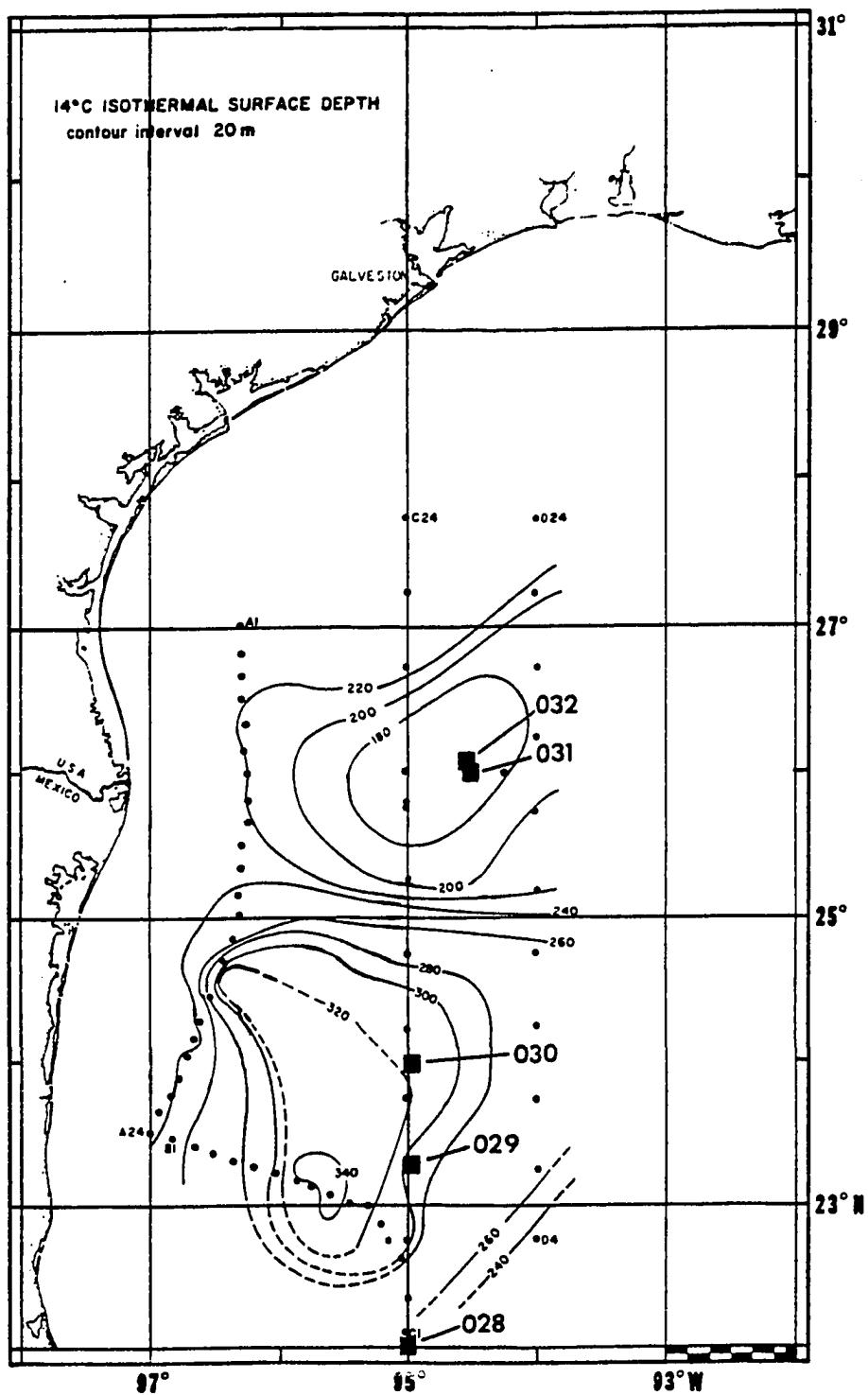


Fig. 3. Number of physonect and calycocephore siphonophores counted during J-080 dives. Histograms display vertical distribution for each of the four consecutive counting intervals. Solid bars represent physonects; stippled bars represent calycocephores. Number in parenthesis beneath dive number is total volume searched per dive.

Fig. 4. Depth contour of the 14°C isothermal surface drawn from XBT and STD data gathered by the R/V Gyre during the spring research cruise, 80-G-1, depicting the northerly cyclone and southerly anticyclone. Small circles represent physical data stations and the squares represent SCUBA dive stations (designated by TAMU dive numbers). Contour drawn by Brooks and Eble' (1982).



influence of either feature. The only area where these distinctions were not entirely useful was at the northern end of the cruise transects where the bottom topography resulted in the upward deflection of the isotherms. This relationship between the depth of the 13°C and 14°C isotherms was relatively constant throughout the year and was used to distinguish between the features during all four cruises.

On each 20-minute dive, the motoring rate was monitored an average of 15 times (range: 12-19). Table 2 lists the average motoring rate ( $\bar{x} \pm s.d.$ ) for each dive as well as the total volume viewed per dive. An average of 22,400 m<sup>3</sup> ( $\pm 4,100$  m<sup>3</sup>) were viewed on dives carried out on 80-G-1.

Physonect abundance varied from 0 to 19 per 25,000 m<sup>3</sup> on dives made on the spring cruise. While few physonects were seen in the cyclone, physonects were present at a standardized density of 19 per 25,000 m<sup>3</sup> on the single dive in the anticyclone (Table 2). These were almost exclusively represented by Agalma sp., a genus typical of subtropical near-surface water. Physophora sp. was also present, but no Forskalia sp. were observed during the grid surveys on this cruise. Diphyid-type calycophores made up the majority of calycophores seen on dives 031 and 032. Fig. 5 displays the vertical and horizontal distribution of the siphonophores seen on

Table 2. Volume searched per dive and calculated abundance estimates (individuals per  $25,000 \text{ m}^3$ ) for physonect and calycoptile siphonophores during spring research cruise 80-G-1 (March-April 1980) in the upper 15 m of the western Gulf of Mexico.

TAMU Dive No. 1	Motoring Rate (m/min.) <sup>2</sup>	Volume Searched (m <sup>3</sup> )	Siphonophores	
			Physonects	Calycoptiles
031 Cyclonic Feature	16.1 ± 1.3 (n=19)	24,150	P.M.	0
032 Oustside Feature	17.7 ± 1.0 (n=12)	26,550	A.M.	1
028 Oustside Feature	16.9 ± 2.0 (n=16)	25,350	P.M.	1
029 Antic-	11.6 ± 1.8 (n=13)	17,400	A.M.	0
030 Cyclonic Feature	12.4 ± 2.0 (n=13)	18,600	P.M.	19
				3

<sup>1</sup> For exact position and time of dive, see Appendix A.

<sup>2</sup> n-value in parenthesis indicates number of times motoring rate was determined during 20-minute SCUBA grid dive.

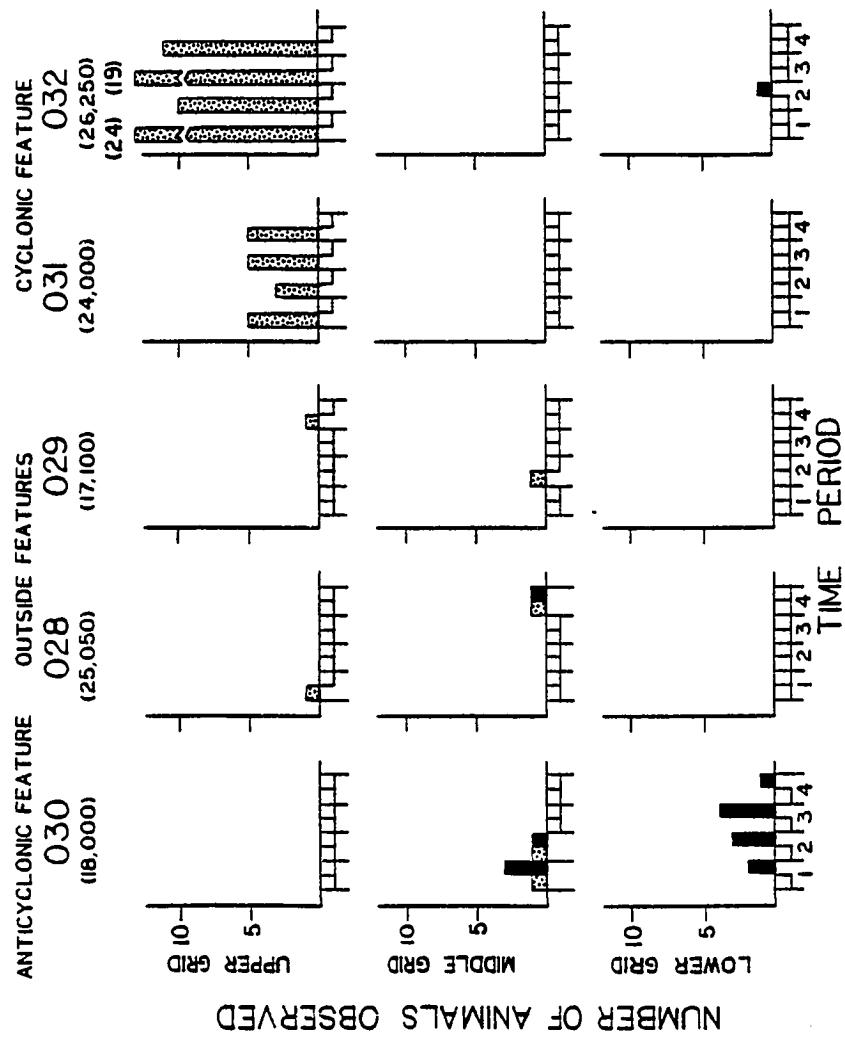


Fig. 5. Number of physonects and calyphophores counted during 80-G-1 dives. Histograms display vertical distribution for each of the four consecutive counting intervals. Solid bars represent physonects; stippled bars represent calyphophores. Number in parentheses beneath dive number is total volume searched per dive.

this series of dives.

Gulf of Mexico, Fall 1980--An anticyclonic and cyclonic mesoscale physical feature were also surveyed on the third cruise, 80-G-11, in the fall of 1980. During the 19-day cruise, 21 SCUBA dives were completed. Sixteen of these dives were grid dives during which abundance estimates were made. Grid dives 050, 051, 053, 054 and 056 took place in the anticyclone. The last four of these dives occurred at a drogued biological sampling station over a 2 1/2-day period. (At all drogued stations occupied during this study, the buoy was drogued below the mixed layer.) Similarly, of the seven dives which took place in the cyclonic feature, dives 065, 066, 067 and 068 were executed at another drogued station over a two-day period (Fig. 6).

The motoring rate was monitored an average of eight times per dive (range: 2-10) and the average volume viewed for these 16 dives was 22,600 m<sup>3</sup> ( $\pm$  5,100 m<sup>3</sup>). Table 3 lists the motoring rate and volume searched for each individual dive.

In contrast to the spring cruise, during the fall physonects were relatively abundant in both the cyclone and anticyclone (Table 3). Physonect siphonophore abundance in the anticyclonic, open Gulf and cyclonic regions averaged 8, 31 and 30 per 25,000 m<sup>3</sup>, respectively. Although calycophoran siphonophore abundance tracked that

Fig. 6. Depth contour of the 14°C isothermal surface drawn from XBT and STD data gathered by the R/V Gyre during the fall research cruise, 80-G-11, depicting the northerly cyclone and southerly anticyclone. Small circles represent physical data stations and the squares represent SCUBA dive stations (designated by TAMU dive numbers). Contour drawn by Brooks and Eble (1982).

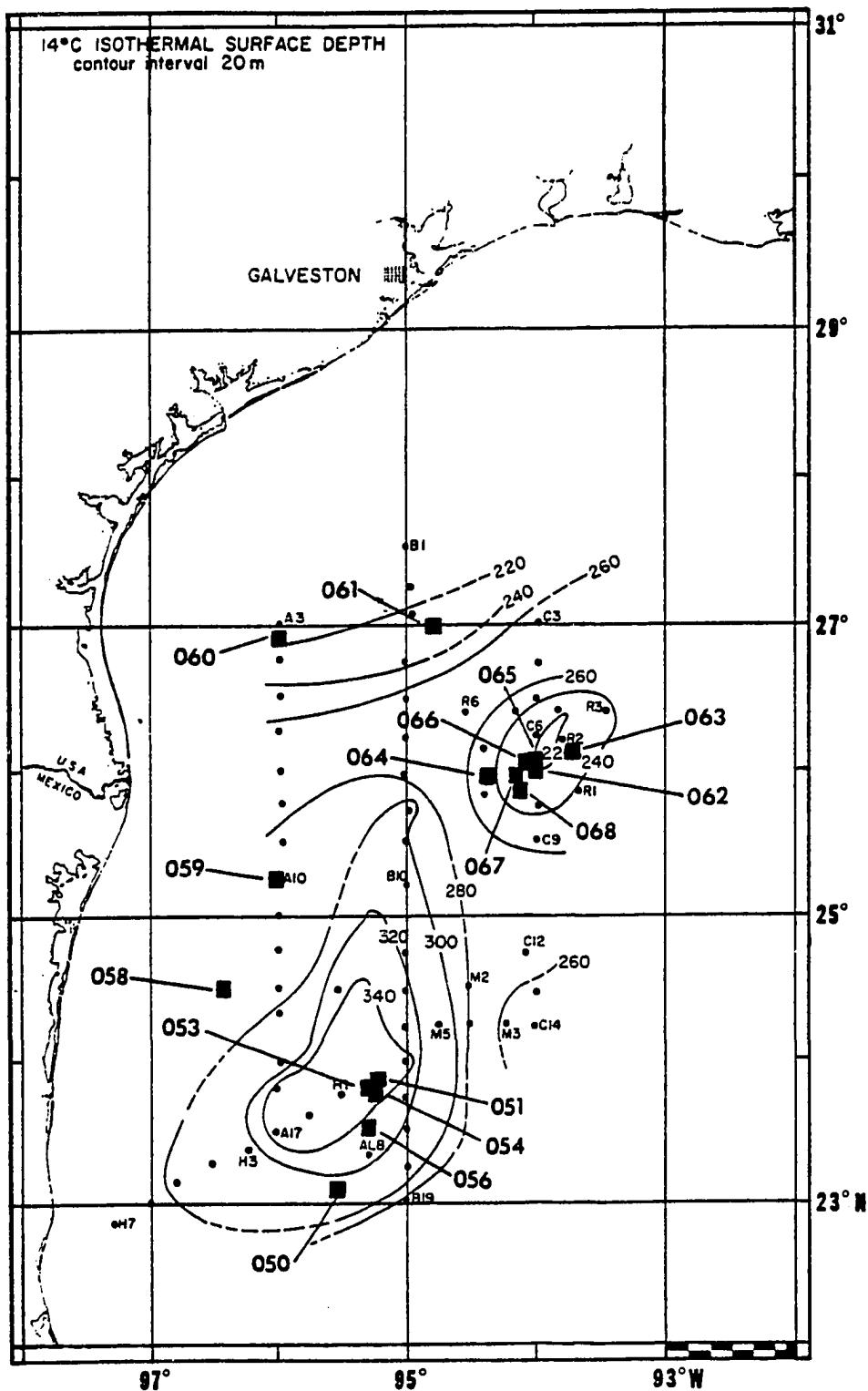


Table 3. Volume searched per dive and calculated abundance estimates (individuals per 25,000 m<sup>3</sup>) for physonect and calycothore siphonophores during fall research cruise 80-G-11 (October-November 1980) in the upper 15 m of the western Gulf of Mexico.

TAMU Dive No. 1	Motoring Rate (m/min.) <sup>2</sup>	Volume Searched (m <sup>3</sup> )	Time of Day <sup>1</sup>	Siphonophores	Calycothores
Cyclonic Features	062 12.5 ± 1.4 (n=7)	18,750	A.M.	4	0
	063 17.0 ± 3.9 (n=9)	25,500	P.M.	34	11
	064 16.5 ± 3.6 (n=9)	24,750	A.M.	55.5	2
	065 14.9 ± 2.1 (n=9)	22,350	P.M.	40	12
	066 11.7 ± 1.4 (n=8)	17,550	A.M.	40	1
	067 17.4 ± 3.9 (n=6)	26,100	A.M.	11.5	3
Dusttide Features	068 18.5 ± 1.9 (n=9)	27,750	P.M.	27	3
	058 13.6 ± 2.0 (n=8)	20,400	A.M.	7	5
	059 15.4 ± 3.6 (n=9)	23,100	P.M.	82	5
	060 13.3 ± 3.7 (n=8)	19,950	A.M.	0	1
	061 12.4 ± 1.4 (n=9)	18,600	P.M.	34	3
Anticyclonic Features	050 11.7 ± 1.4 (n=7)	17,550	P.M.	4	0
	051 8.0 ± 1.2 (n=2)	12,000	P.M.	10	6
	053 18.1 ± 2.1 (n=8)	27,150	P.M.	16	1
	054 20.2 ± 2.0 (n=7)	30,300	A.M.	7	2.5
	056 19.9 ± 2.1 (n=10)	29,850	A.M.	2.5	3

<sup>1</sup> For exact position and time of dive, see Appendix A.

<sup>2</sup> n-value in parenthesis indicates number of times motoring rate was determined during 20-minute SCUBA grid dive.

of physonects, the abundance estimates for large calyco-phores were lower in all three regions (anticyclone--3 per 25,000 m<sup>3</sup>; open Gulf--4 per 25,000 m<sup>3</sup>; and cyclone--5 per 25,000 m<sup>3</sup>).

Unlike physonect siphonophores, many calycophores are rather small and have little salient pigmentation. Consequently, divers would not be able to count them quantitatively during the dives. While the calycophore densities are not absolute, observed trends in the estimates of large calycophore species seen by the divers are useful and provide supporting evidence for the distributional patterns exhibited by the physonect siphono-phores.

Forty percent of the physonect siphonophores encountered in the anticyclone were identified to genus. Forskalia accounted for 93% of those identified. Representatives of the genus Athorybia were also present. In the cyclonic feature, approximately 50% were identified in situ, of which Forskalia made up 85%. Physonect siphonophores of the genera Athorybia, Cordagalma and Agalma were also identified in the cyclone.

No calycophores were identified in the anticyclone, while 58% of the large calycophores present in the cyclone were identified. Stephanophyes sp. accounted for 78% and the genus Rosacea accounted for the remaining 22%. Fig. 7 displays the vertical and horizontal

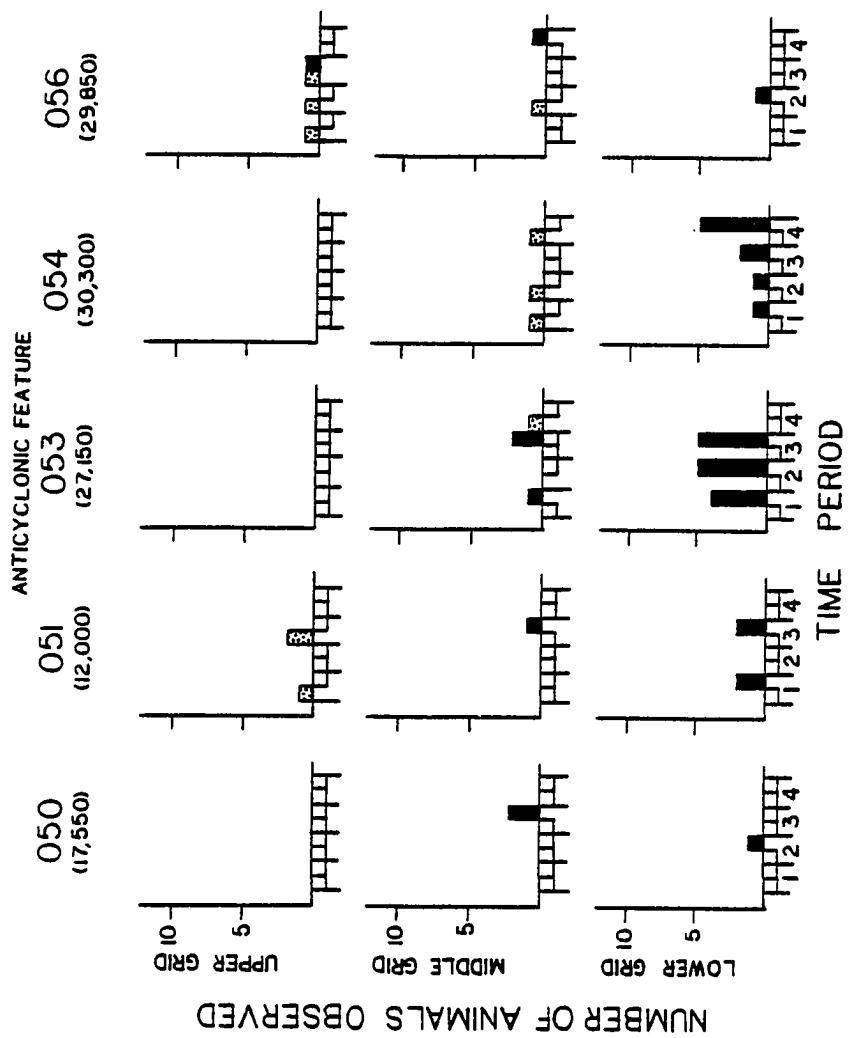


Fig. 7. Number of physonects and calycoephore siphonophores counted during 80-G-11 dives. Histograms display vertical distribution for each of the four consecutive counting intervals. Solid bars represent physonects; stippled bars represent calycoephores. Number in parenthesis beneath dive number is total volume searched per dive.

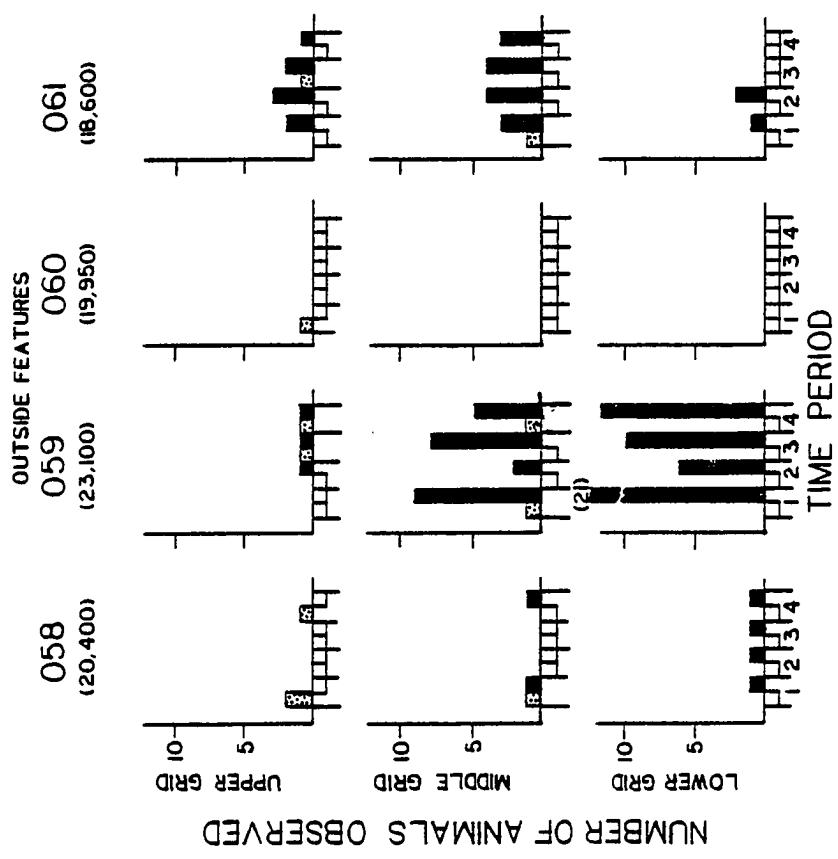


Fig. 7 (continued).

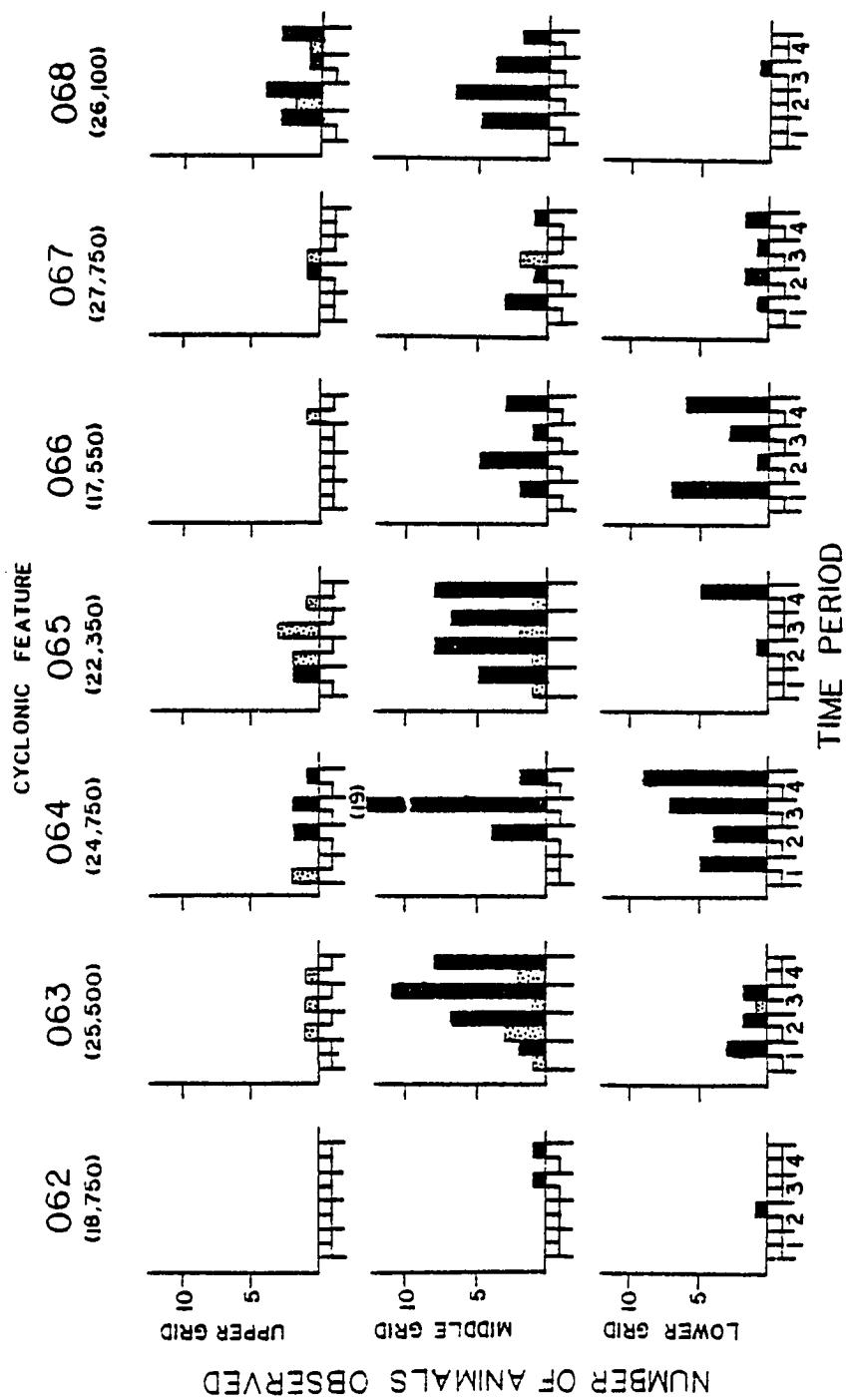


Fig 7 (continued).

distribution of siphonophores viewed during this series of dives.

Gulf of Mexico, Winter 1981--The winter research cruise once again located and charted an anticyclonic and cyclonic physical feature. During cruise 81-G-2, nine grid dives were successfully carried out (Fig. 8). Three of these dives (071, 072, 073) occurred over a 25-hour period at a drogued sampling station, whereas all four dives in the anticyclone were executed over a 2 1/2-day period at another drogued location. While we anticipated that dive 078 occurred in the cyclonic feature, I have classified this dive station as occurring outside either of the two features since this station was at the edge of the XBT coverage during our survey and the dynamic topography (as reflected in the temperature structure (Brooks and Eble 1982)) was rather complex in this general region. Consequently, there were insufficient data to assure this dive occurred in the cyclone.

During this set of dives, the motoring rate was monitored an average of 14 times per dive (range: 3-20). An average of 22,300 m<sup>3</sup> ( $\pm$  4,300 m<sup>3</sup>) were viewed during the dives. The motoring rate and volume searched per dive are listed in Table 4.

The divers observed an average of 16, 8 and 10 physonect siphonophores per 25,000 m<sup>3</sup> in the cyclone, anticyclone and outside the features, respectively.

Fig. 8. Depth contour of the 14°C isothermal surface drawn from XBT data gathered over an 18-day period by the R/V Gyre during the winter research cruises, 81-G-1 and 81-G-2, depicting the northerly cyclone and southerly anticyclone. Small circles represent physical data stations and the squares represent SCUBA dive stations (designated by TAMU dive numbers).

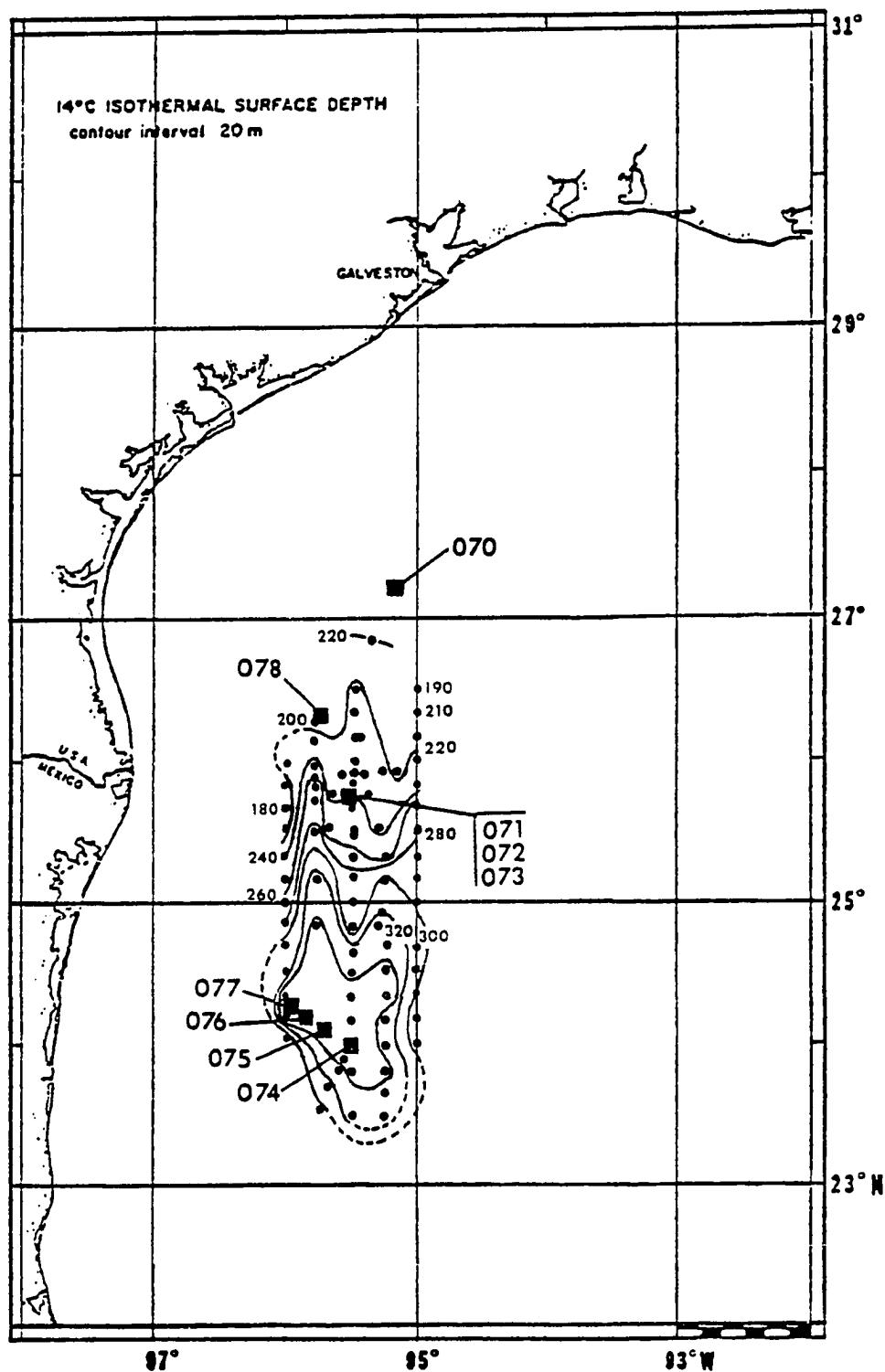


Table 4. Volume searched per dive and calculated abundance estimates (individuals per  $25,000 \text{ m}^3$ ) for Physonect and calyphore siphonophores during winter research cruise 81-G-2 (February 1981) in the upper 15 m of the western Gulf of Mexico.

TAMU Dive No. 1	Motoring Rate (m/min.) <sup>2</sup>	Volume Searched (m <sup>3</sup> )	Time of Day <sup>1</sup>	Siphonophores Calyphores
Cyclonic Features	15.9 ± 1.0 (n=18)	23,850	A.M.	18
071				9
072	14.7 ± 0.9 (n=16)	22,050	P.M.	10
073	11.5 <sup>3</sup>	17,250	A.M.	20
				33
Outsides Features	19.3 ± 1.3 (n=20)	28,950	P.M.	10
070				21.5
078	10.2 ± 0.8 (n=17)	15,300	P.M.	10
				6.5
Anticyclonic Features	16.2 ± 1.2 (n=16)	24,300	P.M.	14
074				6
075	14.1 ± 0.8 (n=11)	21,150	A.M.	5
076	17.94	26,850	P.M.	6.5
077	13.9 ± 0.7 (n=3)	20,850	A.M.	8
				1

<sup>1</sup> For exact position and time of dive, see Appendix A.

<sup>2</sup> n-value in parenthesis indicates number of times motoring rate was determined during 20-minute SCUBA grid dive.

<sup>3</sup> Motoring rate estimated to be about 3/4 of average rate.

<sup>4</sup> Motoring rate estimated using dye.

Large calycophore siphonophores averaged 20, 7 and 14 per 25,000 m<sup>3</sup>, respectively, displaying the same general abundance pattern (Table 4, p. 36).

During the winter cruise, siphonophores were also identified in situ as they drifted through the grids. Ninety-four percent of the physonects seen on the cyclonic dives were identified. Of these, 80% were of the genus Forskalia and the remaining 20% included individuals of the Cordagalma, Agalma and Nanomia genera. In the anticyclone, 84% of the physonects were identified and all were of the genus Forskalia. Although not all the physonects were identified, the cyclone certainly appeared to be more diverse (i.e. a greater number of genera present in the cyclone than the anticyclone).

Ninety-seven percent of the large calycophores were identified in the cyclone; 86% were Rosacea sp. (two species present), 10% were Stephanophyes sp., and the remaining 4% were representatives of the genus Sulculeolaria. During the anticyclonic dives, divers identified 72% of the calycophores encountered. In this group there were approximately the same number (50% and 45%, respectively) of Sulculeolaria sp. as Rosacea sp. (one species present). The other 5% were representatives of the genus Stephanophyes. Fig. 9 shows the vertical and horizontal distribution of siphonophores seen on the winter dives.

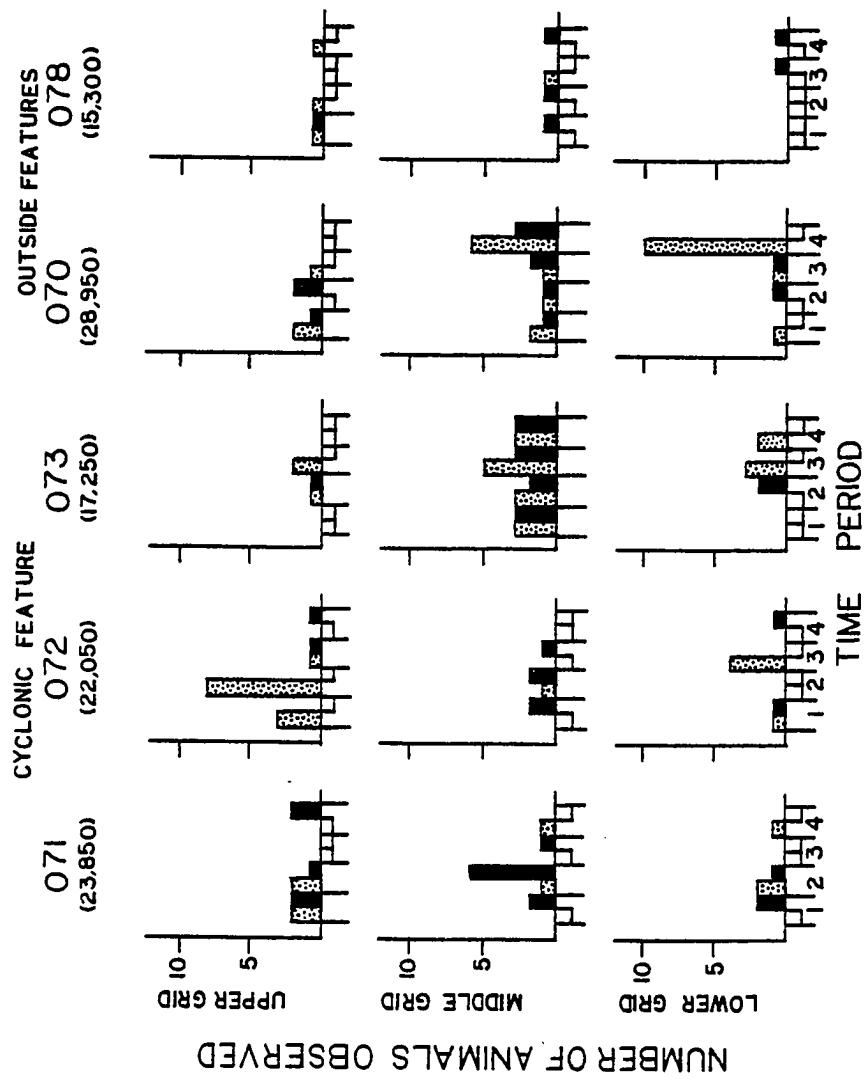


Fig. 9. Number of physonects and calycocephore siphonophores counted during 81-G-2 dives. Histograms display vertical distribution for each of the four consecutive counting intervals. Solid bars represent physonects; stippled bars represent calycocephores. Number in parenthesis beneath dive number is total volume searched per dive.

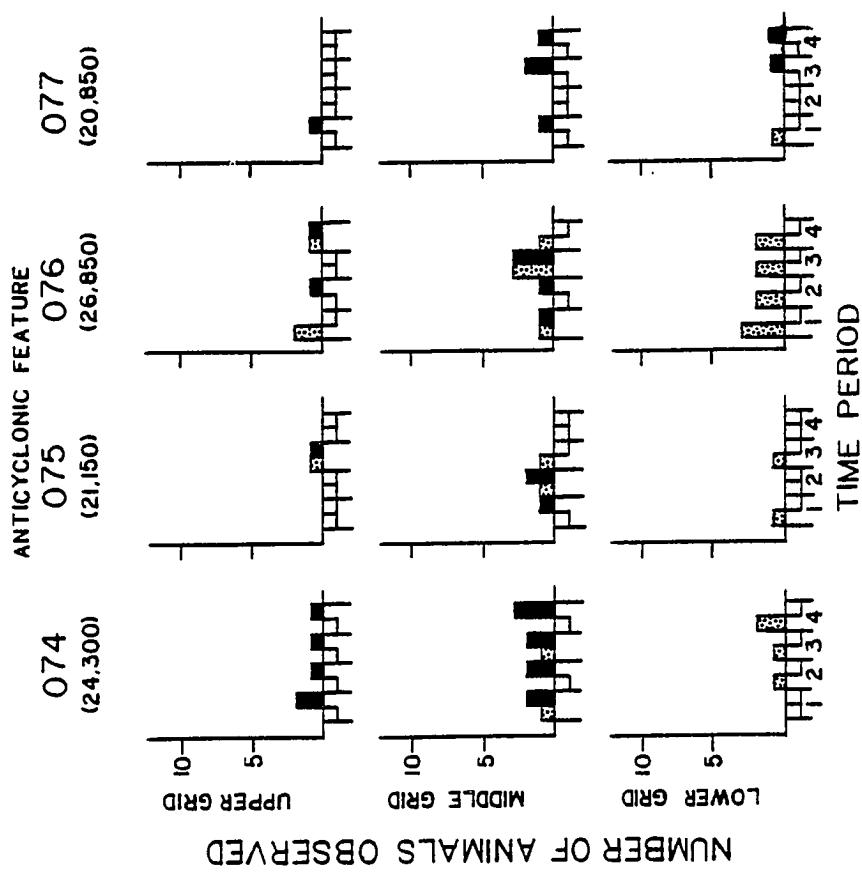


Fig 9 (continued).

Gulf of Mexico, Summer 1980--The summer research cruise (80-I-6) aboard the R/V Iselin also transected both a northerly cyclonic feature and a southerly anticyclonic region. Fourteen dives were made on this cruise, of which nine were successfully completed grid dives. Five of these dives (037, 038, 039, 040, 041) were in the anticyclonic feature and four (036, 043, 044, 055) occurred in the open Gulf of Mexico or in slope water. Three of the five anticyclonic dives (039, 040, 041) occurred at a drogued biological sampling station over a three-day period (Fig. 10).

Table 5 lists the average motoring rate for each dive. This table also displays the volume searched and the abundance of siphonophores on these dives. The average volume viewed on dives occurring on this research cruise was 22,600 m<sup>3</sup> ( $\pm$  2,900 m<sup>3</sup>). The vertical and horizontal distribution of siphonophores during the summer cruise is displayed in Fig. 11.

In contrast to the spring, fall and winter situations, abundance estimates during the summer cruise displayed a preponderance of zeros (Table 5). Over 70% of the observations resulted in zero siphonophores seen. When siphonophores were observed (including representatives of the genera Forskalia and Athorybia), they were small relative to animals viewed during the other three cruises.

Fig. 10. Depth contour of the 14°C isothermal surface drawn from XBT and STD data gathered by the R/V Iselin and R/V Longhorn during the summer of 1980, depicting the northerly cyclone and southerly anticyclone. Small circles represent physical data stations occupied by the Iselin during 80-I-6. Small triangles represent physical data stations occupied by the Longhorn during FSU III at roughly the same period of time. The squares represent SCUBA dive stations occupied during 80-I-6 (designated by TAMU dive numbers). Contour drawn by Brooks and Eble (1982).

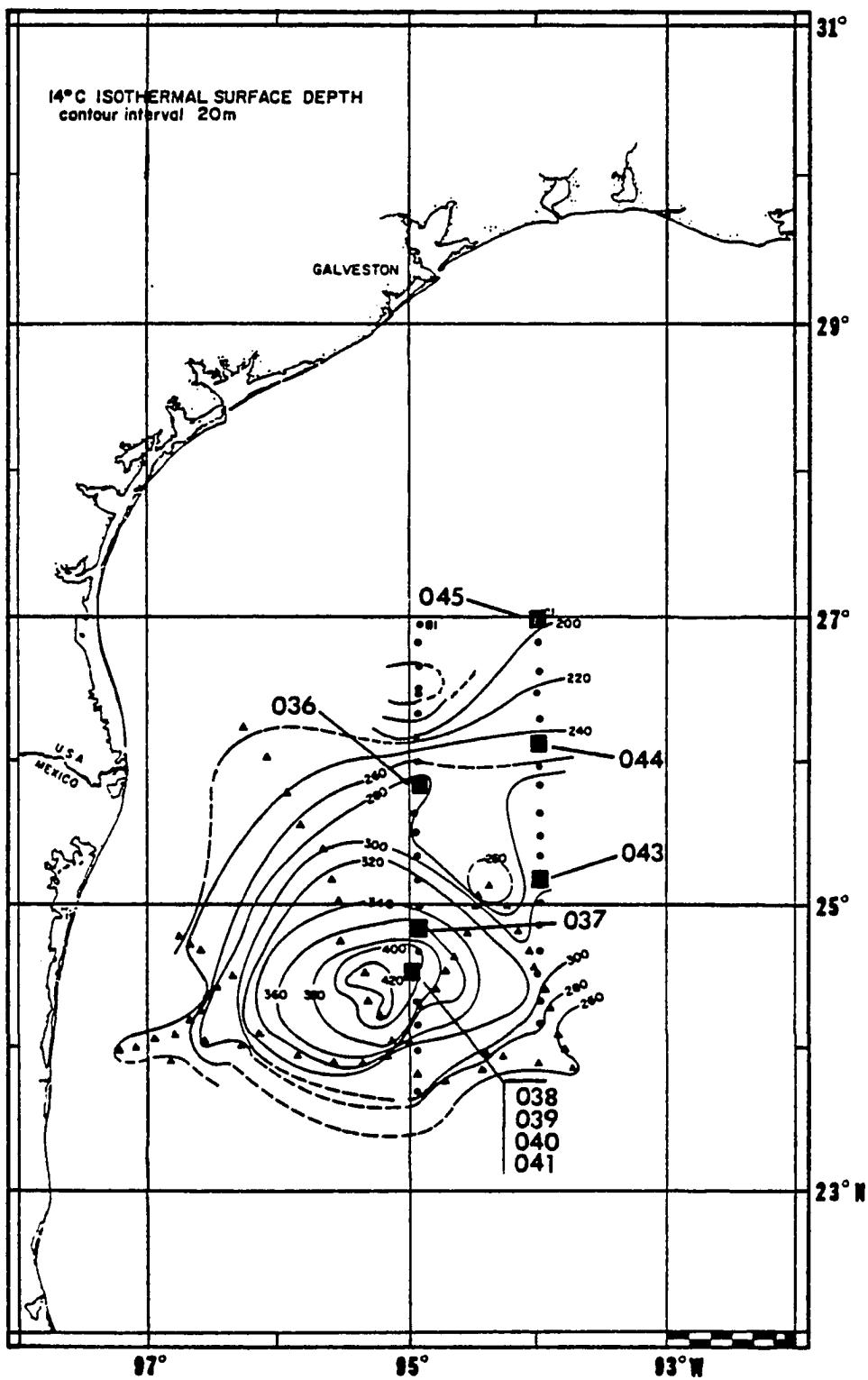


Table 5. Volume searched per dive and calculated abundance estimates (individuals per 25,000 m<sup>3</sup>) for physonect and calyphore siphonophores during summer research cruise 80-1-6 (July 1980) in the upper 15 m of the western Gulf of Mexico.

TAMU Dive No. 1	Motoring Rate (m/min.) <sup>2</sup>	Volume Searched (m <sup>3</sup> )	Time of Day <sup>1</sup>	Siphonophores	Calyphophores
036	14.9 ± 3.3 (n=18)	22,350	A.M.	0	0
043	16.3 ± 4.6 (n=18)	24,450	P.M.	6	0
044	10.6 ± 1.9 (n=18)	15,900	A.M.	1.53	0
045	16.7 ± 6.0 (n=17)	25,050	A.M.	0	0
037	16.3 ± 4.4 (n=8)	24,450	P.M.	0	1
038	14.7 ± 5.0 (n=11)	22,050	A.M.	0	0
039	14.4 ± 4.7 (n=5)	21,600	P.M.	1	0
040	14.8 ± 4.4 (n=15)	22,200	A.M.	0	0
041	16.9 ± 5.3 (n=19)	25,350	P.M.	0	23

<sup>1</sup> For exact position and time of dive, see Appendix A.

<sup>2</sup> n-value in parenthesis indicates number of times motoring rate was determined during 20-minute SCUBA grid dive.

<sup>3</sup> Organisms encountered were very small in size.

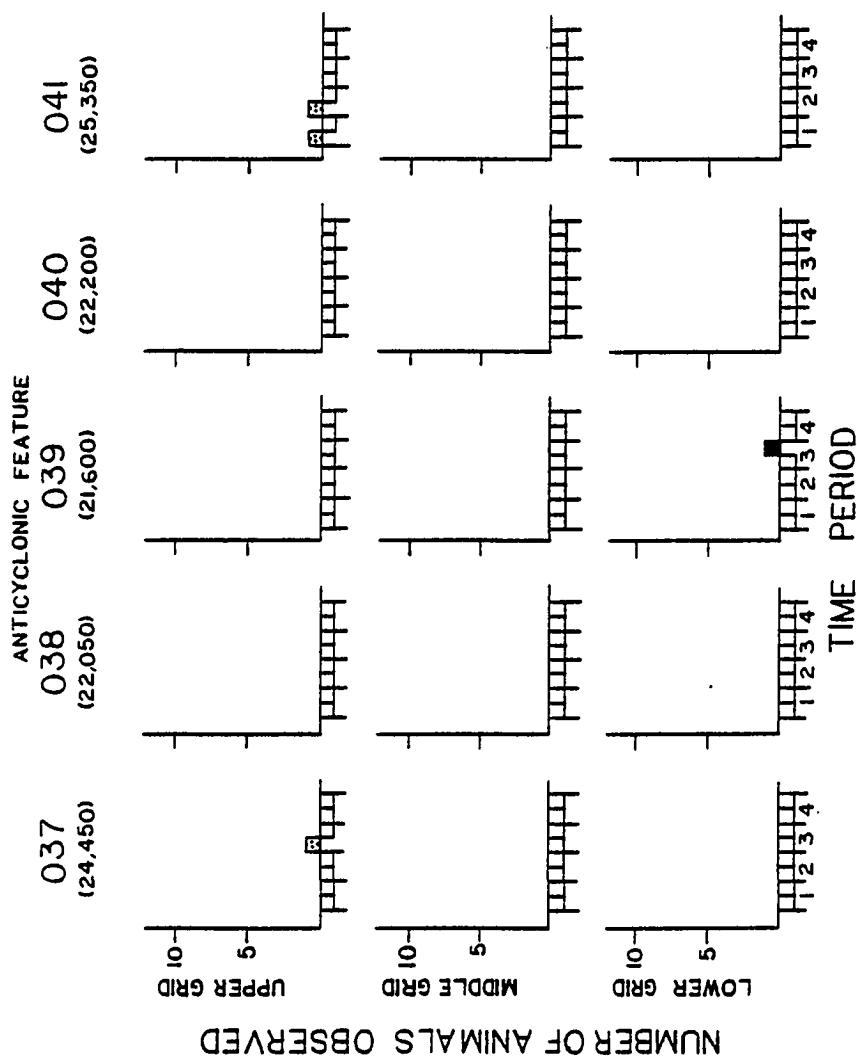


Fig. 11. Number of physonects and calycoaphore siphonophores counted during 80-1-6 dives. Histograms display vertical distribution for each of the four consecutive counting intervals. Solid bars represent physonects; stippled bars represent calycoaphores. Number in parenthesis beneath dive number is total volume searched per dive.

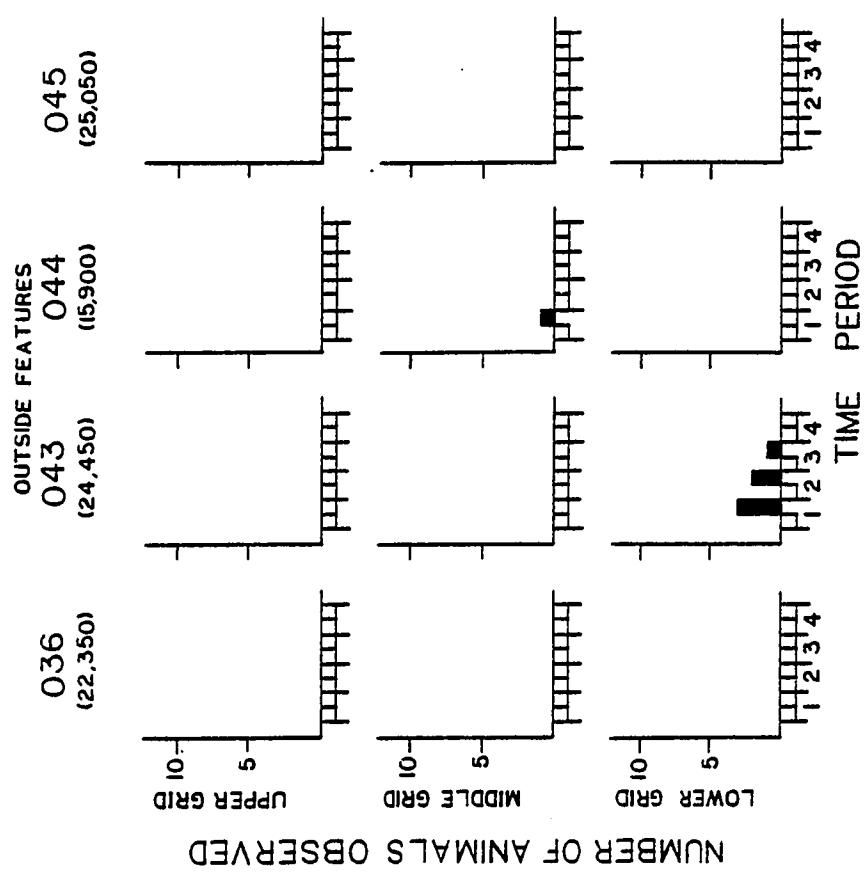


Fig. 11 (continued).

### Discussion

Although the numerical abundance of macrogelatinous zooplankton off the Bahamas was consistently more than an order of magnitude greater on late afternoon dives than on the early morning dives (Biggs et al. 1981), this large deviation was primarily due to the diel changes in density of the two most numerous taxa, the ctenophores and medusae. Examination of the siphonophore abundance data showed no significant differences between dawn-dusk abundance estimates (Wilcoxon Rank Sum test; p-value greater than 0.35 for calycophores, p-value greater than 0.2 for physonects; Hollander and Wolfe 1973).

The relatively large number of abundance estimates for morning-evening dives in both the cyclone and the anticyclone during the fall research cruise in the Gulf of Mexico allows for a similar non-parametric comparison of the dawn-dusk abundance of calycophores or physonects. The Wilcoxon Rank Sum test generates p-values on the order of 0.5 for physonects present in the cyclone and those present in the anticyclone. The same test, when applied to the fall calycophore estimates, results in a p-value of less than 0.057 in the cyclone and greater than 0.6 in the anticyclone. Therefore, there is sufficient evidence to suggest significant dawn-dusk differences for the calycophores in the cyclone only. In the other three cases, there were no significant differences

between dawn-dusk abundance estimates. The latter conclusion is consistent with the situation off the Bahamas.

Since differences between dawn-dusk estimates were not statistically different for physonects during the fall Gulf cruise, a comparison can be made between the observed physonect estimates in the cyclone and anticyclone by lumping the dawn-dusk estimates in each feature. Again using the Wilcoxon Rank Sum test, the resulting p-value was less than 0.05 indicating that physonects were significantly more abundant in the cyclone than the anticyclone during the fall cruise.

Unfortunately, due to the small number of dawn-dusk dives in the cyclone and anticyclone during the other three Gulf cruises, non-parametric comparisons of dawn-dusk estimates were impossible. However, assuming that dawn-dusk differences during the winter Gulf cruise were minimal as during the fall cruise, the lumped physonect estimates in the cyclone and the anticyclone are large enough to also allow comparison using the same test as before. The resulting p-value of 0.10 indicates there were significantly more physonects present in the cyclone than the anticyclone in the winter as well.

Integrated zooplankton displacement volumes to 200 m were determined from MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) samples taken on the spring and summer cruises. During the summer, biomass was

statistically greater in the cyclone. This trend was also apparent from the limited number of spring samples. Similar estimates from fall MOCNESS tows display no statistical difference (Wormuth, personal communication). Biomass estimates, determined from a small number of oblique tows to a depth of 140 m taken during the winter cruise using a 1-m, 333- $\mu$ m zooplankton net, were also greater in the cyclone than the anticyclone.

It is possible that one factor responsible for the observed differences between the cyclone and anticyclone is the temperature-depth signature of the two features (Fig. 12). The upward doming of the isotherms in the cyclone results in cooler, nutrient-rich water being displaced toward the surface. Presumably, the high nutrient levels would be available to the phytoplankton, possibly creating an area of higher productivity. This would not be the case in the anticyclone where isotherms are displaced downward. An examination of the ammonium concentrations in the upper 130 m via a continuously sampling submersible pump does show higher levels in the cyclone during the fall cruise (Johnson 1981). More importantly, a shallower nutricline in the cyclone than the anticyclone on these cruises also lends support to this hypothesis. It is, however, impossible from available data to unequivocally state that productivity was greater in the cyclone as no primary productivity

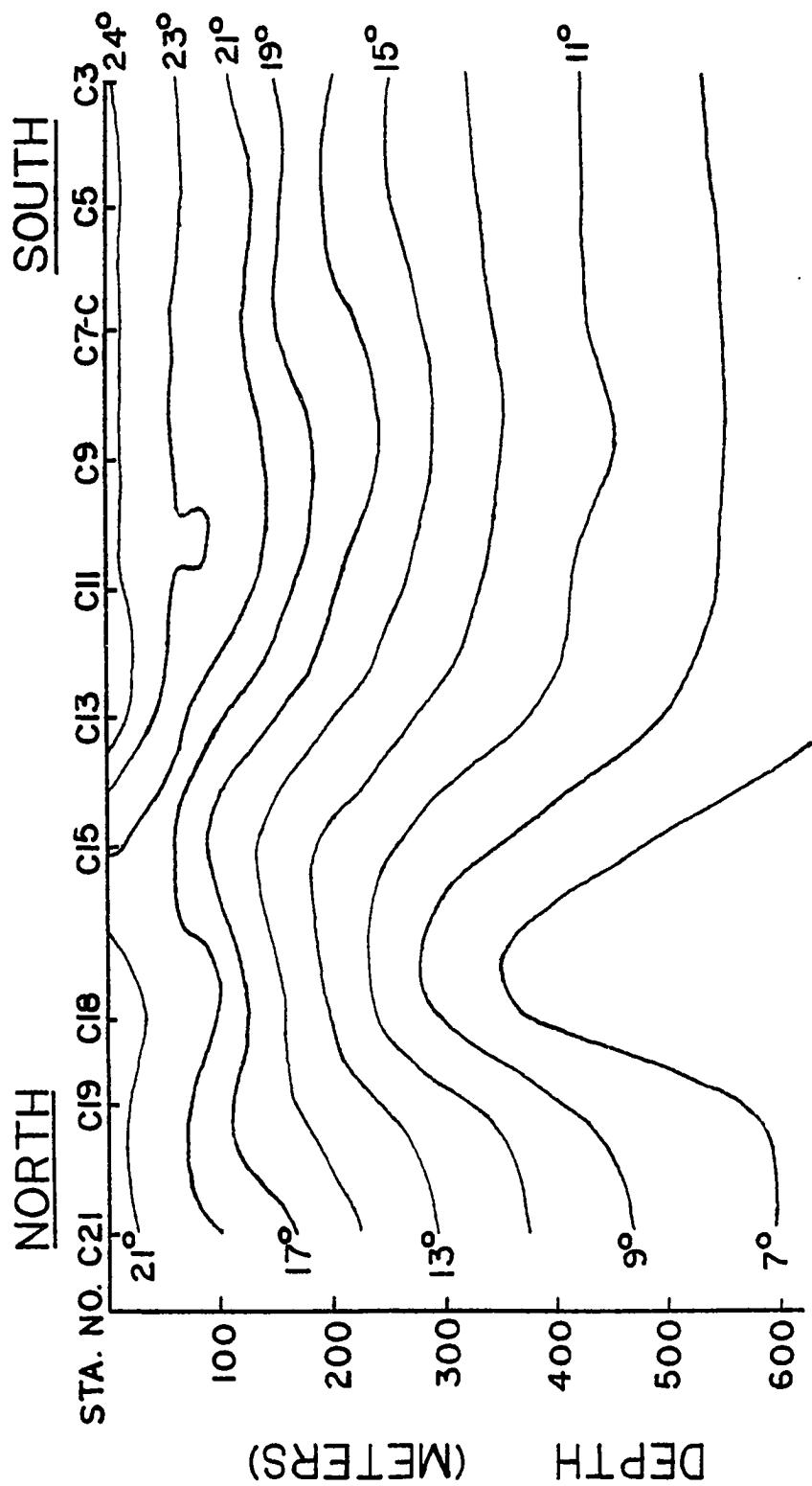


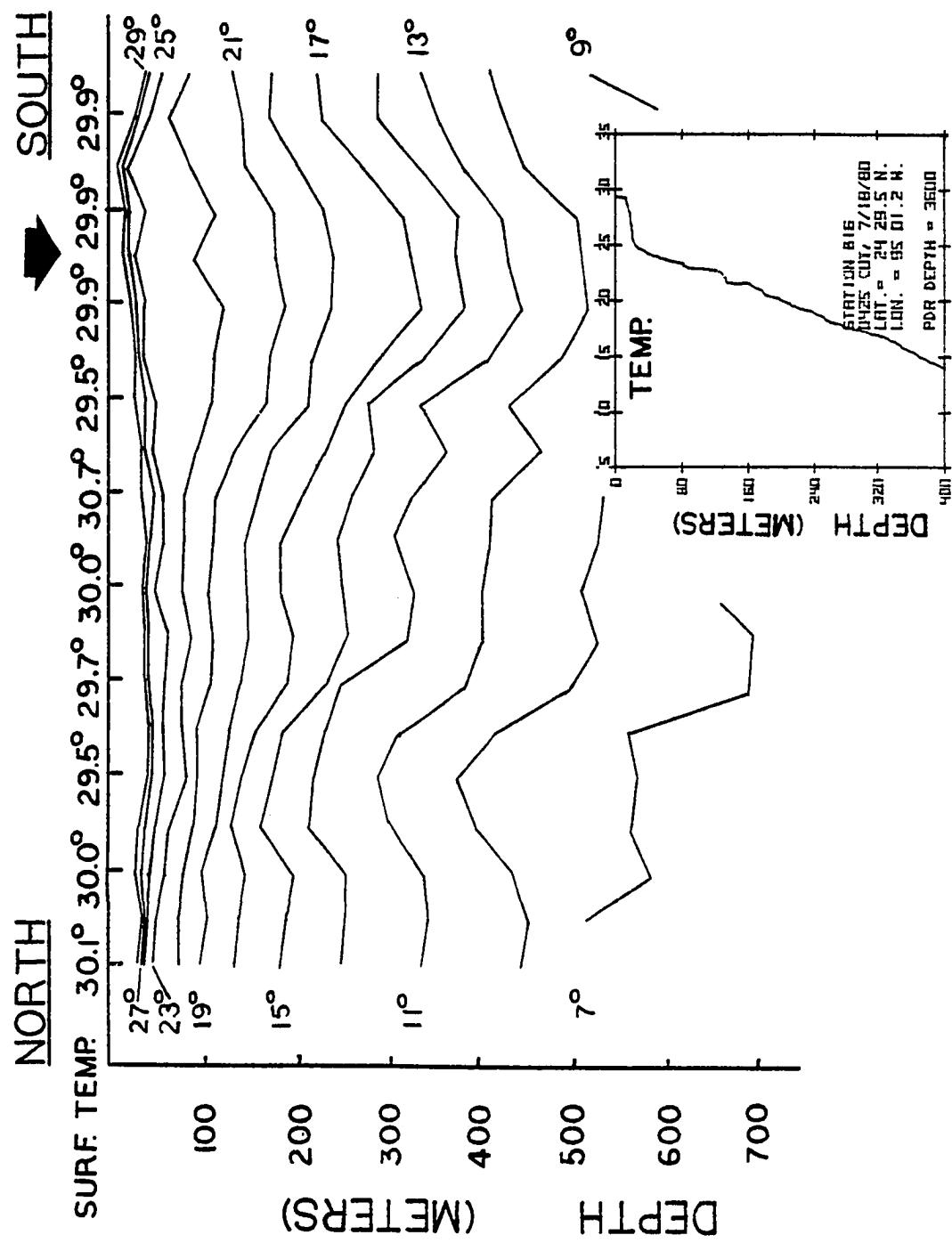
Fig. 12. Temperature section along the  $95^{\circ}\text{W}$  meridian from  $27^{\circ}\text{N}$  to  $22^{\circ}30'\text{N}$  in the western Gulf of Mexico produced from STD data gathered during the spring research cruise, 80-G-1. Section displays typical thermal structure of the northerly cyclone and southerly anticyclone. Redrawn from Brooks and Eble (1982).

experiments were made during this series of cruises. Although the physics of the two features are not well known, entrainment or advection of water from different geographical areas may also enhance the chemical and biological differences recorded in the two features. For example, entrainment of fresher, cooler water from the coastal areas into the cyclone via geostrophic flow could modify the cyclone water mass relative to the anticyclone.

The summer Gulf siphonophore estimates are in sharp contrast to the estimates gathered during the other three cruises. It is likely that the temperature structure of the surface layer contributed to these anomalously low values.

A temperature section along the 95°W meridian in the western Gulf of Mexico from 27°15'N to 24°N was generated from XBT data gathered during the summer cruise (Fig. 13). Present along the entire temperature section is a very warm 29°-30°C surface layer. The inserted XBT trace, taken at the anticyclonic sampling station (designated by the arrow), depicts a strongly stratified warm surface layer. It seems reasonable to speculate, therefore, that during the hot summer months, the difference apparent on the previous cruises relating to surface siphonophore abundance in the cyclone and anticyclone was masked due to the very warm, widespread, strongly stratified surface layer.

Fig. 13. Temperature section along the 95°W meridian from 27°15'N to 24°N in the western Gulf of Mexico produced from XBT data gathered during the summer research cruise, 80-I-6. Inserted XBT trace taken at the anticyclonic station (designated by arrow).



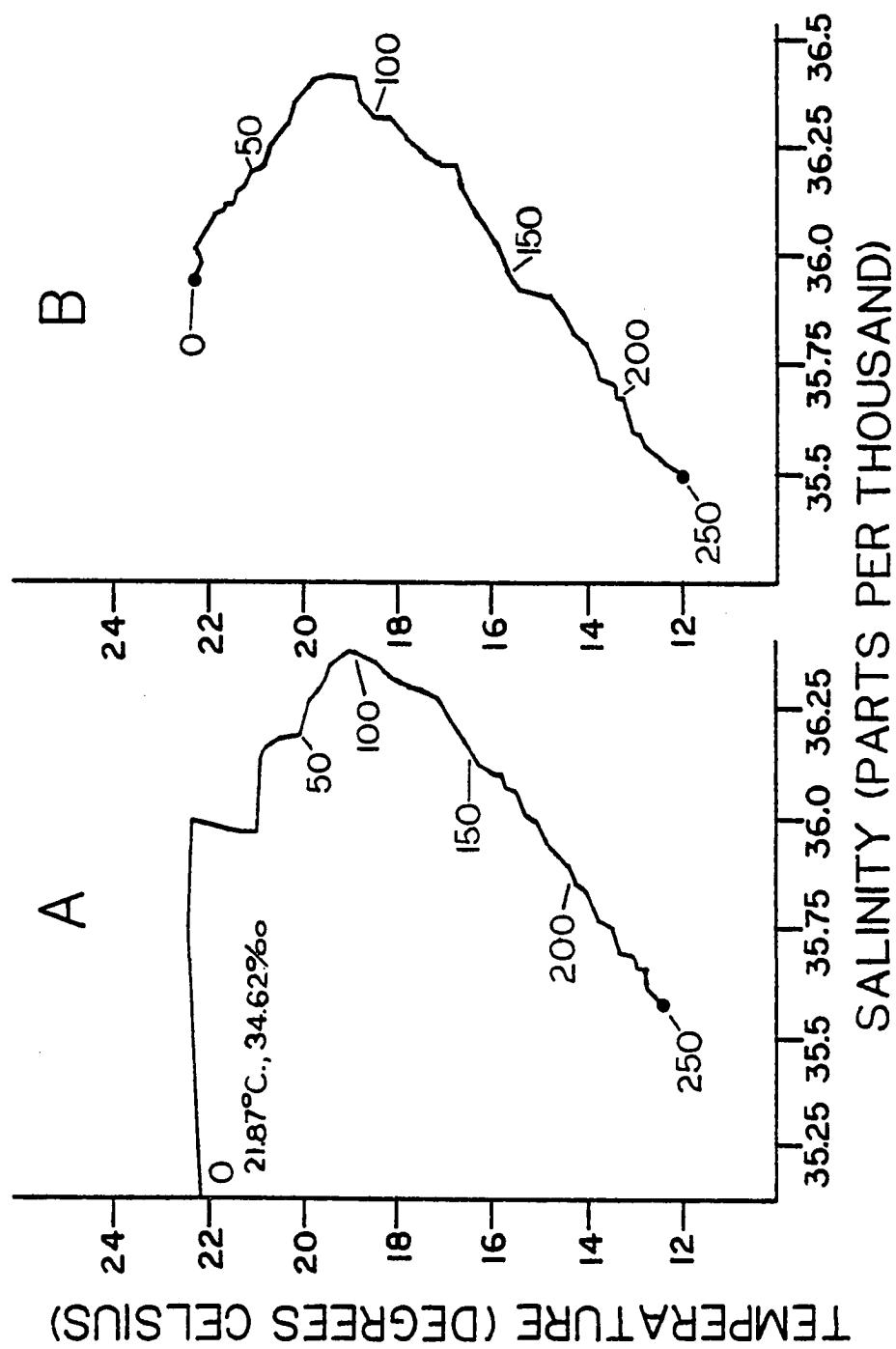
Other investigators have cited relationships between siphonophore distribution and temperature. Alvarino (1971) related the distributional boundaries of siphonophores in the Pacific to hydrographic parameters measured during the sampling cruises. She obtained correlations in most cases with the distribution of the isotherms at 200 m. Specifically, she concluded that "the position of certain 200 m isotherms tends to agree with the limits of the ranges" of the siphonophore species. Pugh (1975), however, in his examination of the distribution of siphonophores in the North Atlantic, has concluded that there was some interrelationship between the physical characteristics of the separate water masses and the composition of the siphonophore populations found in each. He believes that the water mass, as defined by temperature/salinity/depth, and not temperature alone, may have some relationship to the composition of the siphonophore population. The east-west distributional differences which he observed using factor analysis, however, were most pronounced for deep living forms. Finally, in Musayeva's (1971) examination of the siphonophores of the eastern Indian Ocean, she concluded that they lived mainly in the thermocline and other regions where the temperature changed rapidly with depth.

The spring siphonophore abundance estimates, presented above, remain unsettling since physonect

estimates in the cyclone were very low and those in the anticyclone much higher (Table 2, p. 23). Although my sampling of the anticyclone and cyclone was limited to one and two dives, respectively, there is no obvious explanation for this observation. On the spring cruise there was no well-developed warm surface layer similar to that present in the summer and, as stated earlier, integrated zooplankton biomass determinations to 200 m in the spring were greater in the cyclone than anticyclone (Wormuth, personal communication). Fig. 14 displays the temperature-salinity curves generated from STD data taken at the drogued biological sampling station in the cyclone where the spring cyclonic dives occurred. The curve on the left is an STD cast made within 8 hours after we first occupied the station, while that on the right is a cast made as we were preparing to leave the station, 21 hours later. The interesting aspect of these two curves is the presence of a relatively fresh surface layer (0-20 m) which appears to deteriorate with time. Brooks (personal communication) believes that a surface lens of fresher, cooler water from the shelf-slope region may have been advected eastward into the cyclone. This fresher layer may have influenced the local surface physonect distributions.

With respect to species of siphonophores which have been recorded in the Gulf of Mexico, Alvarino's (1971)

Fig. 14. Temperature-salinity diagrams compiled from two STD casts occurring on the spring research cruise, 80-G-1, at the cyclonic sampling station. A: T-S curve from an STD cast taken 8 hours after the ship occupied the station. B: T-S curve from an STD cast taken just before leaving the sampling station (21 hours later).



monograph dealing with siphonophores in the Pacific also includes extensive location lists for various species of siphonophores around the world collated from the literature. Four species of the genus Sulculeolaria have been recorded as occurring in the Gulf of Mexico (Alvarino 1969 as cited by Alvarino 1971; Sears 1954). Moore (1953) has also recorded Sulculeolaria monica and S. biloba in the waters of the Florida Current. Alvarino's compilation also includes two species of Agalma present in the Gulf.

However, a dissertation by Phillips (1972), entitled "The pelagic Cnidaria of the Gulf of Mexico: Zoogeography, ecology and systematics," includes perhaps the most complete species list for siphonophores in the Gulf of Mexico. Phillips sorted and identified the cnidarians found in samples collected along the coast and in the open Gulf. Because of the various types of sampling gear used and the fragmented nature of the collected specimens, he made no attempt to quantify the data. From his samples, he identified eight species of physonect and 35 species of calycophores.

A comparison of the physonect genera Phillips (1972) identified and the genera observed in the surface waters during this study shows four genera in common. They are Nanomia, Agalma, Cordagalma, and Physophora. In addition, Phillips observed physonects of the genera Erenna,

Halistemma, Marrus and Bargmania. Phillips recorded all these genera, with the exception of one, in the epipelagic zone of the open Gulf. Physophora hydrostatica was observed in a bathypelagic sample. We viewed Physophora sp. in the surface waters as well. The physonects Athorybia and Forskalia were also present in the surface waters during this study and were not recorded in the samples that Phillips examined. Indeed, the genus Forskalia was the most numerous physonect on the fall and winter cruises, although none were viewed during the spring cruise.

The fact that Phillips (1972) did not record Forskalia in his samples may be due in part to the rather delicate nature of this siphonophore. The nectophores of Forskalia are very sticky and consequently Forskalia may be easily abraded into an amorphous gelatinous mess as it is funnelled into the cod end of a sampling net.

Phillips' (1972) record of calycophores includes Rosacea cymbiformis and three species of Sulculeolaria present in the Gulf. These two genera were also seen during this study. In addition to Rosacea cymbiformis, R. flaccida (Biggs et al. 1978) was also present in the surface waters of the Gulf.

On dives when siphonophores were abundant ( $>10/25,000 \text{ m}^3$ ), the range in the number of animals observed during each 5-minute counting interval rarely exceeded threefold.

A similar situation is reflected in the siphonophore abundance data from the Bahamas. Since during the grid dives in the Gulf of Mexico the divers transversed an average of 75 m (range: 40-101) per 5-minute counting interval, the above observation supports our previous contention, generated from data gathered along a transect of the North Atlantic, that patch-creating processes operate on these organisms at scales markedly greater (or markedly smaller) than tens-of-meters or tens-of-minutes (Biggs et al. 1981). Similarly, low variability in siphonophore abundance also occurred between dives in the same area. During the Gulf of Mexico dives, the number of siphonophores observed per dive within any group of dives performed on consecutive days at a drogued cyclonic or anticyclonic sampling station generally did not vary by more than threefold. In the surface waters of the North Atlantic, we also found the differences in the abundance estimates for siphonophores between dives separated by less than 40 miles and 5 hours to be low, displaying a variation of about 25% (Biggs et al. 1981).

When there were enough sightings to look for vertical differences, there was no clear vertical distributional pattern within the upper 15 m, at least on a scale of 5 m. This is not surprising since most physical and chemical properties (with the important exceptions of light and turbulence) rarely display significant gradients within

the upper 15 m in an oligotrophic environment such as the open ocean.

A comparison of published siphonophore densities with estimates made during this study immediately highlights the rather limited number of estimates available in the literature. Table 6 summarizes the abundance estimates from a number of locations. As one might expect, the density of siphonophores falls as one moves from the coastal environment to the oceanic region.

Polygastric and eudoxid stages of Muggiaeaa atlantica (a calycophore siphonophore) ranged from 9 to 11 per  $m^3$  in Friday Harbor, Washington (Purcell, 1981d), whereas physonect siphonophores ranged from 0-80 per 25,000  $m^3$  in this study. We observed an average physonect density in the North Atlantic of 11 per 25,000  $m^3$  (Biggs et al. 1981). This is a value within the range of physonect densities observed in this study.

Bias in our abundance estimates could arise from an inconsistent motoring rate or from divers missing animals and not counting them during the grid dives. The uniformity of the motoring rate is measurable ( $s/\bar{x}$ ), and averaged 16.6% in the Gulf of Mexico cruises (Table 7). The error in volume viewed during the Bahamas dives was calculated to be about 8% (Biggs et al. 1981). Both of these figures are lower than the estimated 20% error recorded by Biggs et al. (1981) in the North Atlantic

Table 6. Summary of siphonophore abundance estimates from published sources.

Location	Siphonophore	Density	Reference	Comments
Friday Harbor, Washington	Polygastric colonies of <u>Muggiaeae atlantica</u>	0.6-2.7 m <sup>-3</sup>	Purcell, in press a	Estimated from net tows, no day or night abundance differences
	Eudoxid phase of <u>Muggiaeae atlantica</u>	8.0 ± 3.8 m <sup>-3</sup>		
Surface waters of Santa Catalina Is.,	Polygastric colonies of <u>Sphaeronectes gracilis</u>	6.6 10 m <sup>-3</sup> : Day 11.6 10 m <sup>-3</sup> : Night	Purcell, in press b	Estimated from net tows to 35 m
	Eudoxid phase of <u>S. gracilis</u>	4.6 10 m <sup>-3</sup> : Day 9.5 10 m <sup>-3</sup> : Night		
	Polygastric colonies of <u>Muggiaeae atlantica</u>	6.2 10 m <sup>-3</sup> : Day 6.3 10 m <sup>-3</sup> : Night		
	Eudoxid phase of <u>M. atlantica</u>	10.0 10 m <sup>-3</sup> : Day 15.7 10 m <sup>-3</sup> : Night		
111°15'W, 25°45'N near Puerto Escondido, Baja Calif. Sur, Mexico	<u>Rhizophysa eyenhardti</u>	0-1.8 m <sup>-3</sup> : Day	Purcell, 1981c	Estimated from <u>in situ</u> observation
Gulf of Maine	<u>Nanomia cara</u>	0.1-8.0 m <sup>-3</sup> : Day	Rogers et al., 1978	Estimates made with submersible Nekton Gamma in upper 200 m
North Atlantic, along 40°N parallel	Temperate Region Large calyphores Physonects	25-75 25,000 m <sup>-3</sup> 0-525 25,000 m <sup>-3</sup>	Biggs et al., 1981	Estimated from <u>in situ</u> SCUBA observa- tions, all estimates were made in the daytime
	Temperate-Subtropical Transition Region Large calyphores Physonects	0-75 25,000 m <sup>-3</sup> 0-125 25,000 m <sup>-3</sup>		
	Subtropical Region Large calyphores Physonects	0-200 25,000 m <sup>-3</sup> 0-25 25,000 m <sup>-3</sup>		

Table 7. Data summary of the number of times the motoring rate was monitored during each grid dive, the uniformity during the dive of the motoring rate, and the volume searched per dive on each of the four cruises to the Gulf of Mexico.

Cruise	Uniformity of Motorizing Rate	Time Motorizing Rate Monitored/Dive	Average Volume Searched/Dive (m <sup>3</sup> )
80-G-1	11% (range 6-17)	15	22,400
80-I-6	29% (range 18-36)	14	22,600
80-G-11	16% (range 10-28)	8	22,600
81-G-2	6% (range 5-8)	14	22,300
All cruises	16.6% (range 5-36)	12	22,500

<sup>1</sup> Defined as the coefficient of variation (mean motorizing rate divided by the standard deviation).

where no motor was used during the dives and the Zodiac drifted with the current.

Note that the uniformity of the motoring rate varied between cruises. Weather, sea state, and operator panache influence motoring rate. Since different individuals had primary responsibility for operating the Zodiac during each cruise, a portion of the variability can probably be attributed to individual operator flair in controlling the raft. Note that the average volume viewed during the Gulf of Mexico dives was very similar, about 22,500 m<sup>3</sup> per dive, compared with an average of 22,000 m<sup>3</sup> viewed during the Bahamas dives. This in situ abundance estimate technique resulted in a volume viewed which was 22X the typical 1,000 m<sup>3</sup> volume filtered by a conventional zooplankton net tow. Consequently, motoring the Zodiac during the grid counts served two important functions: it reduced the error in the abundance estimates by providing a more uniform rate of grid movement through the water and it allowed the divers to view relatively large volumes of water.

Increasing the volume viewed beyond 23,000 m<sup>3</sup> per dive would have required that (1) the Zodiac, and consequently the divers, move through the water faster or (2) the dive be extended beyond 20 minutes. Extending the dives would have been difficult as the diver counting the animals in the lower grid would risk running out of

air. Speeding the Zodiac up would only accelerate the use of air and require early termination of the dive. In addition, increasing the motoring rate would have increased the incidence of leg cramps among the divers since the divers would have had to swim harder to keep up and again would have required early termination of the dive.

A second source of bias in these estimates is diver counting error. Underestimates could have resulted from divers missing animals drifting through the grid, as alluded to earlier with respect to small calyptophores. Conversely, counting an animal more than once would result in overestimates of the density. To reduce the error due to different divers participating on different dives, an effort was made to allow the same small group of divers to participate on all the grid dives. In addition, divers with poor eyesight used masks fitted with corrective lenses. While it is not possible to assess this second source of bias, the density of macro-gelatinous animals was relatively low and the divers generally had enough time to adequately survey the whole grid and obtain an accurate count. On the few occasions when the density of the siphonophores was very high, the 5 m x 5 m reference arrangement was too large for the divers to comfortably cover the entire grid. In these situations, a smaller reference area, such as a ring

with area 1 m<sup>2</sup> (Swanberg 1974; Purcell 1981c) suspended within each of the grids, would be preferable.

CHAPTER III  
FORAGING OF PHYSONECT SIPHONOPHORES  
IN THE FOOD-POOR ENVIRONMENT OF THE OPEN OCEAN

Introduction

Quantitative predation studies of gelatinous tentaculate zooplankton have included investigations of ctenophores (Rowe 1971; Anderson 1974; Walter 1976; Reeve et al. 1978), medusae (Clifford and Cargo 1978) and siphonophores (Purcell 1981d; Purcell and Kremer in press). Neritic tentaculate ctenophores, such as Pleurobrachia, have been studied most intensively. Researchers working in the laboratory reported that prey capture by these planktivores was linearly proportional to food concentrations over a wide range of prey densities (e.g.  $1 \times 10^3$  -  $3 \times 10^6$  prey  $m^{-3}$ ; see Rowe 1971; Anderson 1974; Reeve et al. 1978).

In this chapter, the ability of the oceanic physonect siphonophore Forskalia to feed or forage on natural prey is investigated. Forskalia is a "colonial" jellyfish (sensu Totten 1965) which trails a long and ramosc tentacle from each of its multiple polyps (gastrozoooids). The tentacles originate basally from the gastrozoooids, which in this genus are located on long pedicles radiating from the central stem of the animal (Fig. 15).

Fig. 15. In situ photograph of Forskalia sp.



As Reeve et al. (1978) have correctly pointed out, the terms "water clearance," "filtration" and "grazing" rate do not accurately describe the feeding behavior of tentaculate gelatinous carnivores. Therefore, I have used the term "foraging" rate to describe the feeding behavior of the Forskalia test species.

Foraging can be defined as "to wander in search of food." Although Forskalia is an ambush predator, Forskalia does wander in the sense that it periodically contracts its tentacular network, swims to a new location in the ocean, and then resets its fishing network of tentacles. Biggs (1977a) has referred to the fishing network of siphonophores as analogous to the web of an orb-weaving spider. While the analogy is correct in that both animals depend on an ambush prey capture strategy, the siphonophore can rapidly move the spatial location of its original prey-ensnaring "web" by swimming or wandering a short distance.

Unlike previous experimental studies of oceanic tentaculate carnivores in which prey capture behavior was investigated in small containers and/or at abnormally high prey densities, the present study was designed to characterize the ability of Forskalia to forage at low ambient prey densities. Specifically, copepod prey were introduced to siphonophores over a range of densities which approximated daytime abundances in open-ocean

surface waters.

#### Materials and Methods

Forskalia edwardsi and F. tholoides were collected in situ in hand-held jars from subtropical surface waters of the western Gulf of Mexico. Captured siphonophores were transferred aboard ship from the 1-liter collecting jars to larger tanks to minimize their contact with container surfaces.

Forskalia was selected as the predator in these experiments because it was the most numerous physonect encountered. Also, while other common physonects (e.g. Nanomia, Physophora, Agalma, and Athorybia) frequently settled to and rested on the bottom of aquaria, Forskalia floated in the mid-water of the aquaria and did not appear to be adversely affected behaviorally by hand collection or confinement. Forskalia was rarely active (unless disturbed by turbulence or the flash of a camera strobe light) and hung for tens of minutes at a time suspended in a fishing posture.

Oceanic copepods, including species of Euchaeta, Rhincalanus and Candacia, were used as prey in these experiments. The copepods were captured every night during the cruises by oblique plankton tows to 200 m with a 333-um mesh, 1-m zooplankton net fitted with a non-perforated cod end. Analyses of the gut contents of

Forskalia gastrozooids have indicated that over 80% of Forskalia's natural prey are copepods (Purcell 1980). Purcell (1980) reported that copepods less than 2 mm in length could be found in the feeding polyps of field-collected Forskalia. Fig. 16 displays the size range of the prey used in these experiments.

Three criteria were specified in designing the feeding tanks used in this study. First, preliminary observations using a large, cubic tank, with a volume of 1,000 liters, had indicated that both prey and predator congregated in the corners of the tank, suggesting that both behavior and distribution were influenced by a tank of cubic shape. Consequently, the design minimized 90° angles within the tank. Secondly, my design minimized the animals' contact with the tank's surfaces. Oceanic gelatinous zooplankton are delicate and usually contact no surfaces other than the air-sea interface in their natural environment. This criterion was met by designing a tank with a large volume and a reduced surface area/volume ratio. Finally, the tanks had to be practical to work with at sea on a rolling ship.

Consequently, the feeding tanks used in this study were 55-gallon drums that were fitted with a basal, internal, hemispherical fiberglass shell with drain (i.e. test-tube in shape). Each tank had a volume of 177 liters.

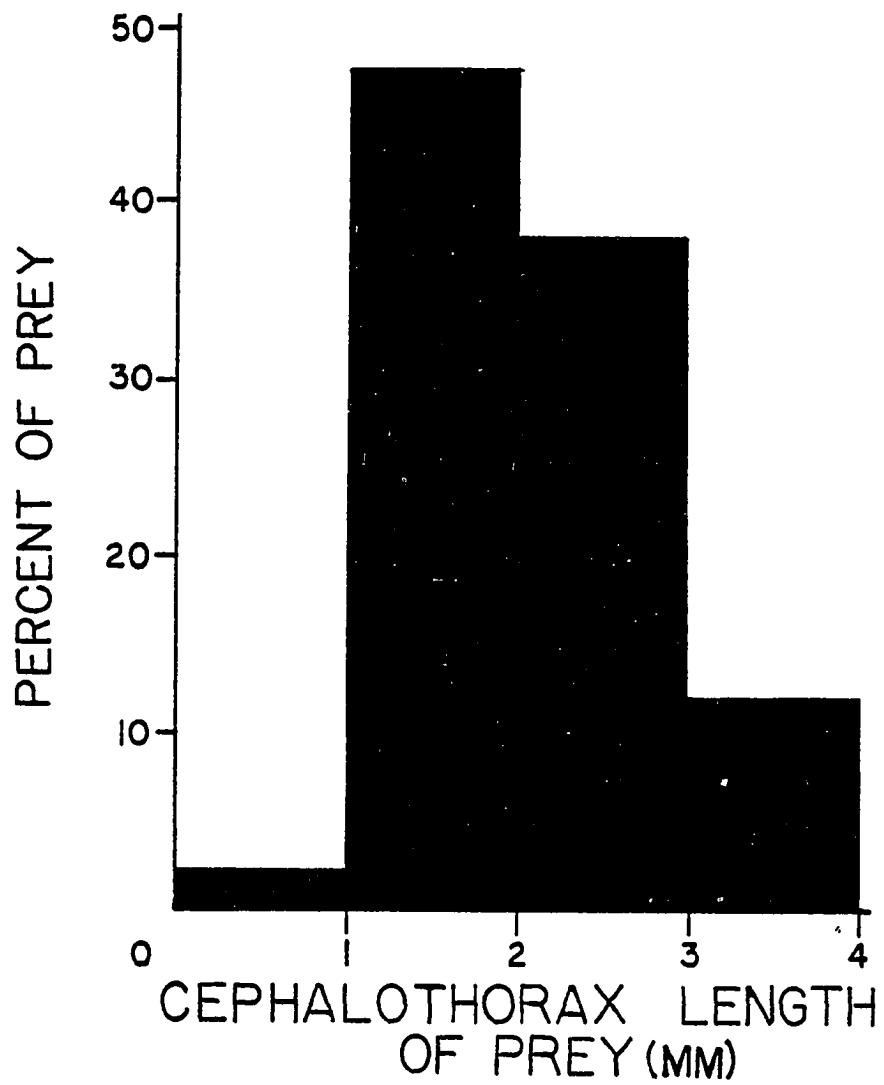


Fig. 16. Size distribution of the oceanic copepods used in the last seven control experiments of Table 8. This distribution curve is representative of the size of prey used in subsequent experiments.

Two sets of tanks were built. One consisted of four tanks and the other of two (six tanks total). Each group was constructed within a fiberglassed wooden box through which ambient temperature surface seawater could be circulated. This procedure kept the water within the tanks at constant, ambient surface temperature. An overhead awning provided additional protection against temperature change.

Two tanks in the set of four were damaged beyond repair during a severe storm in the spring of 1980 on research cruise 80-G-1. Consequently, during the last three research cruises, only four 177-liter tanks were used.

In addition to these 177-liter tanks, two larger plastic tanks were purchased. These tanks were cylindrical with conical bottoms and had a working volume of approximately 1,000 liters.

All tanks were initially filled with surface seawater pumped through a 35-um filter (Sears Cartridge-type Filter System with Extra-fine Cellulose Cartridge) and all experiments were conducted in the dark (i.e. lids on the drums) to prevent visual orientation of the prey.

To determine the prey capture rate, a predetermined number of prey and one predator were released in each large volume feeding chamber. After 2-8 hours, the predator was removed and the water in the tank was

drained basally through a 64 um Nitex sieve to collect the remaining prey. The prey retained on the sieve were preserved in 5% buffered formalin for enumeration ashore. In reporting my data, prey capture rates have been standardized as number of prey ingested/hour.

The range of prey densities was chosen to approximate those in daytime open-ocean surface waters. Howey (1976) estimated the calanoid copepod population of the surface waters of the open Gulf of Mexico at  $10^1$  animals  $m^{-3}$ , whereas Deevey and Brooks (1971) estimated the daytime copepod and total crustacean density in the upper 500 m of the Sargasso Sea at  $10^2$  animals  $m^{-3}$ . A geometric series of prey densities was used in these experiments which included 452 copepods  $m^{-3}$  (80 per tank), 226, 113 and 51 copepods  $m^{-3}$ .

Because of the low prey densities utilized in this study (a density of  $51/m^3$  allowed only 9 copepods per small tank), the accurate sorting of prey was essential. Therefore, prior to introduction, prey had to be hand-sorted at sea under a dissecting microscope. The prey density was never depleted to < 40% of the initial concentration during the course of these experiments.

At the end of the experiment, the predator was bucketed from the feeding tank. After recording its size (number of gastrozooids), the predator was frozen for subsequent determination of total protein content

(Lowry et al. 1951). In all cases, protein was analyzed within one month of collection. Fig. 17 illustrates the relationship between siphonophore protein and the number of gastrozooids.

The very low prey densities used in these experiments mandated that prey remaining in the feeding tank at the termination of the experiment be retrieved with 100% efficiency. It was also necessary to confirm that the prey were distributed in approximately random fashion in the tanks. To monitor prey recovery and distribution, a series of 13 control experiments (no predator) was performed. Bottom, then top, halves of the small tanks were drained separately so that the number of prey in each half could be determined (Table 8). Dye studies indicated that, by draining the tank carefully, mixing between the two halves could be minimized.

In theory, the use of large volume tanks should allow the distribution of individuals in the tanks to change with time while the population remains relatively random, thereby permitting the prey to aggregate and disperse, mimicking the natural environment. Table 8 confirmed that there was a relatively random distribution of prey in the tanks (a 50/50 split in the number of prey between the top and bottom halves). Comparing the mean number of prey in the bottom half of the tank with the expected value, 20 (1/2 of 40), resulted in no

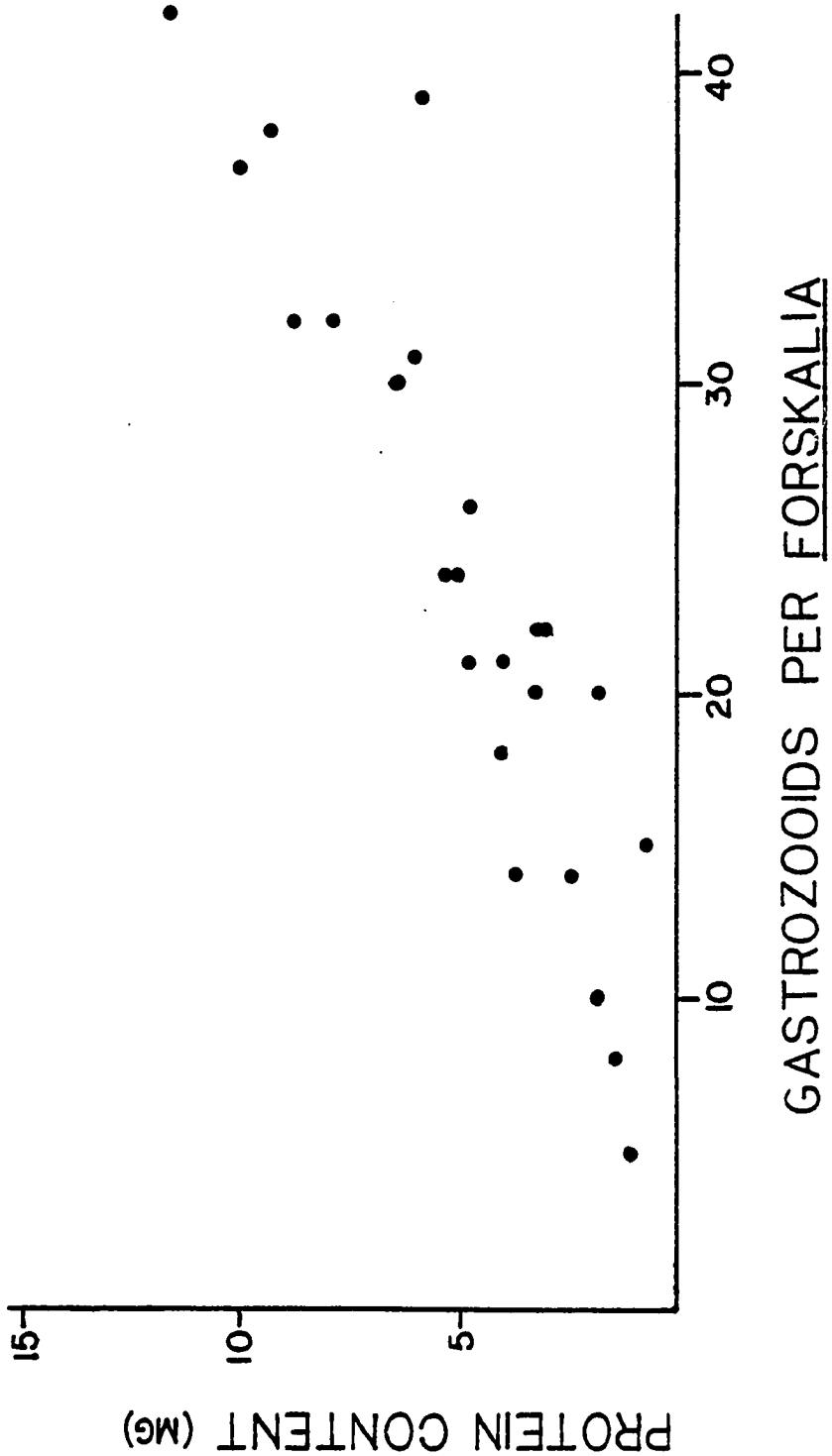


Fig. 17. Protein content versus gastrozooid number for *Forskalia* sp.

Table 8. Efficiency of recovery of prey from, and their distribution within, the feeding tanks in control experiments (no predator introduced).

Duration of Experiment (hrs)	Number of Prey Introduced	Number of Prey Recovered	Distribution in			Prey Used
			Top vs.	Bottom	Halves of Tank	
2	10	10	n.a.	n.a.	n.a.	oceanic copepods
2	10	10	n.a.	n.a.	n.a.	oceanic copepods
1	40	40	n.a.	n.a.	n.a.	<u>Acartia tonsa</u>
1	40	40	30/10	30/10	30/10	<u>Acartia tonsa</u>
1	40	40	21/19	21/19	21/19	<u>Acartia tonsa</u>
3/4	40	40	28/12	28/12	28/12	<u>Acartia tonsa</u>
1 1/2	40	40	18/22	18/22	18/22	oceanic copepods
2 1/4	40	40	24/16	24/16	24/16	oceanic copepods
2 1/4	40	40	9/31	9/31	9/31	oceanic copepods
2 1/4	40	40	15/25	15/25	15/25	oceanic copepods
2	40	40	17/23	17/23	17/23	oceanic copepods
2	40	40	23/17	23/17	23/17	oceanic copepods
2	40	40	10/30	10/30	10/30	oceanic copepods

statistical difference (student's t-test,  $\alpha=0.05$ ).

To evaluate whether the size of the predators used in this study influenced their prey capture rate, the percentage of prey consumed over a four-hour period was plotted against the protein content/predator (Fig. 18) and the number of gastrozooids/predator (Fig. 19).

### Results

Within the limited size range of siphonophores used in this study (as defined by protein content or number of gastrozooids), larger size predators did not consume significantly greater percentages of prey. Linear regressions of prey consumed as a function of either mg protein (Fig. 18) or number of gastrozooids (Fig. 19) produced correlation coefficients ( $r^2$ ) of less than 0.05.

Table 9 illustrates the results of one of my four groups of experiments using the smaller tanks, those conducted using a prey density of 226 copepods  $m^{-3}$ . When data from all four groups of experiments (using the four different prey densities) are presented graphically (Fig. 20), it is evident that the number of prey ingested tracked prey density. For prey densities greater than or equal to about 200 copepods  $m^{-3}$ , the median number of prey ingested was directly proportional to prey density. Prey were seldom captured at a density

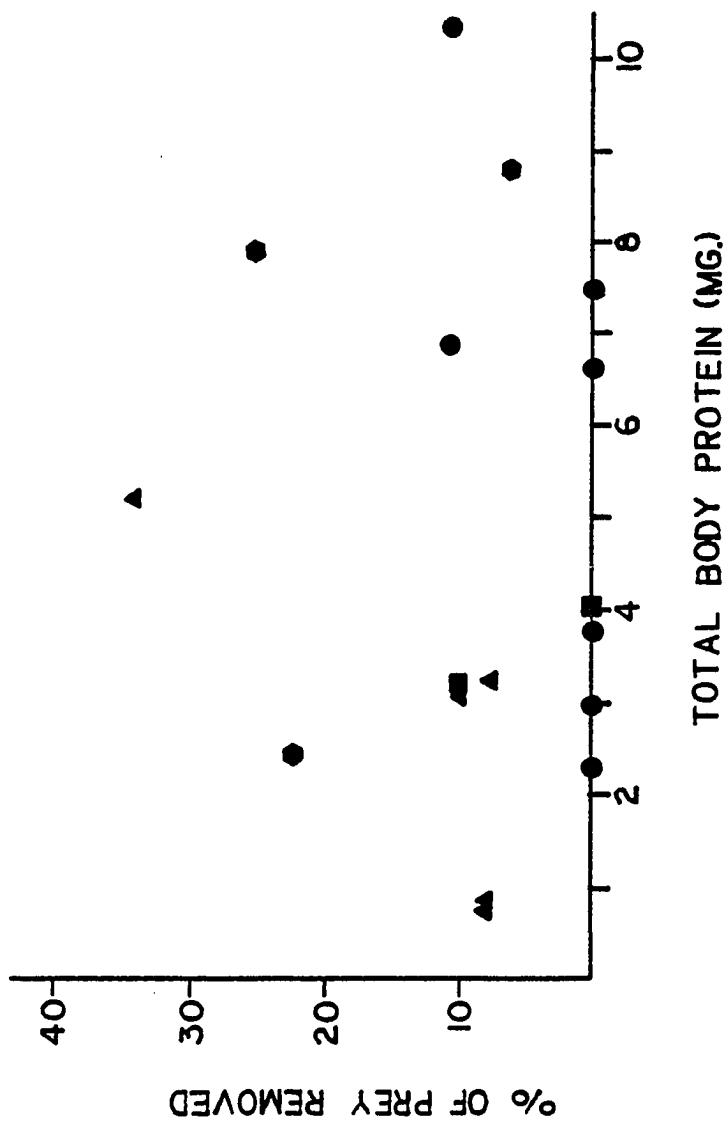


Fig. 18. Size of predator, as defined by protein content versus percentage of prey captured, over an experiment interval of 235-260 minutes ( $\bullet$  - 51 copepods- $m^{-3}$ , ■ - 113 copepods- $m^{-3}$ , ▲ - 226 copepods- $m^{-3}$ , ◆ - 452 copepods- $m^{-3}$ ).

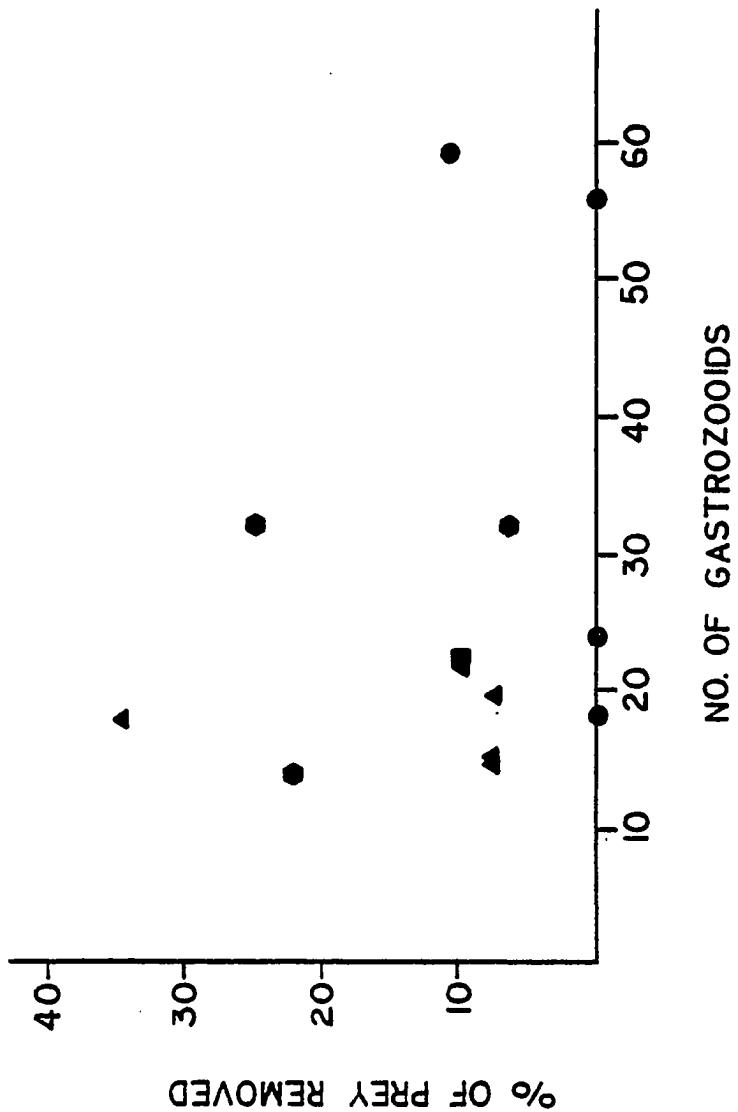
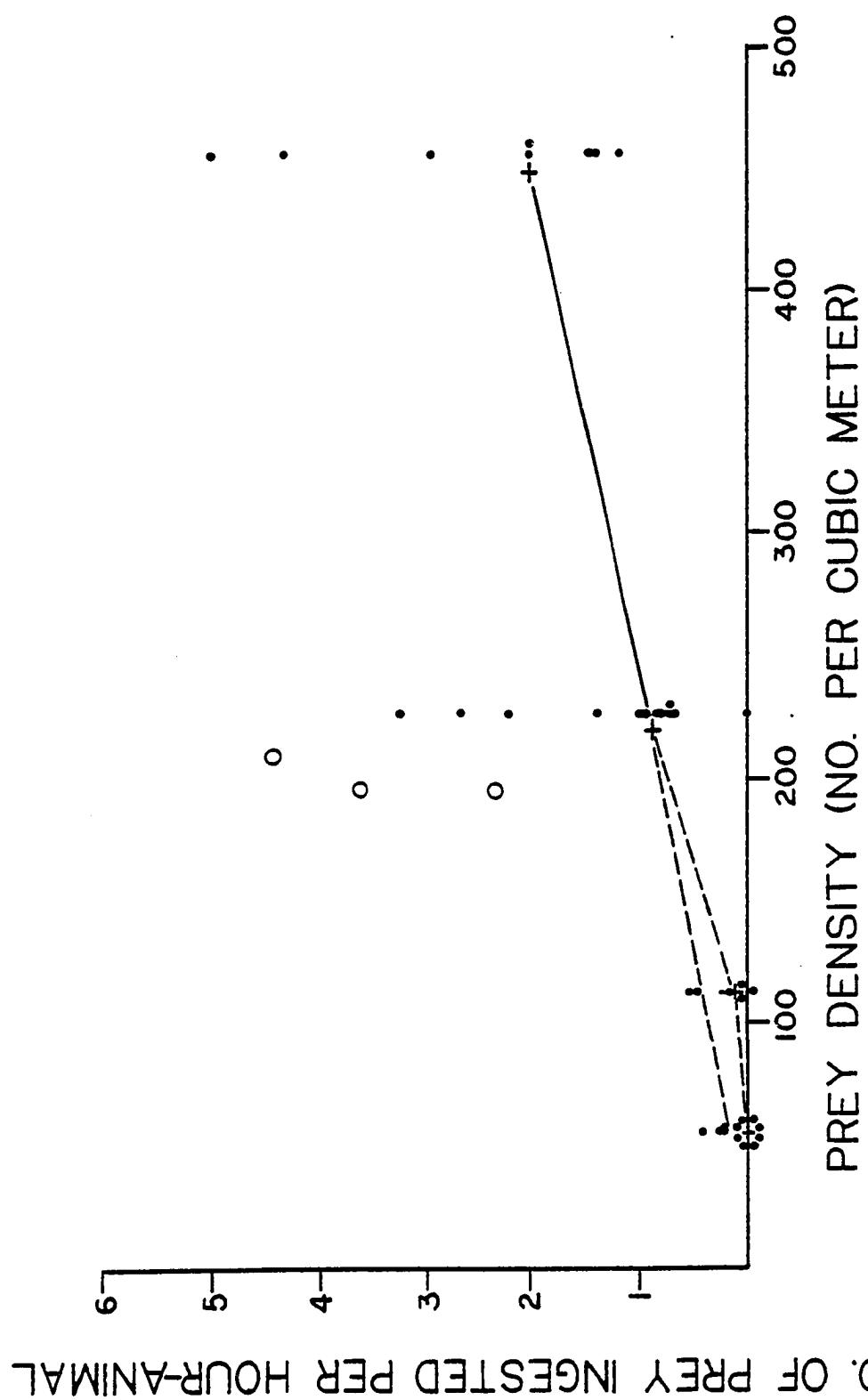


Fig. 19. Size of predator, as defined by gastrozooid number versus percentage of prey captured, over an experiment interval of 235-260 minutes ( $\bullet$  - 51 copepods- $m^{-3}$ ,  $\blacksquare$  - 113 copepods- $m^{-3}$ ,  $\blacktriangle$  - 226 copepods- $m^{-3}$ ,  $\blacklozenge$  - 452 copepods- $m^{-3}$ ).

Table 9. Predation by Forskalia upon oceanic copepods introduced at a density of 226 prey/m<sup>3</sup>. Experiments were performed in the 177-liter tanks.

Duration of Experiment	Number of Prey Consumed	Percent of Prey Consumed	Number of Prey Consumed/Hour	Size of Predator (mg protein)
4 hr	3	8	.8	3.2
6 hr	16	40	2.7	3.7
4 hr	3	8	.8	.7
4 hr	4	10	1.0	3.1
5.2 hr	5	13	1.0	4.8
5.8 hr	5	13	.9	3.2
4.2 hr	3	8	.7	.7
7.8 hr	7	18	.9	1.1
2.3 hr	5	13	2.2	19.5
2.1 hr	0	0	None	--
4 hr	13	33	3.3	--
5 hr	7	18	1.4	10.3

Fig. 20. Number of copepods ingested per hour at each prey density. Crosses represent median values for small tank experiments. (● - experiments run in 177-liter tanks, ○ - experiments run in 1,000-liter tanks.) See text for explanation.



of  $51 \text{ m}^{-3}$ .

The median foraging rate or volume cleared per hour is shown in Fig. 21. Since the length of the foraging experiments was rather short and the percentage of prey consumed low, the foraging rate was determined by dividing the number of prey ingested  $\text{hour}^{-1}$  by the prey density.

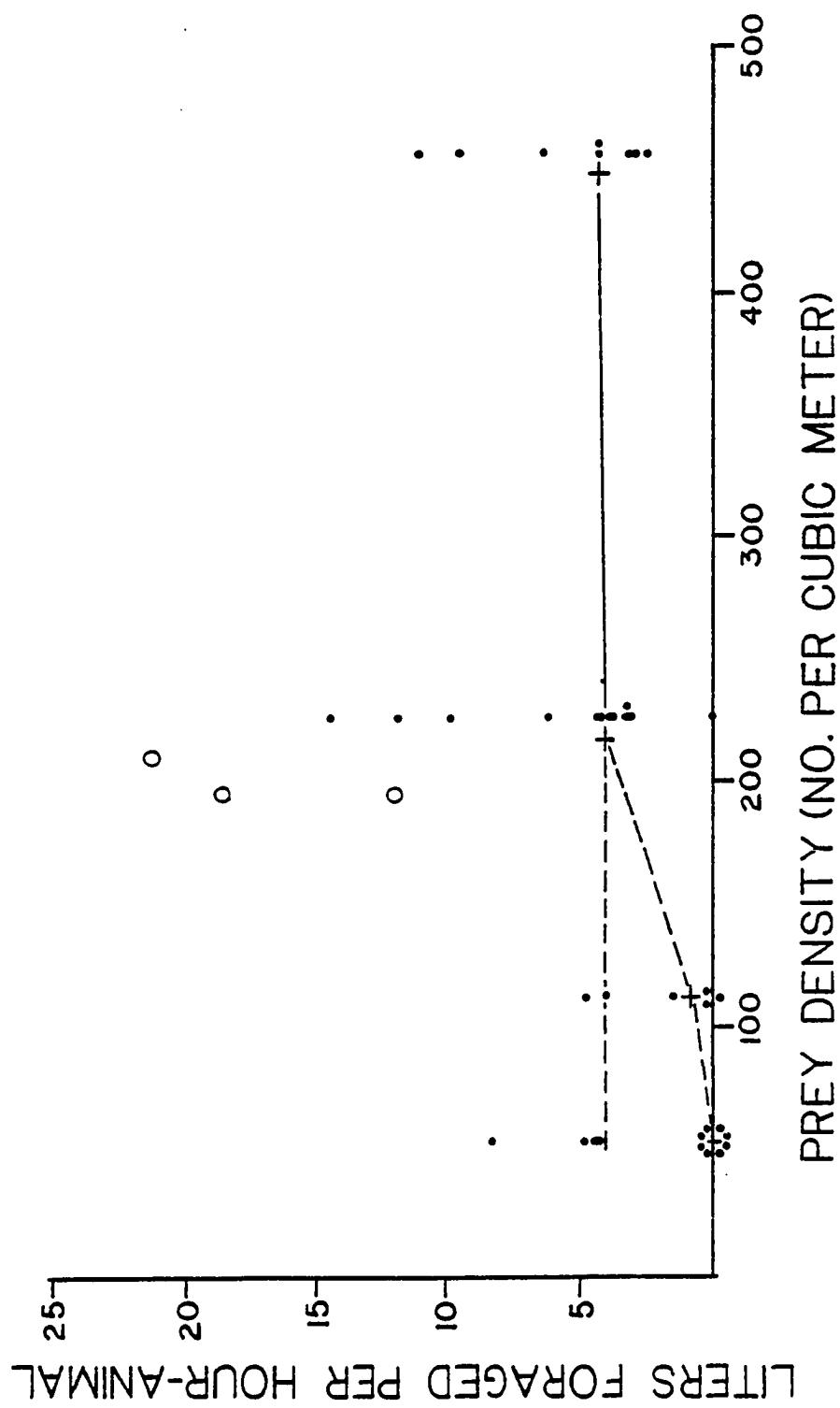
Like the median value, the maximum number of prey ingested  $\text{hour}^{-1}$  at each prey density increased as the prey density increased. Note, however, that the number of predators which ingested no prey (or only one) increased as the prey density decreased.

Three experiments run in the 1,000-liter tanks suggest that prey capture could be underestimated by 2-4 fold using the 177-liter tanks (see Fig. 20, p. 83). While the limited number of experiments run in the larger tanks precludes any conclusions regarding container size in this study, the generally higher ingestion rates in the larger tanks suggest that the ingestion and foraging rates determined using the "small" tanks are conservative.

### Discussion

Aquarium size and choice of prey are potential sources of bias in any investigation of the feeding behavior of macrogelatinous carnivores. Previous investigators have conducted their experiments in feeding

Fig. 21. Calculated foraging rate (liters foraged hour-siphonophore<sup>-1</sup>) at each prey density. Crosses represent median values for small tank experiments. (● - experiments run in 177-liter tanks, O- experiments run in 1,000-liter tanks.) See text for explanation.



aquaria ranging in size from 1-40 liters (Biggs 1977a; Reeve et al. 1978; Reeve 1980), approximately an order of magnitude smaller than those used in this study. For copepod predators, Anraku (1964) has demonstrated that the size of the experimental container used in predation studies with Tortanus discandatus affected his results, and Jamieson (1980) showed that the apparent predation rate of Mesocyclops leuckarti was a function of the size of the beaker in which the experiments were conducted.

The tanks used in the present study were designed to enclose a large volume of water while minimizing the tank's surface area. Since oceanic gelatinous macrozooplankton are delicate, their feeding behavior can be adversely affected by frequent contacts with aquarium surfaces. Because of the delicacy and fragility of these predators, like midwater fish (Robison 1973), it is impossible to maintain them in laboratory aquaria for any extended period.

Most of the foraging experiments were run during the fall and winter cruises in the Gulf of Mexico, as few Forskalia were encountered in surface waters during the spring and summer cruises (see Chapter II). My experiments were run almost exclusively in the smaller tanks to compile a workable data base without having to sort inordinate numbers of prey. In addition, maintaining ambient surface temperature, reducing light, and

retrieving the predator at the end of the experiment from the giant tanks proved to be a formidable task, given the limited time available for experimentation on any one cruise.

A second source of bias relates to the kind of prey used by some investigators. Artemia nauplii, although readily accessible and commonly used, are atypical of the prey species of the open ocean. Their swimming behavior is radically different from the swimming behavior of most open-ocean copepods (Haury and Weihs 1976). In addition, they are seldom dominant elements of the natural plankton assemblages.

Since experiments performed in this study were conducted opportunistically upon capture of the siphonophores, the predators may have had different field nutritional histories. No attempts were made to standardize the nutritional history of the predators (i.e. by pre-experimental feeding or starvation) in order to keep handling, transfer and aquarium time to a minimum.

Purcell (1981a) has investigated the foraging behavior of a select group of siphonophores during the day and at night under both light and dark conditions. It appears that the time of day is less important in determining whether the fishing network of some species is extended than whether it is "light or dark." Her data indicate that Rhizophysa eysenhardtii and Rosacea

cymbiformis fish primarily during lighted conditions, whereas Agalma okeni fishes predominantly during dark periods.

Purcell (1981a) noted that Forskalia extended its tentacles more often during "light" periods than "dark" periods, though the latter observations were made in 1-4 liter containers. Container size is clearly important, since I observed that specimens of Forskalia whose fishing network was contracted in a small, 1-liter collecting jar would relax their tentacles when released in a 177-liter aquarium, both in light and darkness. Moreover, observations I have made during the course of these experiments indicate that Forskalia rarely contracted their tentacles completely regardless of light or dark; rather, there were gradations in the degree to which the tentacles were relaxed.

The functional response of a predator can be defined by the number of prey ingested as the prey density changes (Holling 1959, 1965). The functional response of particle-grazing copepods is characterized as a generally increasing function which eventually levels off at higher prey densities (Frost 1974). Mullin et al. (1975) have approximated the functional response of a filter-feeding herbivore, such as Calanus, as rectilinear or curvilinear. Frost (1972, 1975) believes that the rectilinear model is more realistic, since it is unlikely that copepods

become less efficient at gathering food as the density of food particles increases. Investigators of ctenophore feeding explain the functional response of lobate and cydippid ctenophores as a constant proportionality over wide prey concentrations (Reeve et al. 1978).

Another factor useful in characterizing the shape of the functional response curve is whether or not a threshold prey concentration exists (a prey concentration at which the predator does not forage). This aspect of predation theory has been the focus of controversy.

Steele (1974) has formulated a predation theory to explain the dynamics of the North Sea marine ecosystem. This explanation is centered around the existence of a threshold feeding concentration and switching behavior. Landry (1976) responded with an alternative hypothesis which assumes that mechanisms such as density-dependent predation of herbivores by carnivores prevent over-grazing by the herbivore population.

A generalized functional response curve for gelatinous tentaculate carnivores possesses two distinct regions (Fig. 22). At very high prey densities (Region 1), increasing the prey concentration results in a constant ingestion rate (Rowe 1971; Reeve et al. 1978). Reeve et al. (1978) have attributed the existence of a "critical concentration," above which the ingestion rate is constant, to "mechanical saturation." In other words, the

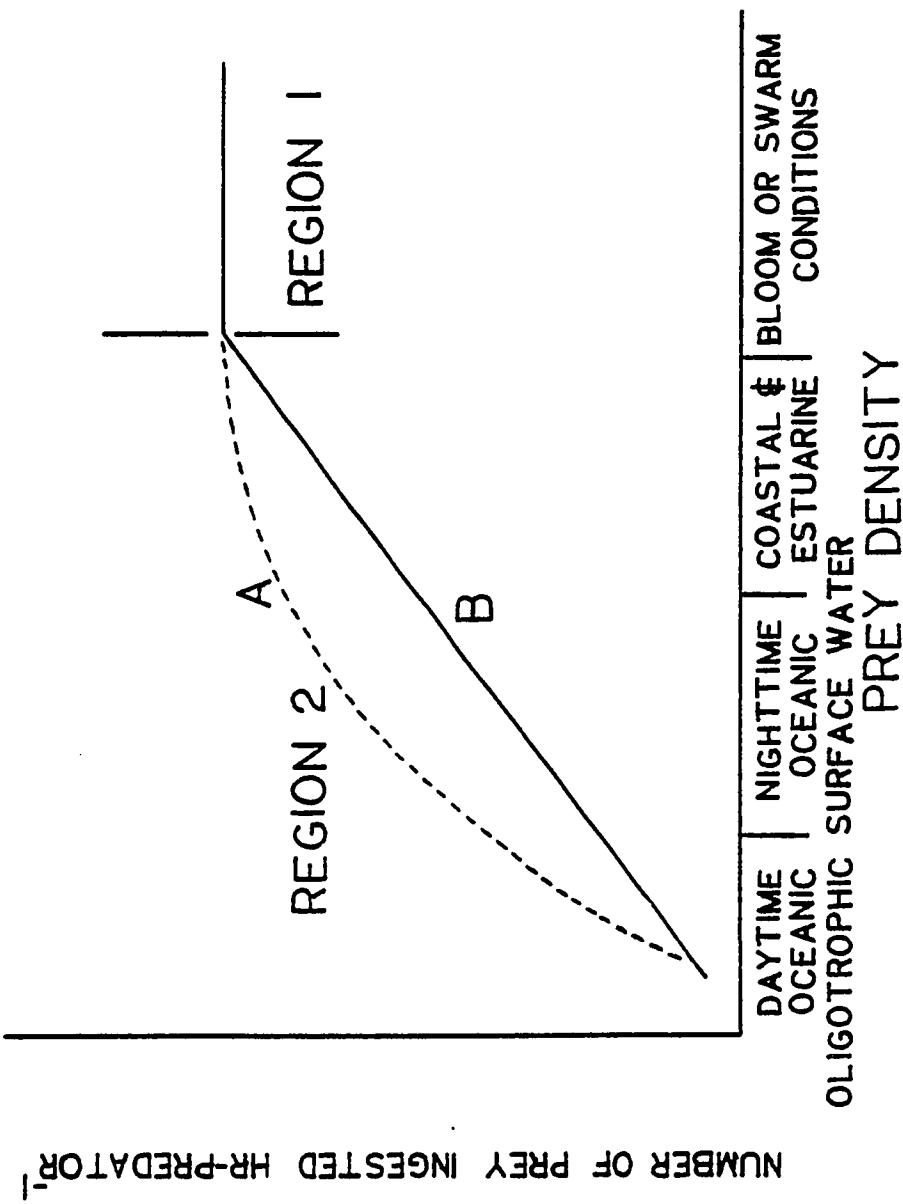


Fig. 22. Theoretical functional-response curves for oceanic gelatinous zooplankton (see text for discussion of curvilinear versus linear slopes of Region 2).

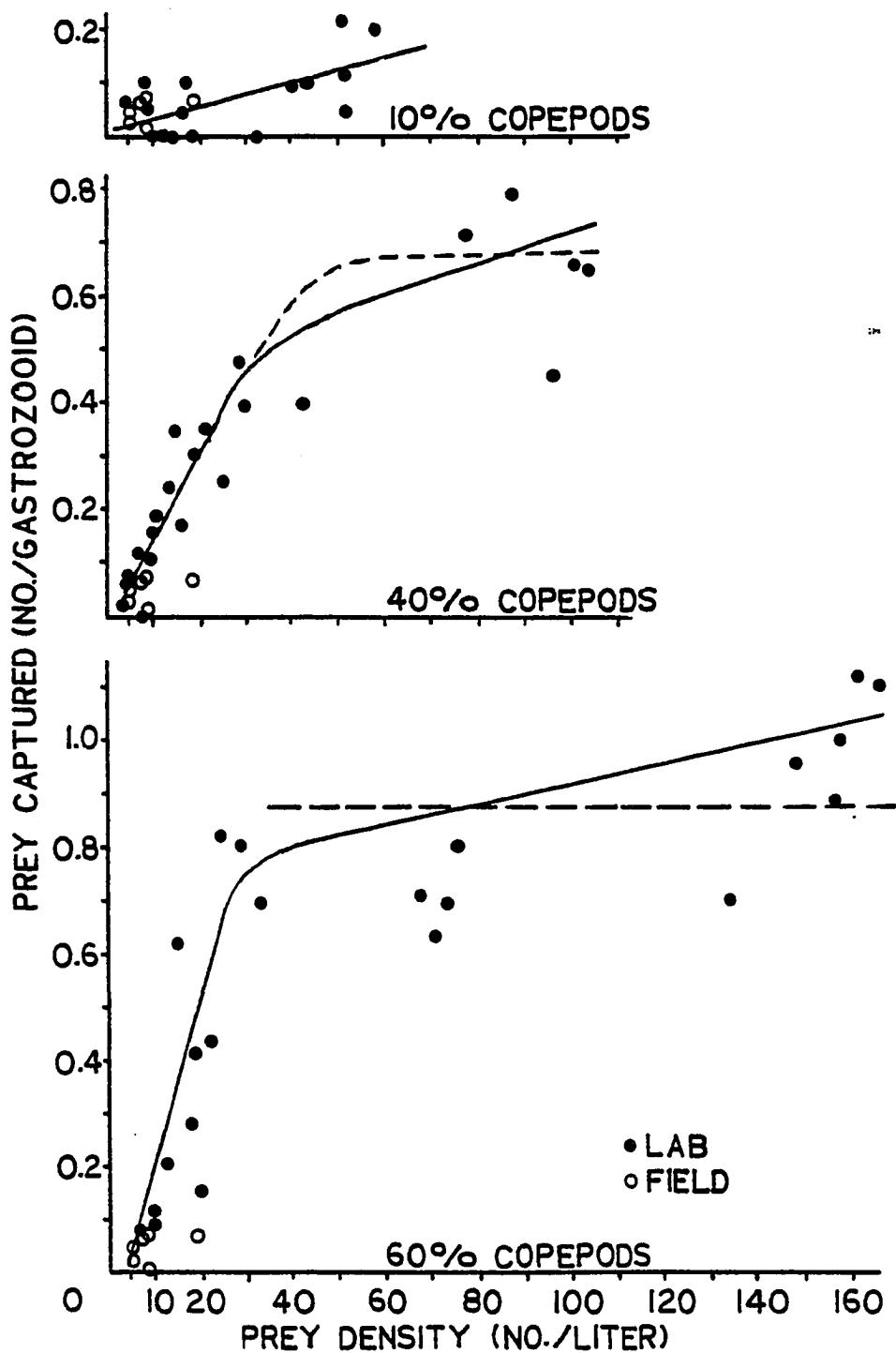
dominant time-consuming feature of feeding at these very high prey concentrations is the transferring of the food items to the mouth, or the handling time, not the time spent searching for prey.

Purcell (1981d) presents a series of functional response curves for the calycophore Muggiae atlantica using different proportions of nauplii and copepods as prey (essentially different prey populations). Her curves, however, never exhibit a constant maximum beyond some critical prey density. According to Purcell, feeding continued to increase slowly after the initial rapid linear increase as the prey density increased.

Fig. 23 is a reproduction of Purcell's (1981d) ingestion curves for M. atlantica, with the second and third curves displaying the slight increase in the number of prey ingested at high prey densities. Note that in the second graph there is a gap in the data to the right of the inflection point (critical concentration) and the curve could be drawn displaying a plateau or constant feeding at high prey densities (inserted dashed curve). In the third case, although the data do indicate a slightly increasing trend to the right of the inflection point, for data beyond a density of 25 prey liter<sup>-1</sup>, the calculated slope was only 0.002.

Region 2 of the functional response curve is characterized by a positive functional relationship between

Fig. 23. Reproduction of Purcell's (1981d) Figure 1 (Chapter IV). Dashed lines indicating constant ingestion have been inserted. See text for details.



prey consumed and prey density. If the relationship is hyperbolic (Holling's (1959, 1965) Type 2 functional response curve), the predator is optimally efficient at foraging at low densities of prey. If the relationship is linear (Holling's (1959, 1965) Type 1 functional response curve), the predator's capture ability is proportional to prey availability.

Behaviorally, siphonophores may be able to modify the effective area and volume of their network of fishing tentacles. Unlike animals with a rigid and fixed feeding structure, siphonophores have a highly extensile feeding arrangement. In situ, Biggs (1977a) has observed that the tentacles of Forskalia which had recently ingested a large prey item were not maximally extended. By corollary, if starving predators extend their tentacles to their maximal length, they should be able to non-linearly increase the efficacy of their foraging.

Physiologically, the control of the excitation threshold of the predator's cnidocysts, the cells which contain the nematocysts, may be modulated by the nervous system depending on the physiological state of the siphonophore (Carre and Carre 1980). While, in theory, siphonophores might become non-linearly more sensitive to the presence of prey in addition to increasing the volume of water they forage, Purcell's (1981d) data for M. atlantica indicates that this siphonophore exhibited a linear

response.

The median values of the foraging rate at the two highest densities used in this study, connected by the solid line in Fig. 21 (p. 86), suggest that Forskalia forages at a constant rate of approximately 4 liters hour-animal<sup>-1</sup> at or above the prey density of 200 prey m<sup>-3</sup>. This is manifest in an amount ingested by the predator that is proportional to the prey concentration (represented by the solid line in Fig. 20, p. 83), a relationship similar to that reported for lobate and cydippid ctenophores by Reeve et al. (1978) and Kremer (1976).

Clearly, at lower prey densities a small change in the ingestion rate will create a large effective change in the foraging rate. Hence, differences in ingestion of only 1 or 2 copepods at a prey density of 51 copepods m<sup>-3</sup> will result in a large deviation in the foraging rate.

The length of time the experiments are run is also influential. The observed median foraging rate at the two highest prey densities, 4 liters hour-animal<sup>-1</sup>, implies that during a one-hour period the predator would forage 2.2% (4 liters/177 liters) of the volume of the tank, consequently consuming about 2.2% of the prey. The total volume of the tank foraged is therefore a function of the length of time of the experiment. A

four-hour experiment would result in about 9% of the prey being captured. (Nine percent of 9 prey, the number present in the tank at a density of 51 prey  $m^{-3}$ , is less than one.)

Consequently, interpretation of the data at the two lowest prey densities is more difficult. The lower dashed line in Fig. 20 (p. 83) connects the median number of prey ingested hour-animal $^{-1}$  and intersects the X-axis at a density of 51 prey  $m^{-3}$ . However, because of the influence of the length of the experiments on prey ingestion at the lower prey densities described above, this median value may be an artifact. Because of the fragility of these predators and their sensitivity to surface contact, it was not possible to sufficiently extend the length of these experiments to avoid this problem. The upper dashed line in Fig. 20 (p. 83) represents a continuation of the proportionality relationship between ingestion and prey density described for prey densities greater than 200  $m^{-3}$ . Therefore, for prey densities less than 200  $m^{-3}$ , the exact nature of the prey ingestion/prey density relationship is not clear, although there is no theoretical reason to believe that the foraging rate decreases (as shown in the lower dashed line in Fig. 21, p. 86) at low prey densities. In Fig. 21 (p. 86), the upper dashed line displays the continuation of a foraging rate of about 4 liters hour-animal $^{-1}$  previously

described for prey densities greater than  $200 \text{ m}^{-3}$ .

The above ingestion and foraging rates allow for a speculative comparison of energy required by Forskalia versus energy available to the predator. Assuming a respiration rate of  $17 \text{ ul-O}_2 \text{ mg-protein-hour}^{-1}$  (Biggs 1977b) and an oxycaloric value of 4.4 calories  $\text{ml-O}_2^{-1}$  (Lehninger 1975), a 5 mg protein Forskalia (4.7 cm, contracted length) would require about 4.5 calories to support its respiration requirements for 12 hours. Table 10 lists the energy theoretically available to a Forskalia feeding at three prey densities on copepods of different caloric value (Shushkina and Sokolova 1972; Wissing et al. 1973). The energy actually available to the siphonophore would be about 80% of these values if Forskalia has an assimilation coefficient similar to that of other gelatinous carnivores (Walter 1976; Reeve et al. 1978; Purcell 1981c). A calculation by Purcell (1981c) for Rosacea cymbiformis indicates that the caloric consumption of R. cymbiformis in the Gulf of California appears to be from 2.4 to 8.2 times that required to balance metabolism.

If the caloric content of the prey is roughly proportional to their physical size, then it is to the advantage of the predator to capture and process large prey. At all prey densities modeled in Table 10, capturing exclusively tiny prey will not provide enough

Table 10. Calculated energy available to *Forskalia* foraging different sizes of prey (as defined by caloric content) at three prey densities. The foraging rate of 4 liter/hr was derived from Fig. 21 (p. 86).

Number of Prey/m <sup>3</sup>	Number of Prey Consumed/12 hrs.	Calorie Content/Prey Item		
		.1	.5	1.0
100	4.8	.5	2.4	4.8
200	9.6	1.0	5.0	10.0
400	19.0	2.0	10.0	23.0

energy for Forskalia's basic energetic requirements. By comparison, a diet of medium and large-size prey at densities of 200 or more  $m^{-3}$  should be adequate. Since the average size of the zooplankton present in daytime open-ocean surface waters is smaller than in eutrophic or coastal areas, it seems that Forskalia must attain a balance between the size of the prey it captures (and, therefore, energy available) and the relative abundance of each size class of prey.

When investigators have looked at size selection by siphonophores, there is a trend for these predators to prefer larger prey to smaller prey. According to Purcell (1981c), small zooplankton were consumed less frequently than their availability would suggest, while large zooplankton were consumed more frequently by the calycophoran siphonophore Rosacea cymbiformis in the Gulf of California. Using the electivity index of Chesson (1978), Purcell and Kremer (in press) have shown that Sphaeronectes gracilis, as well, displayed a preference for larger prey. Muggiaeae atlantica collected in Friday Harbor, Washington behaved similarly (Purcell 1981d).

Apparently, the spatial and temporal distribution of prey in the open ocean may play a key role in determining siphonophore survival. For example, patches with mean densities of greater than 200 prey  $m^{-3}$  should allow Forskalia to process enough energy over the majority of

prey sizes (as defined by caloric content) to allow for respiration plus some growth. Alternatively, in prolonged contact with densities of 100 prey  $m^{-3}$  or less, Forskalia would not be able to obtain adequate energy to meet even its daily respiration needs. Since average daytime prey densities in the subtropical open ocean are commonly in the range of tens to hundreds of copepods- $m^{-3}$  (Deevey and Brooks 1971; Howey 1976), this observation is not trivial.

Purcell (1980) has reported that 20% of the prey in the gastrozooids of field-collected Forskalia represent larger, non-copepod prey. The occasional capture of larger, more energetically-dense prey would seem to be extremely important, especially if the predator has been foraging in an environment of low copepod density.

Although spatial and temporal variability in the number and kind of prey captured will ultimately determine whether or not the predator will survive, a comparison of the foraging rates of Forskalia with other oceanic consumers can emphasize the difference (1) between the coastal and the oceanic environment and (2) between herbivores and carnivores. Any such comparison is, of course, dependent on the kind of food used, but the available literature indicates that Forskalia daily forages greater volumes of water than do coastal taxa (Table 11). While an in-depth comparison is impossible

Table 11. Comparison of foraging rates of coastal and oceanic zooplankton.

Animal	Province	Foraging Rate	Reference
<u><i>Mnemiopsis mccradyi</i></u> <sup>1</sup> (30 mm dia.)	Coastal	20 liters/day	Reeve, Walter & Ikeda 1978
<u><i>Pleurobrachia bachei</i></u> (8 mm dia.)	Coastal	2 liters/day	Reeve, Walter & Ikeda 1978
<u><i>Chrysaora quinquecirrha</i></u> <sup>2</sup> (100 ml vol.)	Coastal	20 liters/day	Calculated from Clifford & Cargo 1978
<u><i>Calanus pacificus</i></u> <sup>3</sup> (adult females)	Coastal	0.2 liters/day	Frost 1972
<u><i>Cyclosalpa affinis</i></u> <sup>3</sup> (10 cm solitary)	Oceanic	80 liters/day	Harbison & McAlister 1979
<u><i>Forskalia</i></u> sp. <sup>4</sup> (4-7 cm, contracted length)	Oceanic	25-100 liters/day	This study

1 Food--copepods, mainly *Acartia tonsa*.

2 Food--*Artemia*, at ambient coastal densities.

3 Food--selected phytoplankton spp.

4 Food--oceanic copepods.

since each consumer has different metabolic rates, is a different size, and feeds with physically different mechanisms, it is clear that the foraging rate of oceanic taxa reflect the generally food-poor environment of the open ocean.

CHAPTER IV  
PREY ENCOUNTER BY A TENTACULATE, PLANKTONIC  
PREDATOR: A STOCHASTIC NUMERICAL MODEL

Introduction

Prey encounter by tentaculate planktivores such as siphonophores, cydippid ctenophores, and medusae is a function of (1) tentacle number and length, (2) tentacle orientation, (3) velocity at which the tentacles are drawn through the water, (4) swimming patterns of the predator, (5) swimming patterns and velocities of the prey, (6) local turbulence or streamlining resulting from swimming of the predator, and (7) diameter of the prey (Mills 1981). Planktivores like hydromedusae feed with tentacles relaxed and extended while swimming and floating. If these animals depend on chance contacts with prey items, then feeding efficiency should have a simple relationship to tentacle length. Mills (1981) observed, however, that variations in the swimming behavior of medusae can significantly modify the "fishing" effectiveness of these predators, and Biggs (1977a) has shown that, for siphonophores, the three-dimensional fishing posture (i.e. linear, curvilinear or radial) will also determine the efficiency of prey encounter.

Unlike most medusae, which fish with tentacles

relaxed and extended as they swim (e.g. Phialidium gregarium), calycophore and physonect siphonophores generally contract their tentacles as they start to swim to change location (Biggs 1977a). As a result, their feeding behavior can be divided into two phases: a fishing phase and a swimming phase. Because siphonophores relax their network of tentacles only after active swimming ceases, the seven parameters listed above which generally dictate prey encounter can be reduced to four by excluding (1) the velocity at which the tentacles are drawn through the water, (2) the swimming pattern of the predator, and (3) local turbulence/streamlining considerations associated with the motion of the predator. Consequently, with but a few assumptions, prey encounter by siphonophores can be modeled in three-dimensional space.

Previous predator/prey encounter models (e.g. Gerritsen and Strickler 1977; Gerritsen 1980) included the assumption that the predator and prey items were points in space. Although this is adequate for most crustacean predators (i.e. net-zooplankton), the multiple feeding polyps of siphonophores and the characteristic three-dimensional shapes of their associated tentacular networks must be considered.

In this chapter, I describe a group of stochastic numerical models developed to investigate the encounter rate by an idealized physonect siphonophore feeding on

three types of prey characterized by different swimming strategies. The prey swimming behaviors which I modeled include:

- 1) Random movement in the X-Y plane and random movement in the Z direction;
- 2) Directed movement along the X-Y plane with a reduced probability of movement in the Z direction; and
- 3) A "hop and sink" type behavior (Haury and Weihs 1976), where the prey sinks passively after darting upward.

The models allow for quantitative conclusions regarding the importance of prey swimming behavior to the encounter rate of macrogelatinous tentaculate zooplankton.

Several studies (Purcell 1981a, 1981d; Purcell and Kremer, in press) have alluded to the importance of prey size and swimming speed to prey encounter with the tentacles of siphonophores. A stochastic model of prey encounter has the advantage of allowing the investigator the opportunity to run an "experiment" on the computer and generate quantitative results from simulated situations which may be logistically or practically impossible to create in the field. The approach is particularly useful for oceanic gelatinous tentaculate predators since these animals are very delicate, rather rare (see Chapter I), and require time and labor intensive techniques

to collect specimens in good physiological shape.

This study focused on (1) determining the importance of prey behavior to encounter rate by tentaculate planktivores, (2) identifying mechanisms available to the predator which increase the rate of encounter, and (3) highlighting areas suitable for further study where available data are rather sparse.

#### Encounter Models

The system includes the prey and three-dimensional predator enclosed in a  $1/8 \text{ m}^3$  volume (500 mm x 500 mm x 500 mm). The system has a physical resolution of 1  $\text{mm}^3$  for the location of a point within this homogeneous space. Any location can be pinpointed by a coordinate set (X,Y,Z) where X, Y and Z range between 1 and 500, inclusive.

Prey were assumed to occupy approximately 1  $\text{mm}^3$  in the space and were, therefore, assigned an X, Y and Z coordinate within the system volume representing their physical location. For example, a prey item with coordinates (100,10,10) was physically located at point (100,10) in the X-Y plane and 10 mm "down," in the positive Z (+Z) direction. During these simulations, a prey density of 112 prey  $\text{m}^{-3}$  was maintained (14 prey within the system space). This concentration was chosen to approximate the ambient daytime copepod and/or crustacean

density in the surface waters of an oligotrophic oceanic environment, such as the open Gulf of Mexico or Sargasso Sea (Deevey and Brooks 1971; Howey 1976), and because it was one of the prey concentrations used in the feeding experiments described in Chapter III.

The prey's initial positions, listed in Table 12, were selected using a random number table (Selby 1972) and were held constant from one simulation to the next (see Fig. 24 for a graphic depiction of these locations). In addition to these coordinates, Table 12 also displays the coordinates of prey introduced to the system to replace those captured. The computer program has the capability, via a subroutine, to replace prey which have been encountered. To maintain a prey density of 112 prey  $m^{-3}$ , the encountered prey item is replaced by assigning a new prey item to a random location. While the instantaneous appearance of a new prey item is unrealistic, the alternative of having a prey item migrate randomly into the system was cost-prohibitive. Replacing prey after an encounter at random locations which are constant from one simulation to the next, along with the constancy of the original prey coordinates, introduces some control in the stochastic models and allows for a common basis for comparison between the simulation results.

The models allow the split-second occupation by two prey items of the same location (i.e. same set of

Table 12. List of initial locations of prey and coordinates at which prey were introduced to the system to replace those captured.

---

Prey Locations at Start of Simulation:

	<u>X</u>	<u>Y</u>	<u>Z</u>
#1	104	465	226
#2	168	61	349
#3	119	253	179
#4	15	51	306
#5	495	103	336
#6	182	26	312
#7	145	47	151
#8	103	252	74
#9	42	411	341
#10	324	72	265
#11	227	424	416
#12	290	351	205
#13	204	145	75
#14	464	350	257

Coordinates of Replacement Prey:

	<u>X</u>	<u>Y</u>	<u>Z</u>
#1	297	119	247
#2	331	321	348
#3	295	359	348
#4	190	87	369
#5	207	421	395

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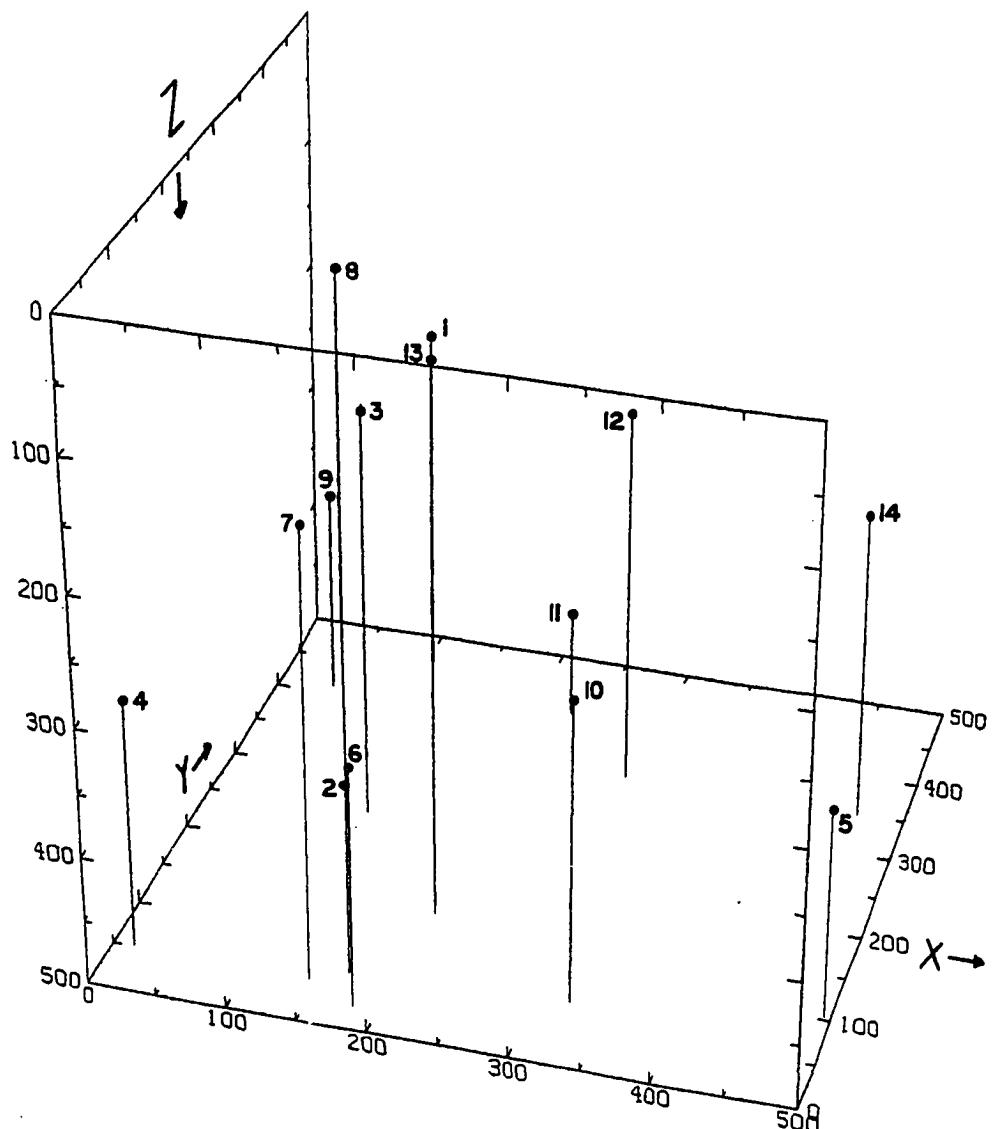


Fig. 24. The system volume, showing the initial location of the fourteen prey items (time=0). The lines extending from the prey points to the X-Y plane provide a reference for comparing the X, Y, and Z coordinates for each prey.

coordinates). Since observations of living oceanic zooplankton in holding aquaria and jars aboard ship confirm that zooplankters occasionally swim very close to one another, this behavior of the system's components is justifiable. I have assumed, however, that cannibalism among prey items did not occur during the course of the simulations.

A physonect siphonophore of the genus Forskalia was chosen as predator for these models. Biggs (1977a) has described the fishing posture of this genus. The feeding polyps are located on the ends of long pedicles which radiate from the center stem like spokes of a wheel (see Fig. 15, p. 68). Consequently, Forskalia has an almost radial symmetry, with the tentacles enclosing a cylindrical or hemispherical volume.

In my models, the predator's tentacular network consisted of 24 tentacles, three levels with eight tentacles each. For convenience, the predator was oriented vertically so that the central stem was normal to the X-Y plane. The tentacles in each row radiated outward from the central stem, one every  $45^{\circ}$  of arc and downward (in the +Z direction) at an angle of  $60^{\circ}$  to the X-Y plane (Fig. 25). From published tentacular dimensions for Forskalia (Biggs 1977a), a length of 46 mm was assigned to each tentacle. The 24 tentacles thus had a combined length of approximately 1.1 m.

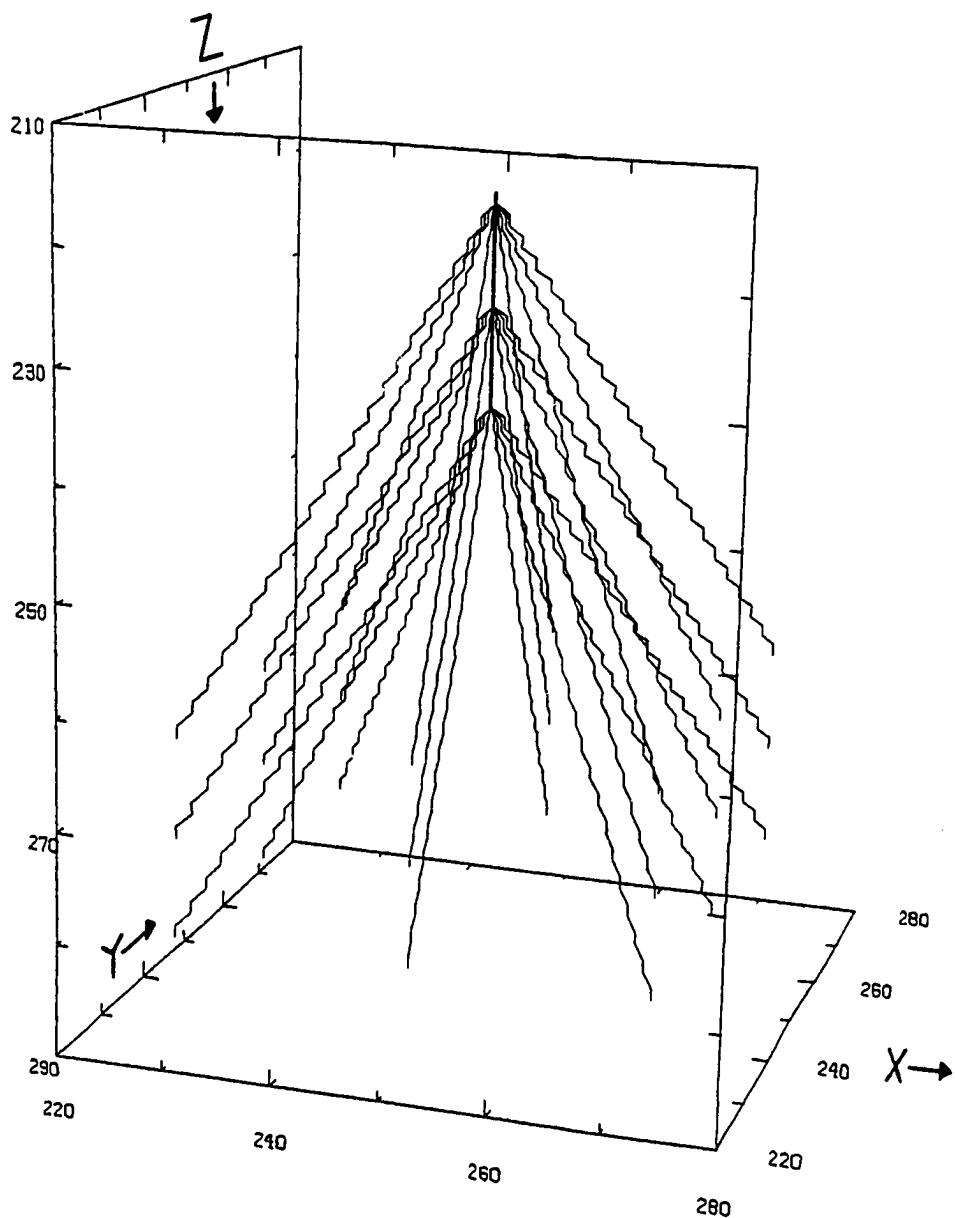


Fig. 25. Computer generated stick diagram of the predator to illustrate its spatial orientation.

The idealized Forskalia was placed in the middle of the system volume (centered around point (250,250,250)), and it was assumed that the predator did not move during the course of the simulations. This assumption is justified since Forskalia relaxes its tentacles only when it is in a fishing posture and is not swimming, and it generally maintains this fishing posture for long periods of time if undisturbed (personal observation; Biggs 1977a).

The stochastic nature of the models arises from probability distributions which govern the movement of prey in space with time. Since the different prey swimming behaviors simulated by these models will be discussed in detail, an explanation of the random number generator used to generate the random variates, and consequently the probability distributions, will be useful. The method employed by the models to generate random variates is a multiplicative congruential method which is a recursion relationship using the modulus function:

$$x_{i+1} = Ax_i \pmod{p}$$

where:  $p$  is a prime number  
 $A$  is a positive primitive root of  $p$   
 $x_i$  is the  $i$ th random number  
 $x_{i+1}$  is the  $i+1$ th random number

This generator was described by Hutchinson (1966) and the version used by the Amdahl 470/V6/V8 computer has

been documented by Lewis et al. (1969). Careful choice of the p and A parameters allows the generated random variate sequence to pass a battery of statistical tests indicating that the sequence behaves as if it were truly random.

The version of the random number generator in the computer's library makes use of the full capacity of the computer's 32-bit registers and generates uniform, real, random variates between 0 and 1. By multiplying the generated variate by 10 and truncating the result, uniform random integers between 0 and 9, inclusive, are created. Also, by changing the initial random number or "seed," which is chosen and supplied by the modeler, different sequences of random variates are processed by the random number generator.

For each simulation run, a total simulation time of four hours (14,400 seconds) was chosen with an iteration time interval of one second. The following is a description of the three different prey swimming behaviors modeled. Appendices C, D and E provide a listing of the computer programs used in the following three models.

Prey Behavior #1--The movement of a particular prey item can be divided into two components: direction and magnitude. These two components combine to define a vector in the three-dimensional system space. By defining

a model iteration time interval of one second over which the movement occurs, the magnitude can then be converted to speed (i.e. mm/second).

The first prey swimming strategy modeled was random swimming movement in the X-Y plane and along the Z-axis with a uniform random magnitude of movement between 1 and 9 mm each iteration. This was accomplished through three independent steps. Directional movement in the X-Y plane was first determined. By definition, the prey item had a 20% probability of remaining in the same X-Y location from one iteration to the next and a 10% probability of moving in any of eight directions in the X-Y plane. Imagining the prey item as a point in the X-Y plane, the eight possible directions of movement can be visualized as spokes radiating from the prey item, separated by an angle of 45° (Fig. 26).

Movement in the Z direction comprised three possibilities: moving "up in space" in the negative Z (-Z) direction, moving "down in space" in the +Z direction, or remaining in the same X-Y plane (no net Z-directional movement). During the first group of simulations, the likelihood of each Z directional possibility, above, was equally weighted. In other words, each was assigned a 33.3% probability of occurrence.

As a result of the above outlined rules and functions detailing prey movement, of the 26 possible directions

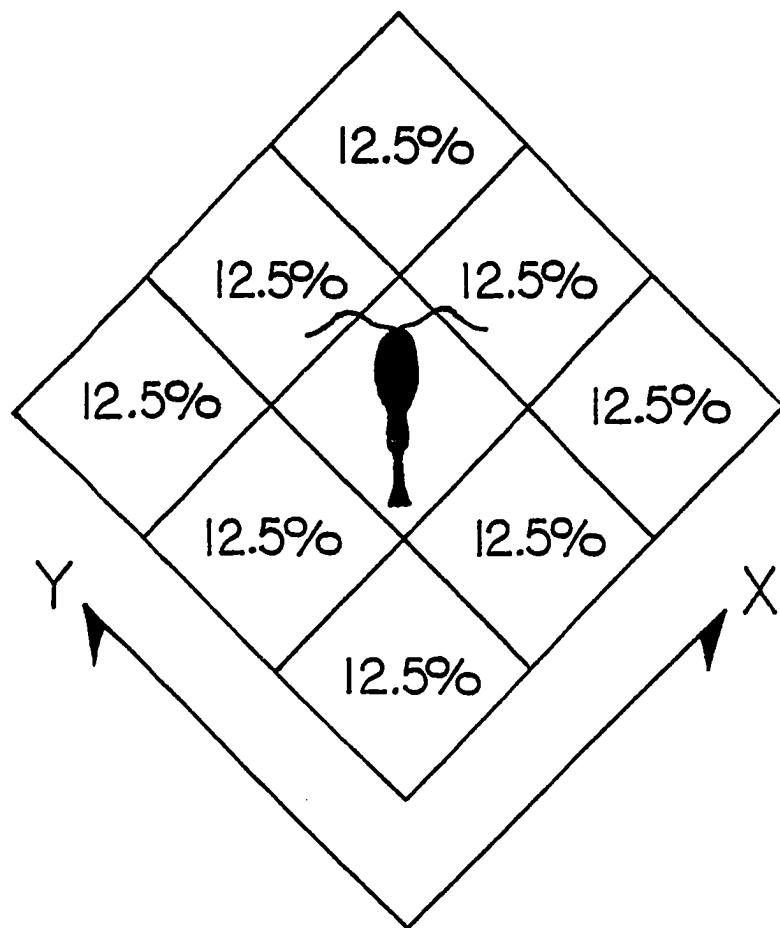


Fig. 26. The eight possible directions of movement for prey in the X-Y plane in model PREY. When the prey move, the percentages represent the probability of movement along each of the eight radiating directions. See text for details.

of prey movement in three-dimensional space, 24 were equally weighted with a probability of occurrence of 3.33%. Due to the greater probability that the prey would remain in the same X-Y position from one iteration to the next, the probability that prey would move upward in the -Z direction or downward in the +Z direction with no X-Y movement was 6.66%. In addition, the probability of no movement in both the X-Y plane and the Z direction was also 6.66%.

The last step required to define prey movement is the determination of movement magnitude. If the prey item moved, it moved from 1-9 mm each iteration (second). In terms of speed, the range was  $1-9 \text{ mm sec}^{-1}$  with an average speed for each prey item during this group of simulations of  $5 \text{ mm sec}^{-1}$ . While choice of direction in the X-Y plane and in the Z direction were independent of one another, magnitude of movement was not. One value for the magnitude of movement was chosen for each prey item during each iteration. Consequently, this value was applied to all movement by a particular prey item during a given iteration. In other words, if prey item #5 was scheduled to move in the +X and -Z directions with a movement magnitude of 5 mm, this magnitude would be applied to both directional movements (new coordinates ( $X+5, Y, Z-5$ )). Except as indicated below, the magnitude of movement for all three encounter models followed

these rules and conditions.

A special set of boundary responses was imposed on prey swimming when the prey item was near the edge of the system space and the next iteration would result in the individual prey moving outside the system volume (e.g. coordinates <1 or >500). If the prey item was scheduled to leave the system during a given iteration, the component of movement which would have resulted in its leaving the system, X and/or Y and/or Z, was reversed and the prey then moved the stochastically-determined magnitude. In this respect, the system volume can be thought of as being confined in a box. When a prey item encounters an edge of the system, it cannot leave and is turned back. For example, if an individual prey with coordinates (498,250,250) is supposed to move 5 mm in the +X direction and +Y direction during the next iteration, the resulting coordinate set of (503,255,250) would place the prey outside the system volume. Consequently, the boundary response is implemented and the prey moves in the -X direction, so that the resulting final coordinates for the prey after the iteration are (493,255,250).

If a prey item was in the immediate vicinity of the predator, so that during the next iteration movement from its initial set of coordinates to its final set may have allowed an encounter with the predator, this

particular prey item was moved 1 mm at a time to test more precisely if it encountered the predator. The predator was idealized as a series of equations in three-dimensional space. An encounter between the predator and prey was flagged when the coordinates of an individual prey solved the equations defining the predator.

Figs. 27 and 28 are two diagrams of the path of prey item #5, which had initial coordinates (495,103,336), during the initial minute of two separate simulations. A different random number generator "seed" was used in each simulation, resulting in different sequences of generated random variates. These figures illustrate that, by varying the "seed" of the random number generator, the specific behavior of the individual prey is altered, although the probability functions governing prey movement remain the same. Consequently, the results of one simulation using a particular prey swimming strategy need not necessarily be the same as those of another run of the model using a different random number generator "seed." This model, which I have designated PREY, was simulated five times to allow the calculation of an average number of prey encountered during the four hours of simulation time.

Prey Behavior #2--As a refinement of random swimming movement, the next swimming strategy modeled involved directed movement in the X-Y plane with a reduced

Fig. 27. Path of prey item #5 during the initial minute of one simulation of model PREY. The prey's path is delineated by the heavy, dark line. Point A represents its original location; point B is the prey position 60 seconds later.

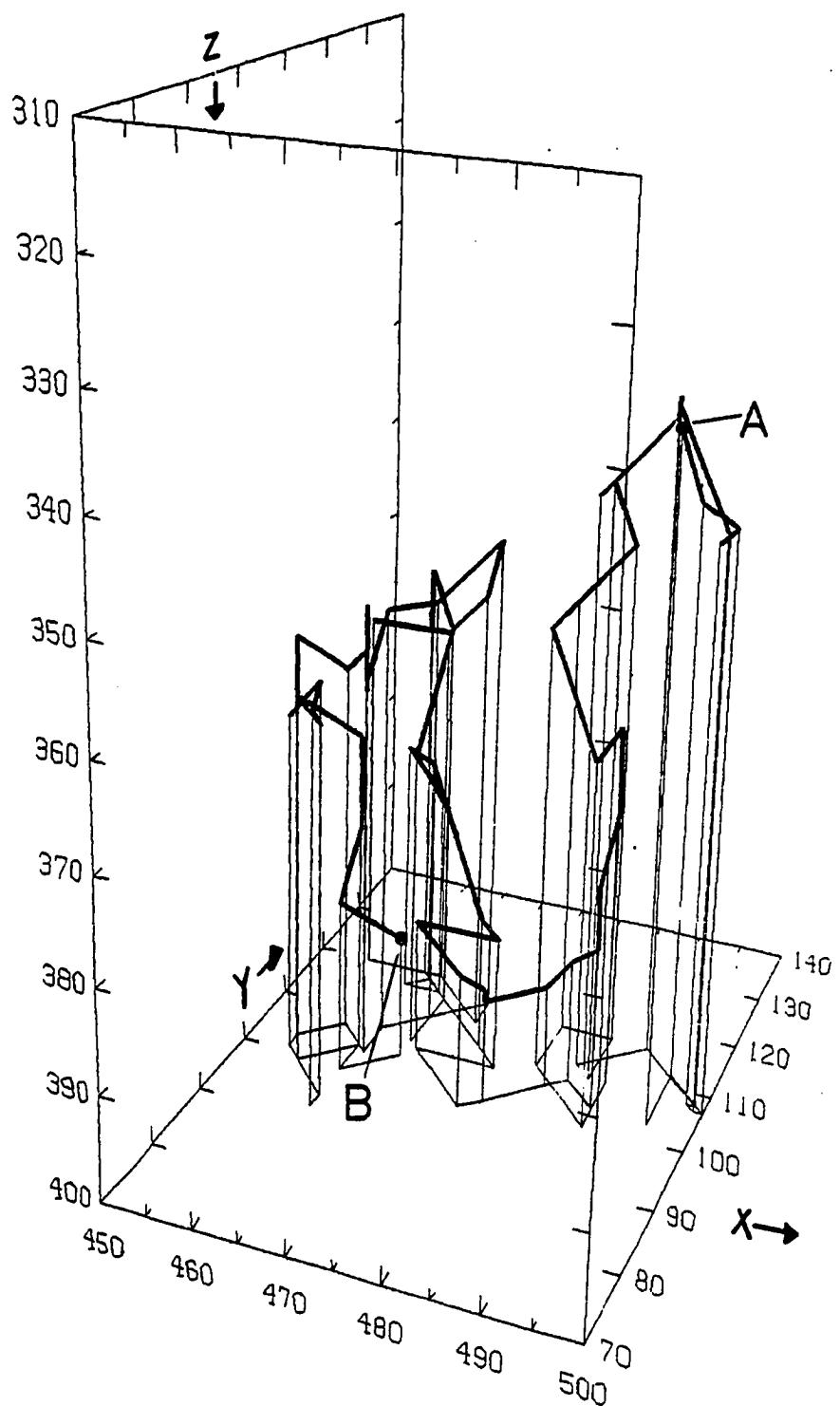
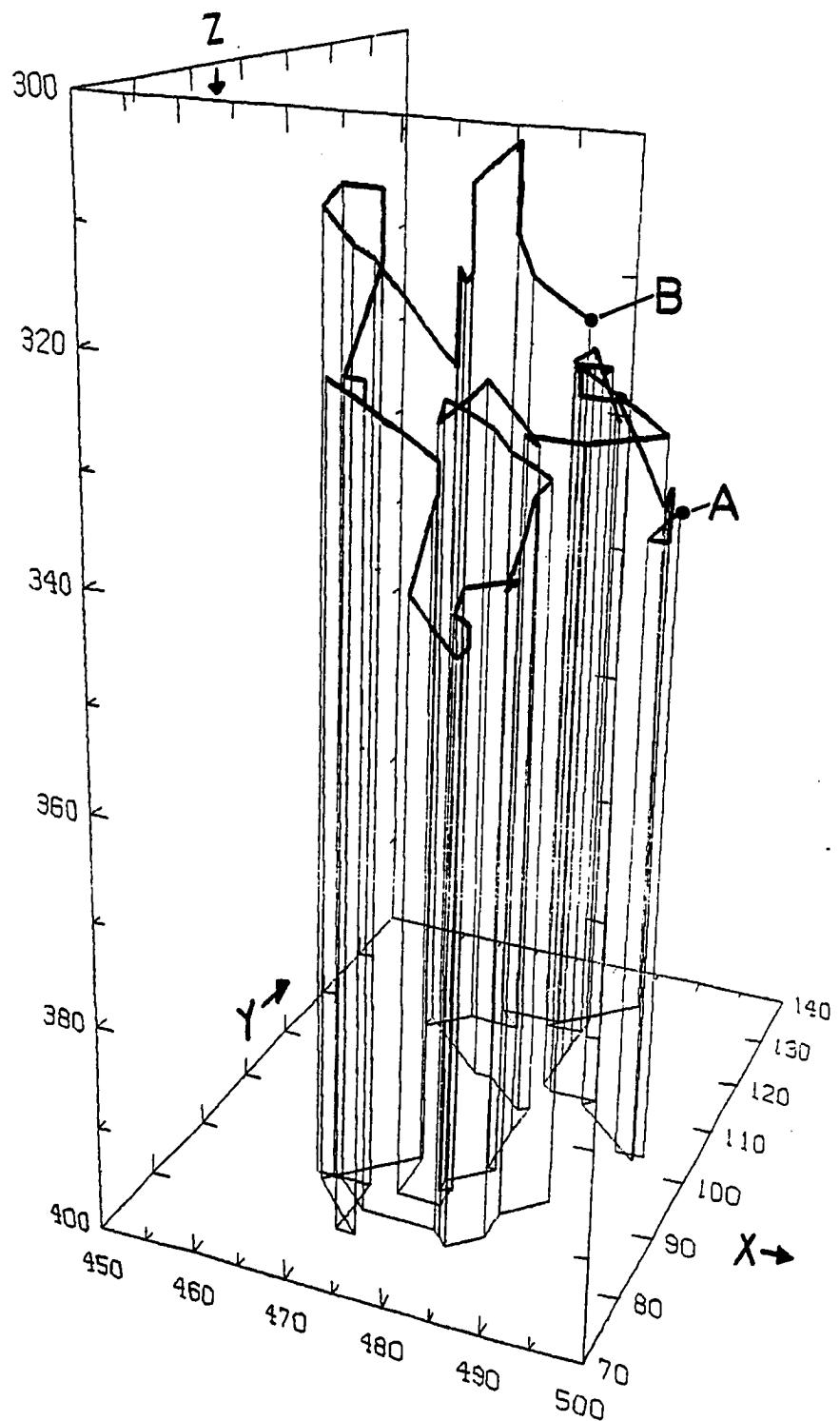


Fig. 28. Path of prey item #5 during the initial minute of a second simulation of model PREY. The prey's path is delineated by the heavy, dark line. Point A represents its original position; point B is the prey position 60 seconds later.



probability of movement in the Z direction. The following assumptions were made to define the probability functions outlining prey movement in the X and Y directions. First, it was assumed that the chance of "forward" movement by a particular prey item was greater than the chance of "lateral" or "backward" movement. The prey were defined as headed in one of four different "favored" directions, each described by an arc of 90° in the X-Y plane. It was further stipulated that the probability of movement in the pre-determined favored direction, the direction in which the prey was headed, was twice the probability that the prey item would swim laterally or backward (Fig. 29). In terms of the physical model and the eight possible directions of movement in the X-Y plane described above, three of the possible movement tracks made up the 90° favored movement arc. Within this group, the probability of moving along any one of the three paths was equal (33.3%). Lateral or backward movement occurred 33.3% of the time and was modeled as movement along one of the five remaining directions in the X-Y plane (Fig. 30), each of which was assigned an equal probability of occurrence (20%).

If the prey moved in a direction other than along one of the three favored tracks, it was assumed that its orientation in space also changed and it was heading in a different direction. Consequently, the index of

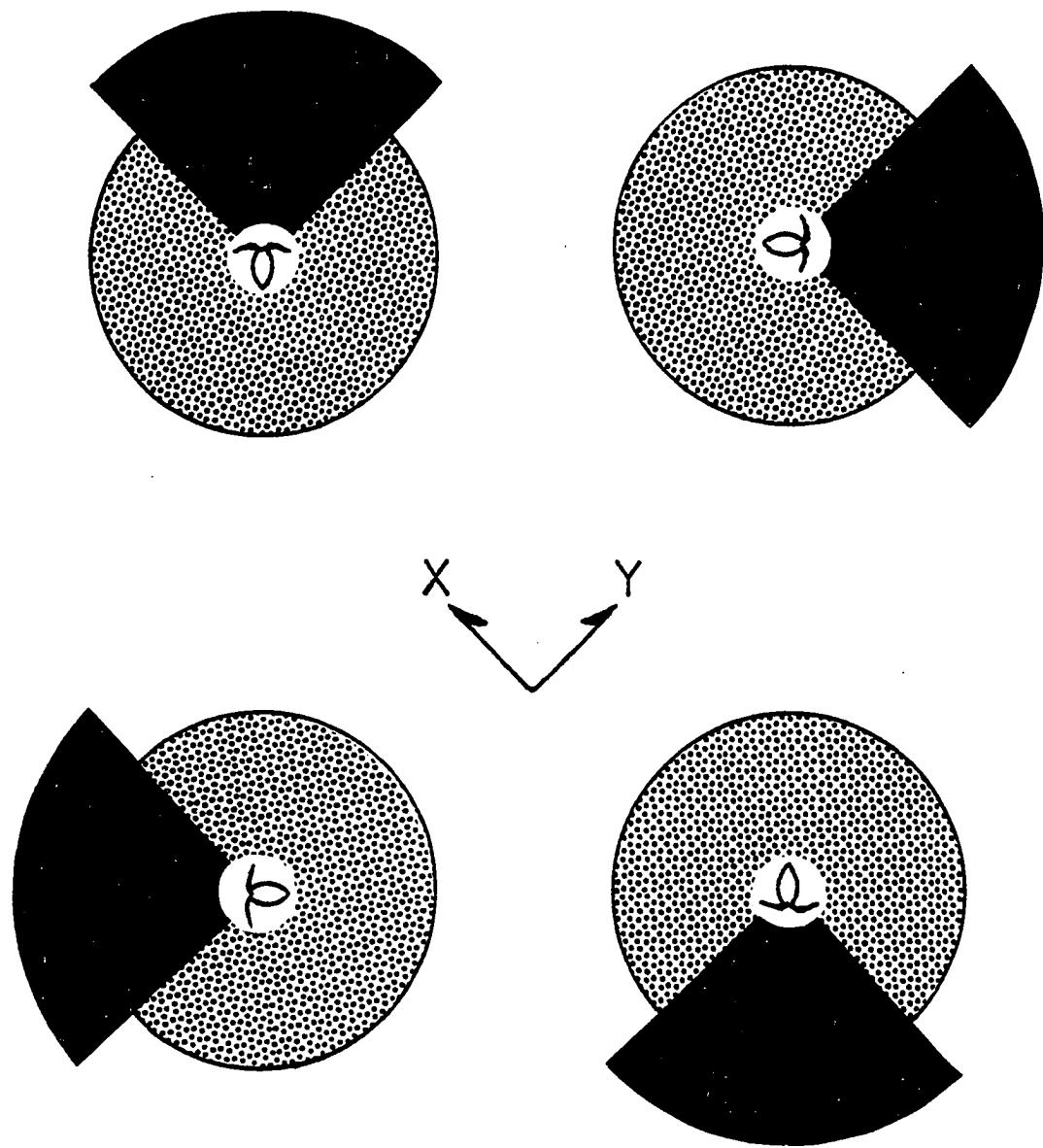


Fig. 29. A display of the four possible "favored" directions of prey movement in the X-Y plane as described in model PREY2. The probability of movement into the black area is twice (66.6%) the probability of movement into the stippled area (33.3%) in each case. See test for details.

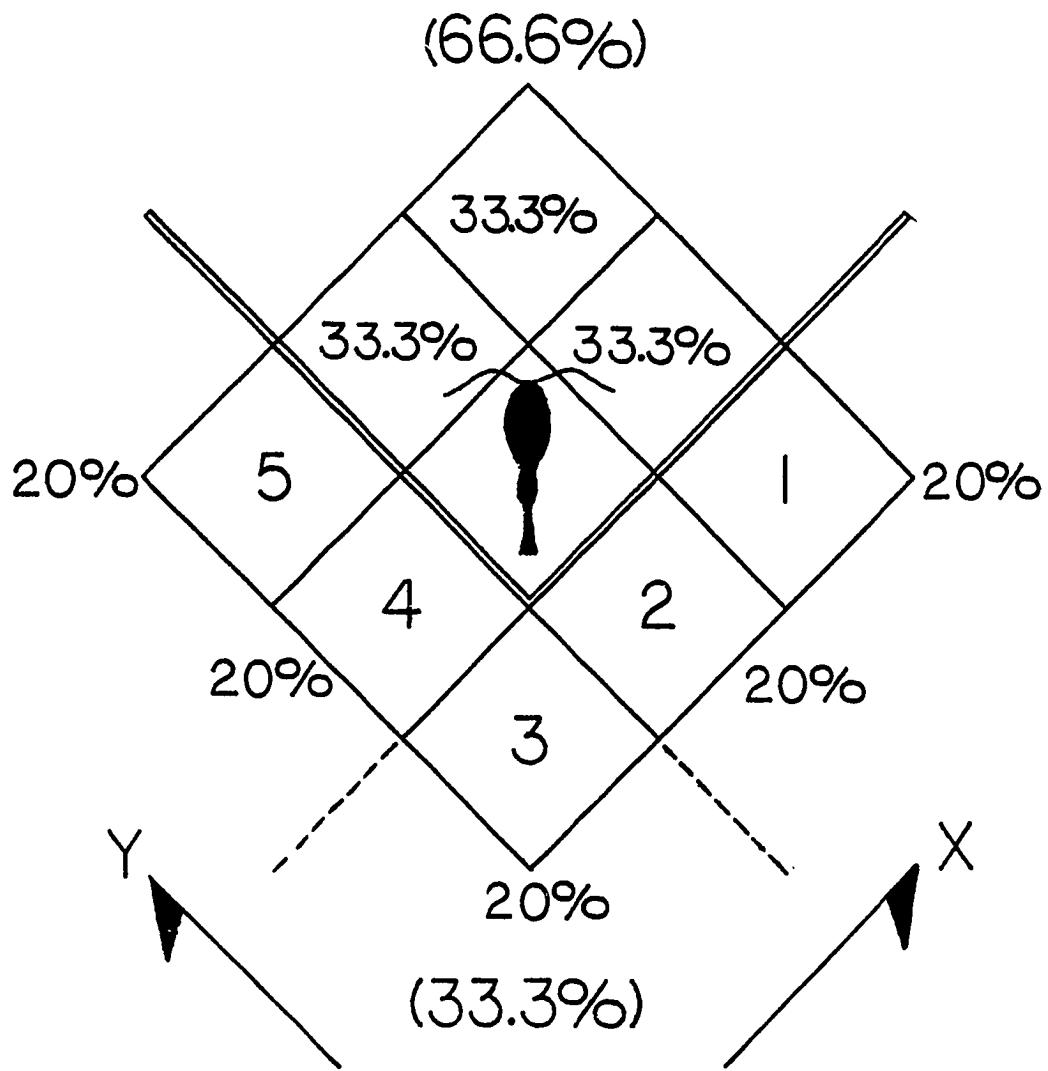


Fig. 30. The eight possible directions of movement for prey in the X-Y plane in model PREY2. In this example, the favored directions of movement by the prey are +X and +Y. The percentage in parenthesis at the top of the figure indicates the probability the prey will move along one of the three paths composing the favored movement arc. The percentage in parenthesis at the bottom is the probability the prey will move in one of the five remaining directions. If the prey moves in the favored arc, it has a 33.3% probability of moving along one of the three tracks. If the prey does not move in the favored directions, it has an equal probability (20.0%) of moving in any of the five remaining directions. See text for further explanation.

orientation was adjusted to comply with the previously selected direction of movement. This procedure is best described graphically. Referring to Fig. 30 (p. 126), if the prey was originally headed in the +X and +Y directions and moved to positions #1 or #2, the new favored directions would be defined as +X and -Y. Movement to positions #4 or #5 would result in a change in the favored directions to -X and +Y. Only movement to position #3, 180° to the original favored direction, would change the favored directions to -X and -Y.

The probability of no movement in the X-Y plane from one time iteration to the next was reduced from 20% in the previous group of simulations to 10% in this model. Consequently, the X-Y movement described above occurred 90% of the time. Further modifications linked the X-Y movement and Z movement portions of the program together with the caveat that, if the prey did not move in the X-Y plane, it did not move in the Z direction either. This constraint was imposed to accentuate the horizontal components of prey movement during this set of simulations. If the prey item did move, the probability function for movement in the Z direction allowed for a 20% probability that the prey would move upward in the -Z direction, a 20% probability that it would move downward in the system space in the +Z direction, and a 60% probability that the Z coordinate would remain unchanged

or the prey would remain in the same X-Y plane from one iteration to the next.

The boundary responses imposed on both the direction of prey movement and prey orientation are complex and can best be explained by detailing the rules governing prey movement near the system boundaries rather than an examination of individual situations. As in the first model, PREY, the only time when the following conditions are implemented is when a particular prey item would leave the system volume during the next iteration.

The rules governing prey movement near boundaries in this model are essentially the same as those described in the preceding model, PREY. If the individual prey item is supposed to move out of the system along the X and/or Y and/or Z axes, the direction of movement along the affected axis is reversed and the prey move back into the system. The prey's index of orientation is determined by the prey's ultimate direction of movement in the same manner as previously described. In the absence of boundary conditions, a prey item with coordinates (498,498,250), favored directions +X and +Y, and a stochastically-determined magnitude of movement of 5 mm in the +X and +Y directions would move out of the system volume along the X- and Y-axes. The boundary constraints result instead in a location of (493,493,250) and favored directions -X and -Y. The rules governing

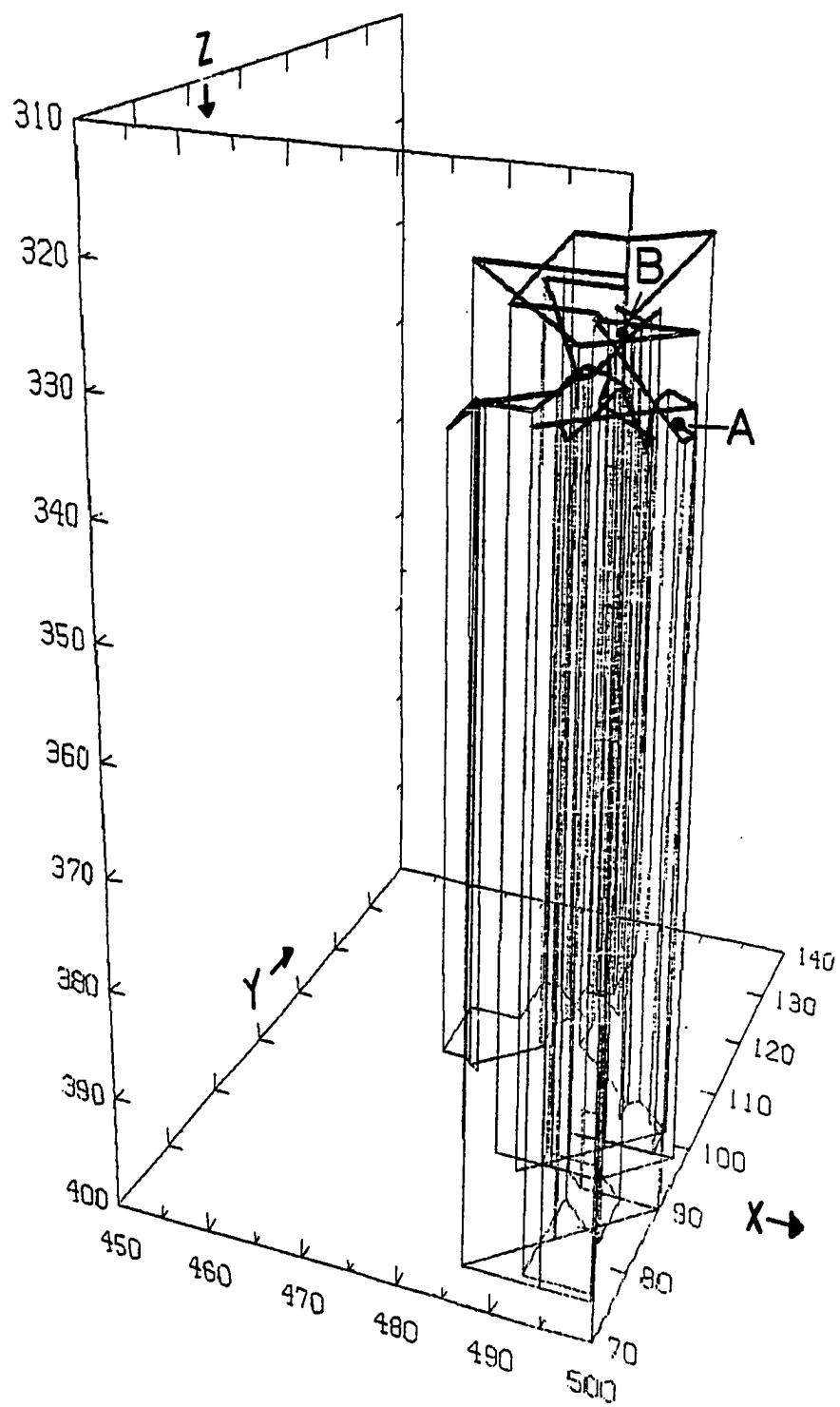
the magnitude of movement in the second model are the same as described for the first group of simulations, model PREY.

Fig. 31 is a computer-generated diagram of the behavior of prey item #5 for the first minute of a simulation. The scale is the same as in Fig. 27 (p. 121). This model will be referred to as PREY 2.

Prey Behavior #3--The final swimming strategy which I modeled was patterned after the "hop and sink" swimming behavior exhibited by copepods such as Calanus finmar- chicus (Haury and Weihs 1976). The prey items were considered negatively buoyant; if they were not actively swimming, they sank passively. The first step in simulating prey movement was to determine a direction of movement in the X-Y plane. Then the magnitude of the prey's "hop" was determined. Once the prey item was moved to its new location, it sank a stochastically determined length of time at a fixed rate after which the process started again.

Movement in the X-Y plane was determined in a manner similar to that used in the model PREY, except that each of the eight possible directions of movement in the X-Y plane, as well as no X-Y movement, was given an equal probability of occurring. The prey item then moved upward in the -Z direction and along the X- and/or Y-axis depending on which direction was chosen in the X-Y

Fig. 31. Path of prey item #5 during the initial minute of one simulation of model PREY2. The prey's path is delineated by the heavy, dark line. Point A represents its original location; point B is the prey position 60 seconds later.



plane. The prey item then "sank" or moved in the +Z direction a stochastically-determined number of seconds at a rate of 1 mm second<sup>-1</sup>.

According to Haury and Weihs (1976), there is usually no appreciable change in the average depth during the "hop and sink" maneuver. Therefore, I programmed the magnitude of the hop to be selected stochastically from a uniform distribution ranging from 1 to 9 mm. Similarly, the period of time spent sinking was determined from a uniform distribution of between 1 and 9 seconds, resulting in a sinking distance of between 1 and 9 mm as well.

The boundary conditions for the X- and Y-axes were the same as described in the section outlining the first model, PREY. The boundary conditions for the Z-axis were as follows. At the "top" of the system space (Z=1), if the next iteration would position the prey outside the system, the prey item was not moved upward but instead allowed to sink for a stochastically-determined number of seconds (as if it had first moved upward) plus an additional number of seconds equal to the magnitude of the scheduled "hop" which would have put the particular prey item outside the system volume. Conversely, if the prey item was slated to sink out of the system volume at a Z coordinate at 500, the prey item would swim upward a stochastically-determined distance plus an additional number of millimeters equal to the remaining number of

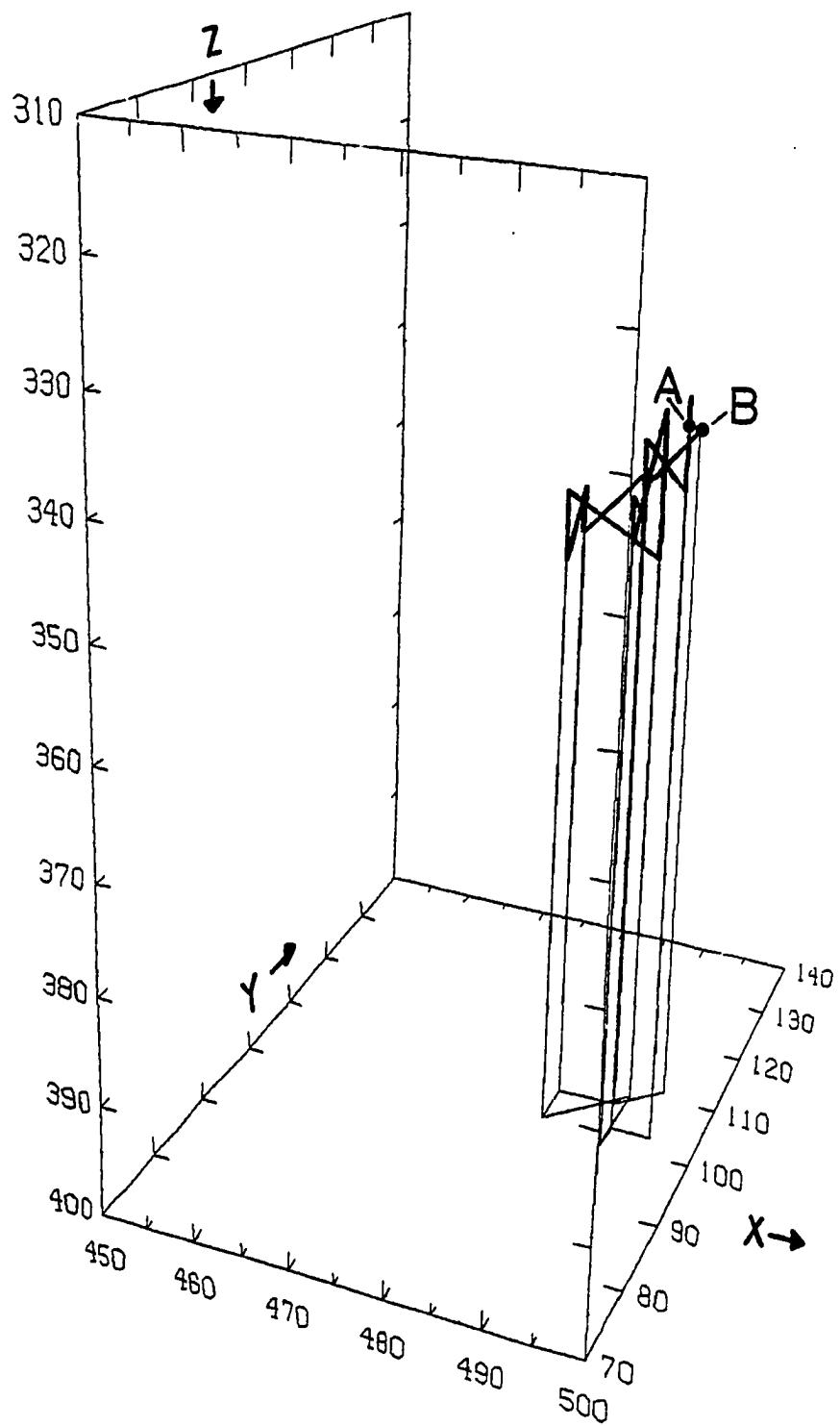
seconds it was supposed to sink when the Z coordinate became 500.

A group of test simulations was run to assure that prey items would not become "caught" along the edges or in the corners of the system due to boundary conditions imposed in the above models. During these simulations, prey were initially positioned along the system edges and in the system corners. Careful examination of prey movement from one second to the next in these test simulations showed that the prey were not congregating along the system boundaries due to the boundary conditions. An examination of these test results also indicated that, after a period of time, most prey were not distributed near the bottom or top or along one edge of the system volume.

Fig. 32 diagrams the path which prey item #5 followed during the initial minute of a simulation. A comparison of Figs. 27 (p. 120), 31 (p. 130), and 32 indicates that prey movement under the latter group of rules and probability functions is predominantly vertical. It can also be seen that the cumulative distance moved by the prey items in this last model is much less than in the previous models due to the time the prey spent sinking and the relatively slow sinking rate.

As in PREY and PREY2, five simulations were performed using this model (which I have designated PREY3) so that

Fig. 32. Path of prey item #5 during the initial minute of one simulation of model PREY3. The prey's path is delineated by the heavy, dark line. Point A represents its original location; point B is the prey position 60 seconds later.



an average number of prey encountered could be calculated.

In addition to the three models just described, a limited number of simulations were run to determine whether or not the predator's three-dimensional shape and/or orientation are important in affecting the prey encounter rate by this predator. A form of sensitivity analysis was used in which two situations were tested: the first doubled the length of the predator's tentacles in each model, while the second rotated the predator 90° in space so that the center stem of the animal now lay normal to the Y-Z plane.

### Results

Table 13 displays the results of the five simulations run for each of the three models, PREY, PREY2, and PREY3. The second model, characterized by directed (non-random) X-Y movement and reduced vertical movement, exhibited the largest number of encounters during the four-hour simulation while the third model, PREY3, never resulted in an encounter. Tables 14 and 15 include specifics of the timing and location of encounters in the first two models.

A nonparametric one-way analysis of variance (Conover 1971) testing the null hypothesis that there was no difference between the number of encounters from one

Table 13. Number of prey encountered over the four-hour simulation period for five runs of each of the three models (PREY, PREY2, PREY3).

Simulation Number	Model Used		
	PREY	PREY2	PREY3
1	2	7	0
2	0	6	0
3	3	5	0
4	4	3	0
5	4	3	0
x ± s.d.	2.5±1.8	4.8±1.8	0

Table 14. Summary of simulation results of model PREY including prey item encountered, prey's original coordinates, coordinates of encounter and time of encounter.

Simulation Number	Prey Item	Original Coordinates	Encounter Coordinates	Time of Encounter (sec)
1	6	182,26,312	252,248,240	1,910
	3	119,253,179	266,266,269	4,651
No Encounters				
3	9	42,411,341	243,243,251	4,107
	13	204,145,75	229,229,278	10,042
	12	290,351,205	231,269,275	11,125
4	12	290,351,205	253,247,242	3,256
	10	324,72,265	269,250,274	3,290
	10	331,321,348	249,249,229	6,392
	8	103,252,74	231,269,256	10,775
5	2	168,61,349	271,250,279	4,745
	13	204,145,75	260,250,238	6,580
	13	331,321,348	250,233,270	7,147
	14	464,350,257	270,230,276	7,965

Table 15. Summary of simulation results of model PREY2 including prey item encountered, prey's original coordinates, coordinates of encounter and time of encounter.

Simulation Number	Prey Item	Original Coordinates	Encounter Coordinates	Time of Encounter (sec)
1	8	103,252,74	259,250,255	1,704
	10	324,72,265	259,259,255	5,313
	14	464,350,257	259,250,254	6,057
	8	297,119,247	234,266,268	9,431
	6	182,26,312	243,250,241	11,287
	3	119,253,179	264,236,265	11,496
	6	207,421,395	250,267,270	13,489
2	10	324,72,265	262,238,242	1,622
	10	297,119,247	250,253,242	2,508
	12	290,351,205	228,250,234	3,167
	7	145,47,151	250,272,280	4,564
	4	15,51,306	238,238,260	10,246
	11	227,424,416	266,250,269	13,071
	3	119,253,179	247,250,234	189
3	3	297,119,247	238,250,260	2,828
	4	15,51,306	245,245,246	9,468
	4	295,359,348	233,267,270	10,465
	14	464,350,257	233,233,253	10,913
	6	182,26,312	264,236,256	7,397
	3	119,253,179	259,241,246	12,001
	12	290,351,205	270,270,277	12,735
5	14	464,350,257	230,262,243	3,948
	2	168,61,349	265,235,249	4,248
	1	104,465,226	257,257,233	13,319

model to the next was performed. At an  $\alpha$ -level of 0.01, there was sufficient evidence to assume that the mean number of encounters was significantly different among the models.

Tables 16, 17 and 18 indicate the coordinates of encounter, time of encounter, and prey item encountered for the three models under the two model modifications (extended tentacles and rotated predator). Table 19 compares the average number of encounters resulting from the modified models with the original models. Extending the tentacles of the predator resulted in more prey encounters than recorded originally, while rotating the predator  $90^\circ$  resulted in little or no change in the number of prey encountered over four hours. Although my limited computer budget allowed few replicates under the modifying conditions, the average number of encounters followed consistent patterns.

### Discussion

The three original models were designed to characterize three very different modes of prey swimming. To contrast with the swimming behavior of model PREY, PREY2 was designed to emphasize the horizontal and directional components of swimming, while PREY3 was programmed so that prey swam with an accentuated vertical component. The observed differences, significant at the  $\alpha=0.01$  level,

Table 16. Summary of results using model modifications for simulation model PREY.

Simulation Number	Prey Item	Original Coordinates	Encounter Coordinates	Time of Encounter (sec)
Modification--Length of Tentacles Doubled				
1	10	324,72,265	274,226,276	3,935
	5	495,103,336	245,245,247	9,156
	14	464,350,257	250,228,281	11,280
Modification--Predator Rotated 90° in the X-Z Plane				
1	12	290,351,205	242,262,250	2,977
	9	42,411,341	261,250,262	3,006
	12	292,119,247	259,250,261	7,654
2	12	290,351,205	221,251,251	11,874
	3	119,253,179	278,250,271	13,414
3	No Encounters			

Table 17. Summary of results using model modifications for simulation model PREY2.

Simulation Number	Prey Item	Original Coordinates	Encounter Coordinates	Time of Encounter (sec)
Modification--Length of Tentacles Doubled				
1	7	145,47,151	205,250,327	7,362
	11	227,424,416	243,243,233	8,249
	7	297,119,247	250,220,287	8,329
	4	15,51,306	228,272,280	8,776
	10	324,72,265	274,246,284	9,515
Modification--Predator Rotated 90° in the X-Z Plane				
1	4	15,51,306	222,222,292	544
	6	182,26,312	295,205,327	3,389
	6	331,321,348	291,291,301	3,413
	14	464,350,257	262,250,261	3,542
	9	42,411,341	293,207,314	9,424
	5	495,103,336	250,286,309	9,483
	1	104,465,226	260,260,248	9,750
2	3	119,253,179	220,249,249	3,445
	4	15,51,306	242,238,262	3,618
	4	331,321,348	240,248,252	8,317
3	12	290,351,205	256,260,240	6,479
	8	103,252,74	253,258,258	7,701
	10	324,72,265	231,250,249	12,308

Table 18. Summary of results using model modifications for simulation model PREY3.

Simulation Number	Prey Item	Original Coordinates	Encounter Coordinates	Time of Encounter (sec)
<b>Modification--Length of Tentacles Doubled</b>				
1	11	227,424,416	262,238,252	5,838
2	6	182,26,312	261,239,249	10,857
<b>Modification--Predator Rotated 90° in the X-Z Plane</b>				
1			No Encounters	
2			No Encounters	
3			No Encounters	

Table 19. Average number of prey encountered during four-hour simulations for the original three models and the two model modifications. See text for detailed explanation of model modifications.

Model	<u>Model Modifications</u>		
	Original Results	Extended Tentacles	Rotated Predator
PREY	2.5 (n=5)	5 (n=2)	1.7 (n=3)
PREY2	4.8 (n=5)	6 (n=2)	4 (n=3)
PREY3	0 (n=5)	1 (n=2)	0 (n=3)

in number of prey encountered during the PREY, PREY2 and PREY3 simulations, as determined by analysis of variance, can be attributed to the qualitative and quantitative differences in prey behavior in the three models.

In terms of qualitative differences, model PREY2 is characterized by non-random, directed swimming behavior in the vertical and horizontal directions, while prey movement in the first model, PREY, is random in the X-Y plane and along the Z-axis. The third model, PREY3, displays both random and non-random directional qualities. For example, prey movement is directionally non-random along the Z-axis since the prey items dart "upward" and then sink. Although the sinking maneuver allows no movement in the X-Y plane, the assignment of an X-Y direction during the prey's "hop" does occur in a random manner.

Quantitative differences in prey behavior are also present in all three models. These differences are particularly apparent when contrasting models PREY and PREY2 with model PREY3. As previously mentioned, the slow sinking rate of prey in the third model substantially reduces the distance traveled by the prey items over a given time interval. Prey movement in the first model, PREY, is also quantitatively different from PREY2 since the reduced probability of vertical prey movement (a qualitative characteristic) in the second model manifests

itself in a reduction in the distance traveled (a quantitative characteristic) by the prey in the vertical direction. Undoubtedly, it is the combination of these qualitative and quantitative aspects of prey behavior which resulted in the differences in the number of prey encountered in these simulations.

Other modelers have reached similar conclusions regarding the importance of prey behavior to prey encounter rates by predators. Gerritsen and Strickler (1977) and Gerritsen (1980) have formulated a predator/prey model to examine the probability of encounter between "point" prey and "point" predators in space. Their results for predators encountering randomly swimming prey indicate two optimal encounter strategies: (1) cruising predators which prey upon slow-moving animals and (2) ambush (non-moving) predators which prey upon fast-swimming prey. From their results, one would expect siphonophores, with their ambush mode of predation, to encounter larger numbers of fast-moving prey than slow-moving prey. The observed preference by some siphonophores of different groups of prey, most often distinguished by size (see Purcell 1981c) is probably in part due to the quantitative and qualitative characteristics of the swimming behavior of the preferred prey.

The results of the simulations performed using the modified models in the sensitivity analysis indicate

that lengthening the predator's tentacles is more effective in increasing the number of prey encounters than rotating the predator 90° in space. It has been suggested (Biggs 1977a) that one way a tentaculate predator might increase its encounter rate would be to assume an optimal fishing configuration in three-dimensional space for the prey present at that particular location at that point in time. The results of the original models and the models with the rotated predators display essentially no difference in the number of prey encountered over a four-hour period. Unfortunately, my limited computer budget did not allow me to run many replicates using this model modification, nor did it allow me to test other predator spatial orientations. However, the hypothesis that a tentaculate predator can affect its prey encounter rate by altering its three-dimensional orientation is worthy of further study.

The quantitative differences in prey encounter simulated for prey with different swimming behaviors emphasizes the importance of the kind of prey used in field and laboratory foraging experiments. Experimentation using prey such as Artemia, which are readily culturable yet atypical of the open-ocean environment, may generate anomalous results. The degree of error will depend on how different the behavior of the experimental prey might be from that of the dominant wild species in

the habitat of interest.

Since a principal goal of this group of models was to determine whether prey swimming behavior influenced prey encounter by tentaculate planktivores, validation of the models involved verifying or debugging the programs to assure the "theoretical" prey swam in the conceptual manner described above and did not artificially accumulate in corners or at the edges of the system. Although the purpose of these models was not to mimic the swimming behavior of any specific prey taxon, the assumptions made in defining prey movement were chosen to be representative of broad groups of marine net-zooplankton.

Published data dealing with the swimming behavior of marine copepods is rather scanty. Most quantitative information dealing with zooplankton swimming is couched in the context of vertical migration studies, and consequently investigators have stressed the importance of "hop and sink" swimming behavior (Bainbridge 1952; Hardy and Bainbridge 1954). It is provocative that hop and sink swimming not only resulted in fewer encounters in these simulations, but has been shown theoretically to save energy relative to continuous swimming at a fixed depth by negatively buoyant zooplankton (Haury and Weihs 1976).

Using new technology and instrumentation, such as video data processing (Cowles 1982) and Schlieren

photography (Strickler 1977), investigators have begun to describe the quantitative swimming behavior of marine zooplankton.

Table 20 is a comparison of the data generated by my three simulation models with experimentally-determined foraging rates from large volume aquaria stocked at a prey density of  $113 \text{ m}^{-3}$  (see Chapter III). I will not imply that this comparison is a form of validation for my simulation models, since the actual swimming behavior of the prey in the large volume foraging experiments was unknown. I do, however, draw attention to the fact that the liters foraged per hour calculated from the simulation results is the same order of magnitude as that determined from the tank experiments.

A direct comparison between experimental foraging results and the results of simulations similar to these will have to await (1) more quantitative data about the behavior of specific prey, (2) experimental foraging results using mono-specific prey as food, and (3) results from models simulating the swimming behavior of specific prey. In addition, the results of foraging experiments and the computer simulations are not directly comparable because the computer simulations flag encounters while the foraging experiments document only successful captures. Shipboard observations of siphonophores in holding tanks by myself and others suggest that not every encounter

Table 20. Average number of prey encountered (range in parenthesis) and calculated liters foraged per hour for each computer simulation model, compared with the number of prey encountered (assuming 100% capture success) and calculated liters foraged per hour from large volume foraging experiments using Forskalia sp. as the predator, at a prey density of  $113 \text{ m}^{-3}$ .

Source	Number Encountered/4 Hrs.	Liters Foraged Per Hour
PREY	2.5 (0-4)	5.5
PREY2	4.8 (3-7)	10.7
PREY3	0	0
Determined Via Foraging Experiment	0.8 (0-2.2)	1.8

results in a capture.

One problem with any shipboard foraging experiment, such as those described in Chapter III, is the variance inherent in the data. The variance in the computer simulations indicates that a substantial portion of the variance in the large-volume foraging experiments may be caused by the behavior of the prey alone. This is particularly important in my large volume experiments since I used a number of different copepod genera as prey (i.e. Euchaeta, Rhincalanus, Candacia, Nannocalanus, Corycaeus, Scolecithrix, and Eucalanus). Any variation in predator fishing behavior would only compound this problem, resulting in still higher variances. On the other hand, simulations such as those I have outlined above can be used as a first approximation to determine the number of replicate experiments the investigator may have to perform to achieve the precision desired.

Gerritsen and Strickler (1977) state that the two types of predator encounter strategies (ambush versus cruising) and their specialization on prey with different speeds, listed above, suggest a mechanism for resource partitioning (MacArthur 1972). However, they are quick to point out that resource partitioning depends on competitive displacement and their encounter model does not consider competition between predators as an input. Yet the results of their model, based on physics and

probability, indicate the potential for different predators to focus on different kinds of prey. In a similar manner, the results of my models and simulations indicate that prey behavior, as determined by prey swimming direction and speed, is also capable of providing a mechanism whereby one predator may be able to have an advantage over another.

This investigation, which is the first to model a three-dimensional open-ocean planktivore, has emphasized the usefulness of simulated predator/prey interactions with three-dimensional predators. Mills was correct in her 1981 paper on hydromedusae feeding when she objected to the notion that the feeding efficiency of gelatinous tentaculate predators could be characterized by a simple relationship with tentacle length. In fact, prey swimming behavior as demonstrated quantitatively by these models, in concert with factors such as tentacle length and number, is important in determining the number of prey encountered by oceanic tentaculate predators.

CHAPTER V  
GENERAL SUMMARY AND SPECULATIONS

Estimates of the daytime population abundance of physonect and selected calycophore siphonophores were made by SCUBA divers during quarterly cruises to the western Gulf of Mexico. This in situ tally program focused upon contrasting the near-surface gelatinous zooplankton distributions in mesoscale cyclonic physical features with those in anticyclonic features. In early spring in the western Gulf, physonect siphonophores averaged 5/25,000 m<sup>3</sup>, while during the summer physonects were rarely observed (<1/25,000 m<sup>3</sup>). In the fall, physonects averaged 30/25,000 m<sup>3</sup> and 8/25,000 m<sup>3</sup> within the upper 15 m of the cyclonic and anticyclonic features, respectively, whereas in winter they averaged 16/25,000 m<sup>3</sup> and 8/25,000 m<sup>3</sup>, respectively.

The 12 dives during which siphonophore abundance estimates were made on the fall research cruise allow for a statistical comparison of early morning/late afternoon and cyclonic/anticyclonic physonect abundances. Morning and late afternoon physonect densities were not significantly different; however, a significant difference between near-surface physonect abundances within cyclonic and anticyclonic features was documented in

both fall and winter, when physonect siphonophores were more abundant in the cyclone.

Both physical and biological factors appear to be responsible for the siphonophore densities encountered in the western Gulf of Mexico. For example, during the summer, the upper 30-40 m of the study region was characterized by uniformly warm temperatures. This 29°-30°C strongly stratified surface layer may have restricted the siphonophore population from moving into the near-surface waters. At other times of the year when the near-surface temperature and density field is more heterogeneous, factors such as differences in primary or secondary productivity between the cyclonic and anticyclonic regions may create different patterns of physonect abundance.

Large volume foraging experiments were also conducted as a part of this study. Specially designed 177-liter feeding aquaria were constructed to minimize container effects on prey and predator behavior. I used the tentaculate predator Forskalia sp. in these experiments which were run at prey densities of 51, 113, 226 and 452 prey  $\text{m}^{-3}$ . When a mixed population of oceanic copepods was provided as prey, ingestion rates for the physonect siphonophore Forskalia were proportional to prey concentration at or above copepod densities of 200 prey  $\text{m}^{-3}$ . The median foraging rate was 4 liters hour<sup>-1</sup>.

At a physonect density of 30/25,000 m<sup>-3</sup> (the highest average physonect density observed in either the cyclone or anticyclone in this study), the resident physonect population in a 12-hour period would forage less than 1% of the 25,000 m<sup>-3</sup>. Assuming a foraging rate three times that observed in the small tank experiments (the foraging rate computed from three feeding experiments in the 1000-liter tanks), the total volume foraged over 12 hours still remains less than 1% of the 25,000 m<sup>-3</sup>.

A simple comparison of the energy required for respiration by a 5 mg protein Forkalia with the food energy theoretically available to Forskalia feeding at different prey densities was also made (Chapter III). This comparison indicates Forskalia may not be able to process enough energy to survive over the range of prey densities typical of oligotrophic environments. However, quality as well as quantity of the prey is important. As shown in Table 10 (p. 99), the "energy density" of the prey captured by Forskalia could make the difference between processing and not processing enough energy to survive at a particular prey density.

Prey behavior is also important to prey encounter by tentaculate planktivores and, consequently, predator survival. The three prey swimming behaviors simulated in Chapter IV resulted in quantitatively different numbers of prey encountered over the four-hour simulation

period. In fact, the observed differences in the simulated number of prey encountered could result in Forskalia starving or thriving at a prey density of  $112 \text{ m}^{-3}$ , due only to the qualitative and quantitative aspects of prey swimming behavior. For example, the model characterized by "hop and sink" prey behavior (PREY3) resulted in no encounters. On the other hand, model PREY2, in which prey behavior was defined as directed in the X-Y plane, with a reduced probability of movement in the Z direction resulted in an average of five prey encountered during the simulation interval. By increasing the number of prey encountered and successfully captured, the necessity that the prey have a high energy density is reduced. Consequently, from the results of this study, it appears that the temporal and spatial distribution of prey, the quality of the prey (in terms of energy density) and prey swimming behavior are important in determining whether or not tentaculate planktivores like Forskalia are resource limited.

This study has generated quantitative estimates of the ecological role and trophic importance of gelatinous predators in the open ocean. Such estimates, made for a variety of different gelatinous planktivores, will ultimately allow gelatinous carnivores to be incorporated into system models of the pelagic ecosystem (Steele and Mullin 1977; Vinogradov and Menshutkin 1977).

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APPENDIX A  
SCUBA Station Log

TAMU Dive No.	Position	Date	Local Time	Abundance Estimates Made
001	Flower Gardens, Gulf of Mexico	16 May 1978	-	No
002	Flower Gardens, Gulf of Mexico	17 May 1978	-	No
003	Flower Gardens, Gulf of Mexico	17 May 1978	-	No
004	Flower Gardens, Gulf of Mexico	18 May 1978	-	No
005	Flower Gardens, Gulf of Mexico	18 May 1978	-	No
006	27°28'N 93°36'W	29 Oct 1978	0904	No
007	26°57'N 93°36'W	29 Oct 1978	1638	No
008	27°13'N 94°43'W	30 Oct 1978	0946	No
009	The Bahamas	20 June 1979	-	No
010	The Bahamas	21 June 1979	0700	Yes
011	The Bahamas	22 June 1979	0700	Yes
012	The Bahamas	23 June 1979	0700	Yes
013	The Bahamas	24 June 1979	1830	Yes
014	The Bahamas	25 June 1979	1830	Yes
015	The Bahamas	26 June 1979	1830	Yes
016	The Bahamas	20 Sep 1979	1800	No
017	The Bahamas	21 Sep 1979	1800	No
018	The Bahamas	22 Sep 1979	1800	No
019	The Bahamas	23 Sep 1979	1800	No
020	The Bahamas	24 Sep 1979	1800	No
021	The Bahamas	25 Sep 1979	1800	No
022	27°59'N 93°32'W	7 Dec 1979	1240	No
023	27°36'N 93°37'W	8 Dec 1979	1040	No
024	27°20'N 93°37'W	8 Dec 1979	1545	No
025	27°19'N 91°49'W	12 Dec 1979	1445	No
026	27°01'N 91°18'W	13 Dec 1979	1628	No
027	22°36'N 95°03'W	2 April 1980	0730	No
028	21°58'N 95°02'W	2 April 1980	1700	Yes
029	23°15'N 95°00'W	3 April 1980	0730	Yes
030	24°05'N 94°59'W	3 April 1980	1715	Yes
031	26°01'N 94°31'W	7 April 1980	1730	Yes
032	26°08'N 94°33'W	8 April 1980	0730	Yes
033	22°31'N 93°58'W	10 April 1980	0730	No
034	23°51'N 94°58'W	12 April 1980	1115	No

TAMU Dive No.	Position	Date	Local Time	Abundance Estimates Made
035	27°00'N 95°00'W	17 July 1980	1821	No
036	25°48'N 95°00'W	18 July 1980	0820	Yes
037	24°50'N 94°59'W	18 July 1980	1840	Yes
038	24°31'N 95°00'W	19 July 1980	0800	Yes
039	24°30'N 95°00'W	19 July 1980	1855	Yes
040	24°26'N 95°06'W	20 July 1980	0815	Yes
041	24°22'N 95°02'W	21 July 1980	1850	Yes
042	24°29'N 94°02'W	22 July 1980	0929	No
043	25°10'N 93°59'W	22 July 1980	1747	Yes
044	26°10'N 94°00'W	23 July 1980	0832	Yes
045	26°59'N 95°07'W	24 July 1980	0800	Yes
046	26°28'N 95°02'W	24 July 1980	1806	No
047	26°20'N 95°04'W	25 July 1980	1650	No
048	26°15'N 95°07'W	26 July 1980	0815	No
049	27°16'N 94°57'W	26 Oct 1980	1445	No
050	23°08'N 95°36'W	28 Oct 1980	1600	Yes
051	23°51'N 95°15'W	31 Oct 1980	1630	Yes
052	23°52'N 95°12'W	1 Nov 1980	0807	No
053	23°49'N 95°12'W	1 Nov 1980	1600	Yes
054	23°39'N 95°13'W	2 Nov 1980	0730	Yes
055	23°34'N 95°13'W	2 Nov 1980	1645	No
056	23°26'N 95°17'W	3 Nov 1980	0635	Yes
057	22°55'N 97°11'W	4 Nov 1980	1615	No
058	24°29'N 96°24'W	5 Nov 1980	0714	Yes
059	25°17'N 96°00'W	5 Nov 1980	1610	Yes
060	26°55'N 96°00'W	6 Nov 1980	0700	Yes
061	27°00'N 94°42'W	6 Nov 1980	1610	Yes
062	25°59'N 93°59'W	7 Nov 1980	0702	Yes
063	26°08'N 93°48'W	7 Nov 1980	1612	Yes
064	25°59'N 94°22'W	8 Nov 1980	0655	Yes
065	26°09'N 94°00'W	8 Nov 1980	1607	Yes
066	26°05'N 94°08'W	9 Nov 1980	0655	Yes
067	25°59'N 94°10'W	9 Nov 1980	1613	Yes
068	25°51'N 94°15'W	10 Nov 1980	0709	Yes
069	25°45'N 94°13'W	10 Nov 1980	1600	No
070	27°08'N 95°12'W	19 Feb 1981	1645	Yes
071	25°49'N 95°30'W	20 Feb 1981	0800	Yes
072	25°45'N 95°30'W	20 Feb 1981	1645	Yes
073	25°43'N 95°30'W	21 Feb 1981	0717	Yes
074	24°00'N 95°30'W	23 Feb 1981	1610	Yes
075	24°07'N 95°43'W	24 Feb 1981	0730	Yes
076	24°13'N 95°49'W	24 Feb 1981	1630	Yes

TAMU Dive No.	Position	Date	Local Time	Abundance Estimates Made
077	24°20'N 95°56'W	25 Feb 1981	0800	Yes
078	26°21'N 95°45'W	26 Feb 1981	1630	Yes
079	26°09'N 95°19'W	27 Feb 1981	0755	No

APPENDIX B

Results of Foraging Experiments  
Performed Using Tentaculate Gelatinous  
Carnivores Other Than Forskalia sp.

<u>Predator</u>	<u>Size of Predator</u>	<u>Initial Prey Density (per m<sup>3</sup>)</u>	<u>No. Prey Consumed</u>	<u>Duration of Experiment (min)</u>	<u>Time Experiment Initiated</u>	<u>Dive Captured</u>
<b>SIPHONOPHORES</b>						
<i>Athorybia rosacea</i>	--	226	3	255	2215	043
<i>Agalma elegans</i>	--	51	2	90	1145	J-080
<i>A. elegans</i>	--	51	0	90	1145	J-080
<i>Physophora hydronota</i>	--	226	3	280	0130	030
<i>P. hydronota</i>	--	226	1	240	2350	030
<b>HYDROMEDUSA</b>						
<i>Orchistoma sp.</i>	18 mm <sup>1</sup>	226	0	240	0300	049
<i>Liriope sp.</i>	22 mm <sup>1</sup>	226	0	315	0300	053
<i>Racostoma sp.</i>	64 mm <sup>1</sup>	226	1	300	0100	057
<b>CTENOPHORES</b>						
<i>Eurhamphaea vexilligera</i>	4.20 mg pro	226	10	240	1000	052
<i>E. vexilligera</i>	--	226	0	180	1215	043
<i>E. vexilligera</i>	1.87 mg. pro	226	1	465	1500	052
Tentaculate ctenophore	--	113	0	150	2258	J-084
Tentaculate ctenophore	--	113	0	210	2335	J-084
Tentaculate ctenophore	--	113	0	98	0352	J-084
Tentaculate ctenophore	--	113	0	120	2150	J-084
Tentaculate ctenophore	--	113	1	155	2155	J-084

<sup>1</sup> Bell diameter.

**APPENDIX C**

**Listing of Computer Program Used  
in Model PREY**

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1. //PREY JOB (S61B,001A,S9B,100,HA),'SMITH'
2. /*LEVEL      0
3. //STEP EXEC WATFIV,REGION=126K
4. //SYSIN DD DATA
5. //OPTIONS
6.          DIMENSION IPRX(14),IPRY(14),IPRZ(14)
7.          INTEGER H,HH,HHH
8.          DOUBLE PRECISION DSEED
9.          IN=1
10.         IM=300
11.         IJ=1
12.         HHH=0
13. C
14. C THIS PART OF THE PROGRAM 'SEEDS' THE RANDOM NUMBER GENERATOR
15. C THE 'SEEDS' USED IN THIS SET OF SIMULATIONS INCLUDE:
16. C 77606252.0 4818.0 7760682922.0 61768.0 353.0
17. C
18. C
19. C DSEED=77606252.00
20. C WRITE (6,999)
21. C WRITE (6,1005) DSEED
22. C
23. C
24. C THIS PART OF THE PROGRAM PUTS THE PREY IN THEIR ORIGINAL
25. C POSITIONS
26. C
27. CALL ORIG (IPRX,IPRY,IPRZ)
28. WRITE (6,1003)
29. WRITE (6,1008)
30. DO 2 IK=1,14
31.        WRITE (6,1004) IPRX(IK),IPRY(IK),IPRZ(IK),HHH
32. 2 CONTINUE
33. C
34. C
35. C THIS PART OF THE PROGRAM BEGINS THE 4-HOUR SIMULATION
36. C
37. DO 105 LI=1,14400
38. I=1
39. DO 100 LJ=1,14
40. C
41. C
42. C THIS PART OF THE PROGRAM DETERMINES THE DIRECTION OF PREY
43. C MOVEMENT STOCHASTICALLY IN THE X-Y PLANE
44. C
45. Y=GGUBFS(DSEED)
46. J=IFIX(Y*10)
47. C
48. C
49. C THIS PART OF THE PROGRAM DETERMINES THE DIRECTION OF PREY
50. C MOVEMENT STOCHASTICALLY IN THE Z DIRECTION
51. C
52. 3 Y=GGUBFS(DSEED)
53. L=IFIX(Y*10)
54. IF (L.EQ.9) GO TO 3
55. C
56. C
57. C THIS PART OF THE PROGRAM DETERMINES THE MAGNITUDE OF PREY
58. C MOVEMENT STOCHASTICALLY IN THE X-Y PLANE AND ALONG THE Z-AXIS
59. C
60. 4 Y=GGUBFS(DSEED)
61. H=IFIX(Y*10)
62. IF (H.EQ.0) GO TO 4
63. HH=H
64. LL=H
65. IF ((L.EQ.0).OR.(L.EQ.1).OR.(L.EQ.2)) LL=-LL
66. IF ((L.EQ.3).OR.(L.EQ.4).OR.(L.EQ.5)) LL=0
67. IF ((IPRX(I).LT.210).OR.(IPRX(I).GT.290)) GO TO 5
68. IF ((IPRY(I).LT.210).OR.(IPRY(I).GT.290)) GO TO 5
69. IF ((IPRZ(I).GT.190).AND.(IPRZ(I).LT.300)) GO TO 45
70. C

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71. C
72. C      IF THE PREY ITEM IS OUTSIDE THE "IMMEDIATE" VICINITY OF THE
73. C      PREDATOR, THIS PART OF THE PROGRAM MOVES THE PREY TO ITS
74. C      NEW LOCATION
75. C
76. 5 IF (J.EQ.1) GO TO 10
77. IF (J.EQ.3) GO TO 15
78. IF (J.EQ.5) GO TO 20
79. IF (J.EQ.7) GO TO 25
80. IF (J.EQ.2) GO TO 30
81. IF (J.EQ.4) GO TO 35
82. IF (J.EQ.6) GO TO 40
83. IF (J.EQ.8) GO TO 44
84. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
85. IPRZ(I)=IPRZ(I)+LL
86. GO TO 99
87. 10 IF (((IPRX(I)+H).GT.500) H=-H
88. IPRX(I)=IPRX(I)+H
89. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
90. IPRZ(I)=IPRZ(I)+LL
91. GO TO 99
92. 15 IF (((IPRY(I)+H).GT.500) H=-H
93. IPRY(I)=IPRY(I)+H
94. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
95. IPRZ(I)=IPRZ(I)+LL
96. GO TO 99
97. 20 IF (((IPRX(I)-H).LT.1) H=-H
98. IPRX(I)=IPRX(I)-H
99. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
100. IPRZ(I)=IPRZ(I)+LL
101. GO TO 99
102. 25 IF (((IPRY(I)-H).LT.1) H=-H
103. IPRY(I)=IPRY(I)-H
104. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
105. IPRZ(I)=IPRZ(I)+LL
106. GO TO 99
107. 30 IF (((IPRX(I)+H).GT.500) H=-H
108. IPRX(I)=IPRX(I)+H
109. IF (((IPRY(I)+HH).GT.500) HH=-HH
110. IPRY(I)=IPRY(I)+HH
111. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
112. IPRZ(I)=IPRZ(I)+LL
113. GO TO 99
114. 35 IF (((IPRX(I)-H).LT.1) H=-H
115. IPRX(I)=IPRX(I)-H
116. IF (((IPRY(I)+HH).GT.500) HH=-HH
117. IPRY(I)=IPRY(I)+HH
118. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
119. IPRZ(I)=IPRZ(I)+LL
120. GO TO 99
121. 40 IF (((IPRX(I)-H).LT.1) H=-H
122. IPRX(I)=IPRX(I)-H
123. IF (((IPRY(I)-HH).LT.1) HH=-HH
124. IPRY(I)=IPRY(I)-HH
125. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
126. IPRZ(I)=IPRZ(I)+LL
127. GO TO 99
128. 44 IF (((IPRX(I)+H).GT.500) H=-H
129. IPRX(I)=IPRX(I)+H
130. IF (((IPRY(I)-HH).LT.1) HH=-HH
131. IPRY(I)=IPRY(I)-HH
132. IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
133. IPRZ(I)=IPRZ(I)+LL
134. GO TO 99
135. C
136. C      IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
137. C      THIS PART OF THE PROGRAM MOVES THE PREY IN THE X-DIRECTION
138. C      AND/OR Y-DIRECTION ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS
139. C      MOVED THE PRE-DETERMINED MAGNITUDE
140.

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141.      C
142.      45 DO 86 LA=1,H
143.          IF (J.EQ.1) IPRX(I)=IPRX(I)+1
144.          IF (J.EQ.3) IPRV(I)=IPRY(I)+1
145.          IF (J.EQ.5) IPRX(I)=IPRX(I)-1
146.          IF (J.EQ.7) IPRY(I)=IPRY(I)-1
147.          IF (J.NE.2) GO TO 46
148.          IPRX(I)=IPRX(I)+1
149.          IPRY(I)=IPRY(I)+1
150.      46 IF (J.NE.4) GO TO 47
151.          IPRX(I)=IPRX(I)-1
152.          IPRY(I)=IPRY(I)+1
153.      47 IF (J.NE.6) GO TO 48
154.          IPRX(I)=IPRX(I)-1
155.          IPRY(I)=IPRY(I)-1
156.      48 IF (J.NE.8) GO TO 49
157.          IPRX(I)=IPRX(I)+1
158.          IPRY(I)=IPRY(I)-1
159.      C
160.      C
161.      C     IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
162.      C     THIS PART OF THE PROGRAM MOVES THE PREY IN THE Z-DIRECTION
163.      C     ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS MOVED THE
164.      C     PRE-DETERMINED MAGNITUDE
165.      C
166.      49 IF ((L.EQ.0).OR.(L.EQ.1).OR.(L.EQ.2)) IPRZ(I)=IPRZ(I)-1
167.          IF ((L.EQ.6).OR.(L.EQ.7).OR.(L.EQ.8)) IPRZ(I)=IPRZ(I)+1
168.      C
169.      C
170.      C     THIS PART OF THE PROGRAM TESTS FOR AN ENCOUNTER BETWEEN THE
171.      C     PREDATOR AND PREY AFTER EACH UNIT MOVED BY THE PREY
172.      C
173.      50 IF (IPRY(I).NE.250) GO TO 59
174.          IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 53
175.          IZ=718-(2*IPRX(I))
176.          DO 51 LK=1,2
177.              IF (IZ.EQ.IPRZ(I)) GO TO 90
178.              IZ=IZ+1
179.      51 CONTINUE
180.          IZ=(2*IPRX(I))-282
181.          DO 52 LK=1,2
182.              IF (IZ.EQ.IPRZ(I)) GO TO 90
183.              IZ=IZ+1
184.      52 CONTINUE
185.      53 IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 56
186.          IZ=727-(2*IPRX(I))
187.          DO 54 LK=1,2
188.              IF (IZ.EQ.IPRZ(I)) GO TO 90
189.              IZ=IZ+1
190.      54 CONTINUE
191.          IZ=(2*IPRX(I))-273
192.          DO 55 LK=1,2
193.              IF (IZ.EQ.IPRZ(I)) GO TO 90
194.              IZ=IZ+1
195.      55 CONTINUE
196.      56 IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 59
197.          IZ=736-(2*IPRX(I))
198.          DO 57 LK=1,2
199.              IF (IZ.EQ.IPRZ(I)) GO TO 90
200.              IZ=IZ+1
201.      57 CONTINUE
202.          IZ=(2*IPRX(I))-264
203.          DO 58 LK=1,2
204.              IF (IZ.EQ.IPRZ(I)) GO TO 90
205.              IZ=IZ+1
206.      58 CONTINUE
207.      59 IF (IPRX(I).NE.250) GO TO 68
208.          IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 62
209.          IZ=718-(2*IPRY(I))
210.          DO 60 LK=1,2

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211.           IF ( IZ.EQ.IPRZ(I) ) GO TO 90
212.           IZ=IZ+1
213. 68   CONTINUE
214.           IZ=(2*IPRY(I))-282
215.           DO 61 LK=1,2
216.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
217.               IZ=IZ+1
218. 61   CONTINUE
219. 62   IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 65
220.           IZ=727-(2*IPRY(I))
221.           DO 63 LK=1,2
222.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
223.               IZ=IZ+1
224. 63   CONTINUE
225.           IZ=(2*IPRY(I))-273
226.           DO 64 LK=1,2
227.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
228.               IZ=IZ+1
229. 64   CONTINUE
230. 65   IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 68
231.           IZ=736-(2*IPRY(I))
232.           DO 66 LK=1,2
233.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
234.               IZ=IZ+1
235. 66   CONTINUE
236.           IZ=(2*IPRY(I))-264
237.           DO 67 LK=1,2
238.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
239.               IZ=IZ+1
240. 67   CONTINUE
241. 68   IY=500-IPRX(I)
242.           IF ( IY.NE.IPRY(I) ) GO TO 77
243.           IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 71
244.           IZ=718-(2*IPRX(I))
245.           DO 69 LK=1,2
246.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
247.               IZ=IZ+1
248. 69   CONTINUE
249.           IZ=(2*IPRX(I))-282
250.           DO 70 LK=1,2
251.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
252.               IZ=IZ+1
253. 70   CONTINUE
254. 71   IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 74
255.           IZ=727-(2*IPRX(I))
256.           DO 72 LK=1,2
257.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
258.               IZ=IZ+1
259. 72   CONTINUE
260.           IZ=(2*IPRX(I))-273
261.           DO 73 LK=1,2
262.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
263.               IZ=IZ+1
264. 73   CONTINUE
265. 74   IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 77
266.           IZ=736-(2*IPRX(I))
267.           DO 75 LK=1,2
268.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
269.               IZ=IZ+1
270. 75   CONTINUE
271.           IZ=(2*IPRX(I))-264
272.           DO 76 LK=1,2
273.               IF ( IZ.EQ.IPRZ(I) ) GO TO 90
274.               IZ=IZ+1
275. 76   CONTINUE
276. 77   IY=IPRX(I)
277.           IF ( IY.NE.IPRY(I) ) GO TO 86
278.           IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 80
279.           IZ=718-(2*IPRX(I))
280.           DO 78 LK=1,2

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281.          IF (IZ.EQ.IPRZ(I)) GO TO 90
282.          IZ=IZ+1
283.    78  CONTINUE
284.          IZ=(2*IPRX(I))-282
285.          DO 79 LK=1,2
286.              IF (IZ.EQ.IPRZ(I)) GO TO 90
287.              IZ=IZ+1
288.    79  CONTINUE
289.    80  IF (((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 83
290.          IZ=727-(2*IPRX(I))
291.          DO 81 LK=1,2
292.              IF (IZ.EQ.IPRZ(I)) GO TO 90
293.              IZ=IZ+1
294.    81  CONTINUE
295.          IZ=(2*IPRX(I))-273
296.          DO 82 LK=1,2
297.              IF (IZ.EQ.IPRZ(I)) GO TO 90
298.              IZ=IZ+1
299.    82  CONTINUE
300.    83  IF (((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 86
301.          IZ=736-(2*IPRX(I))
302.          DO 84 LK=1,2
303.              IF (IZ.EQ.IPRZ(I)) GO TO 90
304.              IZ=IZ+1
305.    84  CONTINUE
306.          IZ=(2*IPRX(I))-264
307.          DO 85 LK=1,2
308.              IF (IZ.EQ.IPRZ(I)) GO TO 90
309.              IZ=IZ+1
310.    85  CONTINUE
311.    86  CONTINUE
312.          GO TO 99
313.
314. C
315. C      THIS PART OF THE PROGRAM RECORDS ENCOUNTERS
316. C
317. 90  WRITE (6,1003)
318.          WRITE (6,1000)
319.          WRITE (6,1001)
320.          WRITE (6,1002) IPRX(I),IPRY(I),IPRZ(I)
321.          WRITE (6,1006) LI
322.          WRITE (6,1007) LJ
323.
324. C
325. C      THIS PART OF THE PROGRAM REPLACES PREY THAT HAVE BEEN
326. C      ENCOUNTERED
327. C
328.          CALL REPL (IPRX,IPRY,IPRZ,I,IJ)
329. 99  I=I+1
330.    100  CONTINUE
331.          IF (LI.NE.IM) GO TO 105
332.          WRITE (6,1003)
333.          DO 101 LK=1,14
334.              WRITE (6,1004) IPRX(LK),IPRY(LK),IPRZ(LK),LI
335.    101  CONTINUE
336.          IN=IN+1
337.          IM=IN*300
338.
339. C
340. C      THIS PART OF THE PROGRAM BEGINS A NEW SIMULATION SECOND
341. C
342. 105  CONTINUE
343. 999 FORMAT ('1')
344. 1000 FORMAT ('0',80X,'A PREY ITEM HAS BEEN ENCOUNTERED')
345. 1001 FORMAT (' ',80X,'AT COORDINATES')
346. 1002 FORMAT (89X,I3,3X,I3,3X,I3)
347. 1003 FORMAT ('0')
348. 1004 FORMAT (' ',20X,I3,5X,I3,5X,I3,5X,I5)
349. 1005 FORMAT (1X,'RANDOM NUMBER GENERATOR SEED IS',F12.1)
350. 1006 FORMAT (' ',80X,'AT TIME',2X,I5,2X,'SECONDS')

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351. 1007 FORMAT (' ',80X,'PREY ITEM',2X,I2,2X,'WAS ENCOUNTERED')
352. 1008 FORMAT (' ',21X,'X',7X,'Y',7X,'Z',5X,'TIME SEC')
353. STOP
354. END
355. C
356. C
357. C THIS SUBROUTINE PLACES THE PREY IN THEIR ORIGINAL POSITIONS
358. C
359. SUBROUTINE ORIG (IPRX,IPRY,IPRZ)
360. DIMENSION IPRX(14),IPRY(14),IPRZ(14)
361. DATA IA,IB,IC,ID,IE,IF,IG,IH,IJ,IK,IL,IM,IN,IO/104,168,
362. C119,015,495,182,145,103,042,324,227,290,204,464/
363. DATA JA,JB,JC,JD,JE,JF,JG,JH,JJ,JK,JL,JM,JN,JO/465,061,
364. C253,051,103,026,047,252,411,072,424,351,145,350/
365. DATA KA,KB,KC,KD,KE,KF,KG,KH,KJ,KK,KL,KM,KN,KO/226,349,
366. C179,306,336,312,151,074,341,265,416,205,075,257/
367. IPRX(1)=IA
368. IPRX(2)=IB
369. IPRX(3)=IC
370. IPRX(4)=ID
371. IPRX(5)=IE
372. IPRX(6)=IF
373. IPRX(7)=IG
374. IPRX(8)=IH
375. IPRX(9)=IJ
376. IPRX(10)=IK
377. IPRX(11)=IL
378. IPRX(12)=IM
379. IPRX(13)=IN
380. IPRX(14)=IO
381. IPRY(1)=JA
382. IPRY(2)=JB
383. IPRY(3)=JC
384. IPRY(4)=JD
385. IPRY(5)=JE
386. IPRY(6)=JF
387. IPRY(7)=JG
388. IPRY(8)=JH
389. IPRY(9)=JJ
390. IPRY(10)=JK
391. IPRY(11)=JL
392. IPRY(12)=JM
393. IPRY(13)=JN
394. IPRY(14)=JO
395. IPRZ(1)=KA
396. IPRZ(2)=KB
397. IPRZ(3)=KC
398. IPRZ(4)=KD
399. IPRZ(5)=KE
400. IPRZ(6)=KF
401. IPRZ(7)=KG
402. IPRZ(8)=KH
403. IPRZ(9)=KJ
404. IPRZ(10)=KK
405. IPRZ(11)=KL
406. IPRZ(12)=KM
407. IPRZ(13)=KN
408. IPRZ(14)=KO
409. RETURN
410. END
411. C
412. C
413. C THIS SUBROUTINE REPLACES A PREY ITEM WHICH HAS BEEN LOST
414. C FROM THE SYSTEM DUE TO ENCOUNTER
415. C
416. SUBROUTINE REPL (IPRX,IPRY,IPRZ,I,IJ)
417. DIMENSION IPRX(14),IPRY(14),IPRZ(14)
418. DATA K1,L1,M1/297,119,247/
419. DATA K2,L2,M2/331,321,348/
420. DATA K3,L3,M3/295,359,348/

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421.      DATA K4,L4,M4/190,87,369/
422.      DATA K5,L5,M5/207,421,395/
423.      IF (IJ.EQ.1) GO TO 10
424.      IF (IJ.EQ.2) GO TO 20
425.      IF (IJ.EQ.3) GO TO 30
426.      IF (IJ.EQ.4) GO TO 40
427.      IF (IJ.EQ.5) GO TO 50
428.      10  IPRX(I)=K1
429.      IPRY(I)=L1
430.      IPRZ(I)=M1
431.      GO TO 60
432.      20  IPRX(I)=K2
433.      IPRY(I)=L2
434.      IPRZ(I)=M2
435.      GO TO 60
436.      30  IPRX(I)=K3
437.      IPRY(I)=L3
438.      IPRZ(I)=M3
439.      GO TO 60
440.      40  IPRX(I)=K4
441.      IPRY(I)=L4
442.      IPRZ(I)=M4
443.      GO TO 60
444.      50  IPRX(I)=K5
445.      IPRY(I)=L5
446.      IPRZ(I)=M5
447.      IJ=0
448.      60  IJ=IJ+1
449.      RETURN
450.      END
451.      //SDATA
```

APPENDIX D

Listing of Computer Program Used  
in Model PREY2

```

1. //PREYZ JOB (S610,001A,100,100,DS),'SMITH'
2. /*LEVEL
3. //STEP EXEC WATFIV,REGION=185K
4. //SYSIN DD DATA
5. //OPTIONS
6.      DIMENSION IPRX(14),IPRY(14),IPRZ(14),ID(14)
7.      INTEGER H,HH,HHH
8.      DOUBLE PRECISION DSEED
9.      IN=1
10.     IM=300
11.     IJ=1
12.     HHH=0
13. C
14. C
15. C   THIS PART OF THE PROGRAM 'SEEDS' THE RANDOM NUMBER GENERATOR
16. C   THE 'SEEDS' USED IN THIS SET OF SIMULATIONS INCLUDE:
17. C   1234567.0 25595.0 521802084.0 843782.0 9773555977.0
18. C
19. DSEED=1234567.0
20. WRITE (6,999)
21. WRITE (6,1005) DSEED
22. C
23. C
24. C   THIS PART OF THE PROGRAM PUTS THE PREY IN THEIR ORIGINAL
25. C   POSITIONS
26. C
27. CALL ORIG (IPRX,IPRY,IPRZ,ID)
28. WRITE (6,1003)
29. WRITE (6,1008)
30. DO 2 IK=1,14
31.     WRITE (6,1004) IPRX(IK),IPRY(IK),IPRZ(IK),HHH,ID(IK)
32. 2 CONTINUE
33. C
34. C
35. C   THIS PART OF THE PROGRAM BEGINS THE 4-HOUR SIMULATION
36. C
37. DO 105 LI=1,14400
38. I=1
39. DO 100 LJ=1,14
40. C
41. C
42. C   THIS PART OF THE PROGRAM DETERMINES THE DIRECTION OF PREY
43. C   MOVEMENT STOCHASTICALLY IN THE X-Y PLANE
44. C
45. Y=GGUBFS(DSEED)
46. J=IFIX(Y*10)
47. C
48. C
49. C   THIS PART OF THE PROGRAM DETERMINES THE DIRECTION OF PREY
50. C   MOVEMENT STOCHASTICALLY IN THE Z DIRECTION
51. C
52. Y=GGUBFS(DSEED)
53. L=IFIX(Y*10)
54. C
55. C
56. C   THIS PART OF THE PROGRAM DETERMINES THE MAGNITUDE OF PREY
57. C   MOVEMENT STOCHASTICALLY IN THE X-Y PLANE AND ALONG THE Z-AXIS
58. C
59. 4 Y=GGUBFS(DSEED)
60. H=IFIX(Y*10)
61. IF (H.EQ.0) GO TO 4
62. HH=H
63. LL=H
64. IF ((L.EQ.0).OR.(L.EQ.1)) LL=-LL
65. IF ((L.EQ.2).OR.(L.EQ.3).OR.(L.EQ.4).OR.(L.EQ.5).OR.(L.EQ.6)
66. C.OR.(L.EQ.7)) LL=0
67. IF (((IPRX(I).LT.210).OR.(IPRX(I).GT.290)) GO TO 5
68. IF (((IPRY(I).LT.210).OR.(IPRY(I).GT.290)) GO TO 5
69. IF (((IPRZ(I).GT.190).AND.(IPRZ(I).LT.300)) GO TO 45
70. C

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71. C      IF THE PREY ITEM IS OUTSIDE THE "IMMEDIATE" VICINITY OF THE
72. C      PREDATOR, THIS PART OF THE PROGRAM MOVES THE PREY TO ITS
73. C      NEW LOCATION
74. C
75. C
76.      5 IF (J.EQ.0) GO TO 99
77.      IF ((ID(I).EQ.1) GO TO 280
78.      IF ((ID(I).EQ.2) GO TO 380
79.      IF ((ID(I).EQ.3) GO TO 480
80.      IF ((ID(I).EQ.4) GO TO 580
81.      280 IF ((J.EQ.1).OR.(J.EQ.2).OR.(J.EQ.3)) GO TO 210
82.      281 Y=GGUBFS(DSEED)
83.      JJ=IFIX(Y*10)
84.      IF ((JJ.EQ.0) GO TO 281
85.      IF (((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 282
86.      IF (((JJ.EQ.4).OR.(JJ.EQ.5).OR.(JJ.EQ.6)) GO TO 283
87.      IF (((JJ.EQ.7).OR.(JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 286
88.      282 IF (((IPRY(I)-HH).LT.1) HH=-HH
89.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
90.      IPRY(I)=IPRY(I)-HH
91.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
92.      IPRZ(I)=IPRZ(I)+LL
93.      GO TO 99
94.      283 IF (((IPRY(I)-HH).LT.1) HH=-HH
95.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
96.      IPRY(I)=IPRY(I)-HH
97.      IF (((IPRX(I)+H).GT.500).AND.(ID(I).EQ.2)) GO TO 284
98.      IF (((IPRX(I)+H).GT.500) ID(I)=4
99.      GO TO 285
100.     284 ID(I)=3
101.     285 IF ((IPRX(I)+H).GT.500) H=-H
102.     IPRX(I)=IPRX(I)+H
103.     IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
104.     IPRZ(I)=IPRZ(I)+LL
105.     GO TO 99
106.     286 IF ((IPRX(I)+H).GT.500) H=-H
107.     IF ((IPRX(I)+H).GT.500) ID(I)=4
108.     IPRX(I)=IPRX(I)+H
109.     IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
110.     IPRZ(I)=IPRZ(I)+LL
111.     GO TO 99
112.     210 Y=GGUBFS(DSEED)
113.     JJ=IFIX(Y*10)
114.     IF ((JJ.EQ.0).OR.(JJ.EQ.1)) GO TO 211
115.     IF ((JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 214
116.     IF ((JJ.EQ.4).OR.(JJ.EQ.5)) GO TO 215
117.     IF ((JJ.EQ.6).OR.(JJ.EQ.7)) GO TO 218
118.     IF ((JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 219
119.     211 ID(I)=2
120.     IF ((IPRX(I)+H).GT.500) H=-H
121.     IF ((IPRX(I)+H).GT.500) ID(I)=3
122.     IPRX(I)=IPRX(I)+H
123.     IF (((IPRY(I)+HH).GT.500).AND.(ID(I).EQ.3)) GO TO 212
124.     IF ((IPRY(I)+HH).GT.500) ID(I)=1
125.     GO TO 213
126.     212 ID(I)=4
127.     213 IF ((IPRY(I)+HH).GT.500) HH=-HH
128.     IPRY(I)=IPRY(I)+HH
129.     IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
130.     IPRZ(I)=IPRZ(I)+LL
131.     GO TO 99
132.     214 ID(I)=2
133.     IF ((IPRY(I)+HH).GT.500) HH=-HH
134.     IF ((IPRY(I)+HH).GT.500) ID(I)=1
135.     IPRY(I)=IPRY(I)+HH
136.     IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
137.     IPRZ(I)=IPRZ(I)+LL
138.     GO TO 99
139.     215 ID(I)=3
140.     IF ((IPRY(I)+HH).GT.500) HH=-HH

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141.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
142.      IPRY(I)=IPRY(I)+HH
143.      IF (((IPRX(I)-H).LT.1).AND.(ID(I).EQ.4)) GO TO 216
144.      IF (((IPRX(I)-H).LT.1) ID(I)=2
145.      GO TO 217
146. 216 ID(I)=1
147. 217 IF (((IPRX(I)-H).LT.1) H=-H
148.      IPRX(I)=IPRX(I)-H
149.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
150.      IPRZ(I)=IPRZ(I)+LL
151.      GO TO 99
152. 218 ID(I)=4
153.      IF (((IPRX(I)-H).LT.1) H=-H
154.      IF (((IPRX(I)-H).LT.1) ID(I)=1
155.      IPRX(I)=IPRX(I)-H
156.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
157.      IPRZ(I)=IPRZ(I)+LL
158.      GO TO 99
159. 219 ID(I)=4
160.      IF (((IPRX(I)-H).LT.1) H=-H
161.      IF (((IPRX(I)-H).LT.1) ID(I)=1
162.      IPRX(I)=IPRX(I)-H
163.      IF (((IPRY(I)-HH).LT.1).AND.(ID(I).EQ.1)) GO TO 220
164.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
165.      GO TO 221
166. 220 ID(I)=2
167. 221 IF (((IPRY(I)-HH).LT.1) HH=-HH
168.      IPRY(I)=IPRY(I)-HH
169.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
170.      IPRZ(I)=IPRZ(I)+LL
171.      GO TO 99
172. 300 IF ((J.EQ.1).OR.(J.EQ.2).OR.(J.EQ.3)) GO TO 310
173. 301 Y=GGUBFS(DSEED)
174.      JJ=IFIX(Y*10)
175.      IF (JJ.EQ.0) GO TO 301
176.      IF ((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 302
177.      IF ((JJ.EQ.4).OR.(JJ.EQ.5).OR.(JJ.EQ.6)) GO TO 303
178.      IF ((JJ.EQ.7).OR.(JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 306
179. 302 IF (((IPRX(I)+H).GT.500) H=-H
180.      IF (((IPRX(I)+H).GT.500) ID(I)=3
181.      IPRX(I)=IPRX(I)+H
182.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
183.      IPRZ(I)=IPRZ(I)+LL
184.      GO TO 99
185. 303 IF (((IPRX(I)+H).GT.500) H=-H
186.      IF (((IPRX(I)+H).GT.500) ID(I)=3
187.      IPRX(I)=IPRX(I)+H
188.      IF (((IPRY(I)+HH).GT.500).AND.(ID(I).EQ.3)) GO TO 304
189.      IF (((IPRY(I)+HH).GT.500) ID(I)=1
190.      GO TO 305
191. 304 ID(I)=4
192. 305 IF (((IPRY(I)+HH).GT.500) HH=-HH
193.      IPRY(I)=IPRY(I)+HH
194.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
195.      IPRZ(I)=IPRZ(I)+LL
196.      GO TO 99
197. 306 IF (((IPRY(I)+HH).GT.500) HH=-HH
198.      IF (((IPRY(I)+HH).GT.500) ID(I)=1
199.      IPRY(I)=IPRY(I)+HH
200.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
201.      IPRZ(I)=IPRZ(I)+LL
202.      GO TO 99
203. 310 Y=GGUBFS(DSEED)
204.      JJ=IFIX(Y*10)
205.      IF ((JJ.EQ.0).OR.(JJ.EQ.1)) GO TO 311
206.      IF ((JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 314
207.      IF ((JJ.EQ.4).OR.(JJ.EQ.5)) GO TO 315
208.      IF ((JJ.EQ.6).OR.(JJ.EQ.7)) GO TO 318
209.      IF ((JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 319
210. 311 ID(I)=3

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211.      IF (((IPRY(I)+HH).GT.500) HH=-HH
212.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
213.      IPRY(I)=IPRY(I)+HH
214.      IF (((IPRX(I)-H).LT.1).AND.(ID(I).EQ.4)) GO TO 312
215.      IF (((IPRX(I)-H).LT.1) ID(I)=2
216.      GO TO 313
217. 312  ID(I)=1
218.      IF (((IPRX(I)-H).LT.1) H=-H
219.      IPRX(I)=IPRX(I)-H
220.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
221.      IPRZ(I)=IPRZ(I)+LL
222.      GO TO 99
223. 314  ID(I)=3
224.      IF (((IPRX(I)-H).LT.1) H=-H
225.      IF (((IPRX(I)-H).LT.1) ID(I)=2
226.      IPRX(I)=IPRX(I)-H
227.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
228.      IPRZ(I)=IPRZ(I)+LL
229.      GO TO 99
230. 315  ID(I)=4
231.      IF (((IPRX(I)-H).LT.1) H=-H
232.      IF (((IPRX(I)-H).LT.1) ID(I)=1
233.      IPRX(I)=IPRX(I)-H
234.      IF (((IPRY(I)-HH).LT.1).AND.(ID(I).EQ.1)) GO TO 316
235.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
236.      GO TO 317
237. 316  ID(I)=2
238. 317  IF (((IPRY(I)-HH).LT.1) HH=-HH
239.      IPRY(I)=IPRY(I)-HH
240.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
241.      IPRZ(I)=IPRZ(I)+LL
242.      GO TO 99
243. 318  ID(I)=1
244.      IF (((IPRY(I)-HH).LT.1) HH=-HH
245.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
246.      IPRY(I)=IPRY(I)-HH
247.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
248.      IPRZ(I)=IPRZ(I)+LL
249.      GO TO 99
250. 319  ID(I)=1
251.      IF (((IPRY(I)-HH).LT.1) HH=-HH
252.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
253.      IPRY(I)=IPRY(I)-HH
254.      IF (((IPRX(I)+H).GT.500).AND.(ID(I).EQ.2)) GO TO 320
255.      IF (((IPRX(I)+H).GT.500) ID(I)=4
256.      GO TO 321
257. 320  ID(I)=3
258. 321  IF (((IPRX(I)+H).GT.500) H=-H
259.      IPRX(I)=IPRX(I)+H
260.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
261.      IPRZ(I)=IPRZ(I)+LL
262.      GO TO 99
263. 400  IF ((J.EQ.1).OR.(J.EQ.2).OR.(J.EQ.3)) GO TO 410
264. 401  Y=GGUBFS(DSEED)
265.      JJ=IFIX(Y*10)
266.      IF (JJ.EQ.0) GO TO 401
267.      IF ((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 402
268.      IF ((JJ.EQ.4).OR.(JJ.EQ.5).OR.(JJ.EQ.6)) GO TO 403
269.      IF ((JJ.EQ.7).OR.(JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 406
270. 402  IF (((IPRY(I)+HH).GT.500) HH=-HH
271.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
272.      IPRY(I)=IPRY(I)+HH
273.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
274.      IPRZ(I)=IPRZ(I)+LL
275.      GO TO 99
276. 403  IF (((IPRY(I)+HH).GT.500) HH=-HH
277.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
278.      IPRY(I)=IPRY(I)+HH
279.      IF (((IPRX(I)-H).LT.1).AND.(ID(I).EQ.4)) GO TO 404
280.      IF (((IPRX(I)-H).LT.1) ID(I)=2

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281.      GO TO 405
282. 404 ID(I)=1
283. 405 IF (((IPRX(I)-H).LT.1) H=-H
284.      IPRX(I)=IPRX(I)-H
285.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
286.      IPRZ(I)=IPRZ(I)+LL
287.      GO TO 99
288. 406 IF (((IPRX(I)-H).LT.1) H=-H
289.      IF (((IPRX(I)-H).LT.1) ID(I)=2
290.      IPRX(I)=IPRX(I)-H
291.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
292.      IPRZ(I)=IPRZ(I)+LL
293.      GO TO 99
294. 410 Y=GGUBFS(DSEED)
295.      JJ=IFIX(Y*10)
296.      IF (((JJ.EQ.0).OR.(JJ.EQ.1)) GO TO 411
297.      IF (((JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 414
298.      IF (((JJ.EQ.4).OR.(JJ.EQ.5)) GO TO 415
299.      IF (((JJ.EQ.6).OR.(JJ.EQ.7)) GO TO 418
300.      IF (((JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 419
301. 411 ID(I)=4
302.      IF (((IPRX(I)-H).LT.1) H=-H
303.      IF (((IPRX(I)-H).LT.1) ID(I)=1
304.      IPRX(I)=IPRX(I)-H
305.      IF (((IPRY(I)-HH).LT.1).AND.(ID(I).EQ.1)) GO TO 412
306.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
307.      GO TO 413
308. 412 ID(I)=2
309. 413 IF (((IPRY(I)-HH).LT.1) HH=-HH
310.      IPRY(I)=IPRY(I)-HH
311.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
312.      IPRZ(I)=IPRZ(I)+LL
313.      GO TO 99
314. 414 ID(I)=4
315.      IF (((IPRY(I)-HH).LT.1) HH=-HH
316.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
317.      IPRY(I)=IPRY(I)-HH
318.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
319.      IPRZ(I)=IPRZ(I)+LL
320.      GO TO 99
321. 415 ID(I)=1
322.      IF (((IPRY(I)-HH).LT.1) HH=-HH
323.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
324.      IPRY(I)=IPRY(I)-HH
325.      IF (((IPRX(I)+H).GT.500).AND.(ID(I).EQ.2)) GO TO 416
326.      IF (((IPRX(I)+H).GT.500) ID(I)=4
327.      GO TO 417
328. 416 ID(I)=3
329. 417 IF (((IPRX(I)+H).GT.500) H=-H
330.      IPRX(I)=IPRX(I)+H
331.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
332.      IPRZ(I)=IPRZ(I)+LL
333.      GO TO 99
334. 418 ID(I)=2
335.      IF (((IPRX(I)+H).GT.500) H=-H
336.      IF (((IPRX(I)+H).GT.500) ID(I)=3
337.      IPRX(I)=IPRX(I)+H
338.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
339.      IPRZ(I)=IPRZ(I)+LL
340.      GO TO 99
341. 419 ID(I)=2
342.      IF (((IPRX(I)+H).GT.500) H=-H
343.      IF (((IPRX(I)+H).GT.500) ID(I)=3
344.      IPRX(I)=IPRX(I)+H
345.      IF (((IPRY(I)+HH).GT.500).AND.(ID(I).EQ.3)) GO TO 420
346.      IF (((IPRY(I)+HH).GT.500) ID(I)=1
347.      GO TO 421
348. 420 ID(I)=4
349. 421 IF (((IPRY(I)+HH).GT.500) HH=-HH
350.      IPRY(I)=IPRY(I)+HH

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351.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
352.      IPRZ(I)=IPRZ(I)+LL
353.      GO TO 99
354. 500 IF ((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 510
355. 501 Y=GGUBFS(DSEED)
356.      JJ=IFIX(Y*10)
357.      IF (JJ.EQ.0) GO TO 501
358.      IF ((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 502
359.      IF ((JJ.EQ.4).OR.(JJ.EQ.5).OR.(JJ.EQ.6)) GO TO 503
360.      IF ((JJ.EQ.7).OR.(JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 506
361. 502 IF (((IPRX(I)-H).LT.1) H=-H
362.      IF (((IPRX(I)-H).LT.1) ID(I)=1
363.      IPRX(I)=IPRX(I)-H
364.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
365.      IPRZ(I)=IPRZ(I)+LL
366.      GO TO 99
367. 503 IF (((IPRX(I)-H).LT.1) H=-H
368.      IF (((IPRX(I)-H).LT.1) ID(I)=1
369.      IPRX(I)=IPRX(I)-H
370.      IF (((IPRY(I)-HH).LT.1).AND.(ID(I).EQ.1)) GO TO 504
371.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
372.      GO TO 505
373. 504 ID(I)=2
374. 505 IF (((IPRY(I)-HH).LT.1) HH=-HH
375.      IPRY(I)=IPRY(I)-HH
376.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
377.      IPRZ(I)=IPRZ(I)+LL
378.      GO TO 99
379. 506 IF (((IPRY(I)-HH).LT.1) HH=-HH
380.      IF (((IPRY(I)-HH).LT.1) ID(I)=3
381.      IPRY(I)=IPRY(I)-HH
382.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
383.      IPRZ(I)=IPRZ(I)+LL
384.      GO TO 99
385. 510 Y=GGUBFS(DSEED)
386.      JJ=IFIX(Y*10)
387.      IF ((JJ.EQ.0).OR.(JJ.EQ.1)) GO TO 511
388.      IF ((JJ.EQ.2).OR.(JJ.EQ.3)) GO TO 514
389.      IF ((JJ.EQ.4).OR.(JJ.EQ.5)) GO TO 515
390.      IF ((JJ.EQ.6).OR.(JJ.EQ.7)) GO TO 516
391.      IF ((JJ.EQ.8).OR.(JJ.EQ.9)) GO TO 519
392. 511 ID(I)=1
393.      IF (((IPRY(I)-HH).LT.1) HH=-HH
394.      IF (((IPRY(I)-HH).LT.1) ID(I)=2
395.      IPRY(I)=IPRY(I)-HH
396.      IF (((IPRX(I)+H).GT.500).AND.(ID(I).EQ.2)) GO TO 512
397.      IF (((IPRX(I)+H).GT.500) ID(I)=4
398.      GO TO 513
399. 512 ID(I)=3
400. 513 IF (((IPRX(I)+H).GT.500) H=-H
401.      IPRX(I)=IPRX(I)+H
402.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
403.      IPRZ(I)=IPRZ(I)+LL
404.      GO TO 99
405. 514 ID(I)=1
406.      IF (((IPRX(I)+H).GT.500) H=-H
407.      IF (((IPRX(I)+H).GT.500) ID(I)=4
408.      IPRX(I)=IPRX(I)+H
409.      IF (((IPRZ(I)+LL).GT.500).OR.((IPRZ(I)+LL).LT.1)) LL=-LL
410.      IPRZ(I)=IPRZ(I)+LL
411.      GO TO 99
412. 515 ID(I)=2
413.      IF (((IPRX(I)+H).GT.500) H=-H
414.      IF (((IPRX(I)+H).GT.500) ID(I)=3
415.      IPRX(I)=IPRX(I)+H
416.      IF (((IPRY(I)+HH).GT.500).AND.(ID(I).EQ.3)) GO TO 516
417.      IF (((IPRY(I)+HH).GT.500) ID(I)=1
418.      GO TO 517
419. 516 ID(I)=4
420. 517 IF (((IPRY(I)+HH).GT.500) HH=-HH

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421.      IPRY(I)=IPRY(I)+HH
422.      IF (((IPRZ(I)+LL).GT.500).OR.(((IPRZ(I)+LL).LT.1)) LL=-LL
423.      IPRZ(I)=IPRZ(I)+LL
424.      GO TO 99
425. 518 ID(I)=3
426.      IF (((IPRY(I)+HH).GT.500) HH=-HH
427.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
428.      IPRY(I)=IPRY(I)+HH
429.      IF (((IPRZ(I)+LL).GT.500).OR.(((IPRZ(I)+LL).LT.1)) LL=-LL
430.      IPRZ(I)=IPRZ(I)+LL
431.      GO TO 99
432. 519 ID(I)=3
433.      IF (((IPRY(I)+HH).GT.500) HH=-HH
434.      IF (((IPRY(I)+HH).GT.500) ID(I)=4
435.      IPRY(I)=IPRY(I)+HH
436.      IF (((IPRX(I)-H).LT.1).AND.(ID(I).EQ.4)) GO TO 528
437.      IF (((IPRX(I)-H).LT.1) ID(I)=2
438.      GO TO 521
439. 520 ID(I)=1
440. 521 IF (((IPRX(I)-H).LT.1) H=-H
441.      IPRX(I)=IPRX(I)-H
442.      IF (((IPRZ(I)+LL).GT.500).OR.(((IPRZ(I)+LL).LT.1)) LL=-LL
443.      IPRZ(I)=IPRZ(I)+LL
444.      GO TO 99
445. C
446. C
447. C   IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
448. C   THIS PART OF THE PROGRAM MOVES THE PREY IN THE X-DIRECTION
449. C   AND/OR Y-DIRECTION ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS
450. C   MOVED THE PRE-DETERMINED MAGNITUDE
451. C
452. 45 IF (J.EQ.0) GO TO 99
453.      IF ((J.EQ.1).OR.(J.EQ.2).OR.(J.EQ.3)) GO TO 605
454. 600 Y=GGUBFS(DSEED)
455.      JJ=IFIX(Y*10)
456.      IF ((JJ.EQ.0) GO TO 600
457.      IF (((JJ.EQ.1).OR.(JJ.EQ.2).OR.(JJ.EQ.3)) IDD=7
458.      IF (((JJ.EQ.4).OR.(JJ.EQ.5).OR.(JJ.EQ.6)) IDD=8
459.      IF (((JJ.EQ.7).OR.(JJ.EQ.8).OR.(JJ.EQ.9)) IDD=1
460.      GO TO 609
461. 605 Y=GGUBFS(DSEED)
462.      JJ=IFIX(Y*10)
463.      IF ((JJ.EQ.0).OR.(JJ.EQ.1)) IDD=2
464.      IF ((JJ.EQ.2).OR.(JJ.EQ.3)) IDD=3
465.      IF ((JJ.EQ.4).OR.(JJ.EQ.5)) IDD=4
466.      IF ((JJ.EQ.6).OR.(JJ.EQ.7)) IDD=5
467.      IF ((JJ.EQ.8).OR.(JJ.EQ.9)) IDD=6
468. 609 IF (ID(I).NE.2) GO TO 610
469.      IDD=IDD+2
470.      IF (IDD.GT.8) IDD=IDD-8
471. 610 IF (ID(I).NE.3) GO TO 615
472.      IDD=IDD+4
473.      IF (IDD.GT.8) IDD=IDD-8
474. 615 IF (ID(I).NE.4) GO TO 618
475.      IDD=IDD+6
476.      IF (IDD.GT.8) IDD=IDD-8
477. 618 IF (ID(I).NE.1) GO TO 620
478.      IF ((IDD.EQ.2).OR.(IDD.EQ.3)) ID(I)=2
479.      IF (IDD.EQ.4) ID(I)=3
480.      IF ((IDD.EQ.5).OR.(IDD.EQ.6)) ID(I)=4
481.      GO TO 635
482. 620 IF (ID(I).NE.2) GO TO 625
483.      IF ((IDD.EQ.4).OR.(IDD.EQ.5)) ID(I)=3
484.      IF (IDD.EQ.6) ID(I)=4
485.      IF ((IDD.EQ.7).OR.(IDD.EQ.8)) ID(I)=1
486.      GO TO 635
487. 625 IF (ID(I).NE.3) GO TO 630
488.      IF ((IDD.EQ.6).OR.(IDD.EQ.7)) ID(I)=4
489.      IF (IDD.EQ.8) ID(I)=1
490.      IF ((IDD.EQ.1).OR.(IDD.EQ.2)) ID(I)=2

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491.      GO TO 635
492. 630 IF ( ID(I).NE.4) GO TO 635
493.      IF ((IDD.EQ.8).OR.(IDD.EQ.1)) ID(I)=1
494.      IF ( IDD.EQ.2) ID(I)=2
495.      IF ((IDD.EQ.3).OR.(IDD.EQ.4)) ID(I)=3
496. 635 DO 86 LA=1,H
497.      IF ( IDD.EQ.1) IPRX(I)=IPRX(I)+1
498.      IF ( IDD.EQ.3) IPRY(I)=IPRY(I)+1
499.      IF ( IDD.EQ.5) IPRX(I)=IPRX(I)-1
500.      IF ( IDD.EQ.7) IPRY(I)=IPRY(I)-1
501.      IF ( IDD.NE.2) GO TO 46
502.      IPRX(I)=IPRX(I)+1
503.      IPRY(I)=IPRY(I)+1
504. 46   IF ( IDD.NE.4) GO TO 47
505.      IPRX(I)=IPRX(I)-1
506.      IPRY(I)=IPRY(I)+1
507. 47   IF ( IDD.NE.6) GO TO 48
508.      IPRX(I)=IPRX(I)-1
509.      IPRY(I)=IPRY(I)-1
510. 48   IF ( IDD.NE.8) GO TO 49
511.      IPRX(I)=IPRX(I)+1
512.      IPRY(I)=IPRY(I)-1
513.
514. C
515. C      IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
516. C      THIS PART OF THE PROGRAM MOVES THE PREY IN THE Z-DIRECTION
517. C      ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS MOVED THE
518. C      PRE-DETERMINED MAGNITUDE
519. C
520. 49   IF ((L.EQ.0).OR.(L.EQ.1)) IPRZ(I)=IPRZ(I)-1
521.      IF ((L.EQ.8).OR.(L.EQ.9)) IPRZ(I)=IPRZ(I)+1
522.
523. C
524. C      THIS PART OF THE PROGRAM TESTS FOR AN ENCOUNTER BETWEEN THE
525. C      PREDATOR AND PREY AFTER EACH UNIT MOVED BY THE PREY
526. C
527. 50   IF ( IPRY(I).NE.250) GO TO 59
528.      IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 53
529.      IZ=718-(2*IPRX(I))
530.      DO 51 LK=1,2
531.          IF (IZ.EQ.IPRZ(I)) GO TO 90
532.          IZ=IZ+1
533. 51   CONTINUE
534.      IZ=(2*IPRX(I))-292
535.      DO 52 LK=1,2
536.          IF (IZ.EQ.IPRZ(I)) GO TO 90
537.          IZ=IZ+1
538. 52   CONTINUE
539. 53   IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 56
540.      IZ=727-(2*IPRX(I))
541.      DO 54 LK=1,2
542.          IF (IZ.EQ.IPRZ(I)) GO TO 90
543.          IZ=IZ+1
544. 54   CONTINUE
545.      IZ=(2*IPRX(I))-273
546.      DO 55 LK=1,2
547.          IF (IZ.EQ.IPRZ(I)) GO TO 90
548.          IZ=IZ+1
549. 55   CONTINUE
550. 56   IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 59
551.      IZ=736-(2*IPRX(I))
552.      DO 57 LK=1,2
553.          IF (IZ.EQ.IPRZ(I)) GO TO 90
554.          IZ=IZ+1
555. 57   CONTINUE
556.      IZ=(2*IPRX(I))-264
557.      DO 58 LK=1,2
558.          IF (IZ.EQ.IPRZ(I)) GO TO 90
559.          IZ=IZ+1
560. 58   CONTINUE

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561.      59   IF (IPRX(I).NE.250) GO TO 68
562.      IF (((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 62
563.      IZ=718-(2*IPRY(I))
564.      DO 60 LK=1,2
565.          IF (IZ.EQ.IPRZ(I)) GO TO 90
566.          IZ=IZ+1
567.      CONTINUE
568.      IZ=(2*IPRY(I))-282
569.      DO 61 LK=1,2
570.          IF (IZ.EQ.IPRZ(I)) GO TO 90
571.          IZ=IZ+1
572.      CONTINUE
573.      62   IF (((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 65
574.      IZ=727-(2*IPRY(I))
575.      DO 63 LK=1,2
576.          IF (IZ.EQ.IPRZ(I)) GO TO 90
577.          IZ=IZ+1
578.      CONTINUE
579.      IZ=(2*IPRY(I))-273
580.      DO 64 LK=1,2
581.          IF (IZ.EQ.IPRZ(I)) GO TO 90
582.          IZ=IZ+1
583.      64   CONTINUE
584.      65   IF (((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 68
585.      IZ=736-(2*IPRY(I))
586.      DO 66 LK=1,2
587.          IF (IZ.EQ.IPRZ(I)) GO TO 90
588.          IZ=IZ+1
589.      66   CONTINUE
590.      IZ=(2*IPRY(I))-264
591.      DO 67 LK=1,2
592.          IF (IZ.EQ.IPRZ(I)) GO TO 90
593.          IZ=IZ+1
594.      67   CONTINUE
595.      68   IY=500-IPRX(I)
596.      IF (IY.NE.IPRY(I)) GO TO 77
597.      IF (((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 71
598.      IZ=718-(2*IPRX(I))
599.      DO 69 LK=1,2
600.          IF (IZ.EQ.IPRZ(I)) GO TO 90
601.          IZ=IZ+1
602.      69   CONTINUE
603.      IZ=(2*IPRX(I))-282
604.      DO 70 LK=1,2
605.          IF (IZ.EQ.IPRZ(I)) GO TO 90
606.          IZ=IZ+1
607.      70   CONTINUE
608.      71   IF (((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 74
609.      IZ=727-(2*IPRX(I))
610.      DO 72 LK=1,2
611.          IF (IZ.EQ.IPRZ(I)) GO TO 90
612.          IZ=IZ+1
613.      72   CONTINUE
614.      IZ=(2*IPRX(I))-273
615.      DO 73 LK=1,2
616.          IF (IZ.EQ.IPRZ(I)) GO TO 90
617.          IZ=IZ+1
618.      73   CONTINUE
619.      74   IF (((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 77
620.      IZ=736-(2*IPRX(I))
621.      DO 75 LK=1,2
622.          IF (IZ.EQ.IPRZ(I)) GO TO 90
623.          IZ=IZ+1
624.      75   CONTINUE
625.      IZ=(2*IPRX(I))-264
626.      DO 76 LK=1,2
627.          IF (IZ.EQ.IPRZ(I)) GO TO 90
628.          IZ=IZ+1
629.      76   CONTINUE
630.      77   IY=IPRX(I)

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631. IF (IY.NE.IPRY(I)) GO TO 86
632. IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 88
633. IZ=718-(2*IPRX(I))
634. DO 78 LK=1,2
635.     IF (IZ.EQ.IPRZ(I)) GO TO 90
636.     IZ=IZ+1
637. 78 CONTINUE
638.     IZ=(2*IPRX(I))-282
639.     DO 79 LK=1,2
640.         IF (IZ.EQ.IPRZ(I)) GO TO 90
641.         IZ=IZ+1
642. 79 CONTINUE
643. 80 IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 83
644. IZ=727-(2*IPRX(I))
645. DO 81 LK=1,2
646.     IF (IZ.EQ.IPRZ(I)) GO TO 90
647.     IZ=IZ+1
648. 81 CONTINUE
649.     IZ=(2*IPRX(I))-273
650.     DO 82 LK=1,2
651.         IF (IZ.EQ.IPRZ(I)) GO TO 90
652.         IZ=IZ+1
653. 82 CONTINUE
654. 83 IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 86
655. IZ=736-(2*IPRX(I))
656. DO 84 LK=1,2
657.     IF (IZ.EQ.IPRZ(I)) GO TO 90
658.     IZ=IZ+1
659. 84 CONTINUE
660.     IZ=(2*IPRX(I))-264
661.     DO 85 LK=1,2
662.         IF (IZ.EQ.IPRZ(I)) GO TO 90
663.         IZ=IZ+1
664. 85 CONTINUE
665. 86 CONTINUE
666. GO TO 99
667.
668. C
669. C      THIS PART OF THE PROGRAM RECORDS ENCOUNTERS
670. C
671. 90 WRITE (6,1003)
672.     WRITE (6,1000)
673.     WRITE (6,1001)
674.     WRITE (6,1002) IPRX(I),IPRY(I),IPRZ(I),ID(I)
675.     WRITE (6,1006) LI
676.     WRITE (6,1007) LJ
677.
678. C
679. C      THIS PART OF THE PROGRAM REPLACES PREY THAT HAVE BEEN
680. C      ENCOUNTERED
681. C
682. CALL REPL (IPRX,IPRY,IPRZ,I,IJ,ID)
683. 99 I=I+1
684. 100 CONTINUE
685.     IF (LI.NE.IM) GO TO 105
686.     WRITE (6,1003)
687.     DO 101 LK=1,14
688.         WRITE (6,1004) IPRX(LK),IPRY(LK),IPRZ(LK),LI,ID(LK)
689. 101 CONTINUE
690.     IN=IN+1
691.     IM=IN*300
692.
693. C
694. C      THIS PART OF THE PROGRAM BEGINS A NEW SIMULATION SECOND
695. C
696. 105 CONTINUE
697. 999 FORMAT ('1')
698. 1000 FORMAT ('0',80X,'A PREY ITEM HAS BEEN ENCOUNTERED')
699. 1001 FORMAT (' ',80X,'AT COORDINATES')
700. 1002 FORMAT (89X,I3.3X,I3.3X,I3.5X,'(.,II.)')

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701.    1003 FORMAT ('B')
702.    1004 FORMAT (' ',20X,I3.5X,I3.5X,I3.5X,I5,10X,I1)
703.    1005 FORMAT (1X,'RANDOM NUMBER GENERATOR SEED IS',F12.1)
704.    1006 FORMAT (' ',80X,'AT TIME',2X,I5,2X,'SECONDS')
705.    1007 FORMAT (' ',80X,'PREY ITEM',2X,I2.2X,'WAS ENCOUNTERED')
706.    1008 FORMAT (' ',21X,'X',7X,'Y',7X,'Z',5X,'TIME SEC',7X,'ID')
707.    STOP
708.    END
709.    C
710.    C
711.    C      THIS SUBROUTINE PLACES THE PREY IN THEIR ORIGINAL POSITIONS
712.    C
713.    SUBROUTINE ORIG (IPRX,IPRY,IPRZ,ID)
714.        DIMENSION IPRX(14),IPRY(14),IPRZ(14),ID(14)
715.        DATA IA,IB,IC,IP,IE,IF,IG,IH,IJ,IK,IL,IM,IN,IO/104,168,
716.          C119,015,495,182,145,103,042,324,227,290,204,464/
717.          DATA JA,JB,JC,JD,JE,JF,JG,JH,JJ,JK,JL,JM,JN,JO/465,061,
718.          C253,051,103,026,047,252,411,072,424,351,145,350/
719.          DATA KA,KB,KC,KD,KE,KF,KG,KH,KJ,KK,KL,KM,KN,KO/226,349,
720.          C179,306,336,312,151,074,341,265,415,205,075,257/
721.          DATA LA,LB,LC,LD,LE,LF,LG,LH,LJ,LK,LL,LM,LN,LO/1,2,3,4,1,2,
722.          C3,4,1,2,3,4,2,3/
723.          IPRX(1)=IA
724.          IPRX(2)=IB
725.          IPRX(3)=IC
726.          IPRX(4)=IP
727.          IPRX(5)=IE
728.          IPRX(6)=IF
729.          IPRX(7)=IG
730.          IPRX(8)=IH
731.          IPRX(9)=IJ
732.          IPRX(10)=IK
733.          IPRX(11)=IL
734.          IPRX(12)=IM
735.          IPRX(13)=IN
736.          IPRX(14)=IO
737.          IPY(1)=JA
738.          IPY(2)=JB
739.          IPY(3)=JC
740.          IPY(4)=JD
741.          IPY(5)=JE
742.          IPY(6)=JF
743.          IPY(7)=JG
744.          IPY(8)=JH
745.          IPY(9)=JJ
746.          IPY(10)=JK
747.          IPY(11)=JL
748.          IPY(12)=JM
749.          IPY(13)=JN
750.          IPY(14)=JO
751.          IPRZ(1)=KA
752.          IPRZ(2)=KB
753.          IPRZ(3)=KC
754.          IPRZ(4)=KD
755.          IPRZ(5)=KE
756.          IPRZ(6)=KF
757.          IPRZ(7)=KG
758.          IPRZ(8)=KH
759.          IPRZ(9)=KJ
760.          IPRZ(10)=KK
761.          IPRZ(11)=KL
762.          IPRZ(12)=KM
763.          IPRZ(13)=KN
764.          IPRZ(14)=KO
765.          ID(1)=LA
766.          ID(2)=LB
767.          ID(3)=LC
768.          ID(4)=LD
769.          ID(5)=LE
770.          ID(6)=LF

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771.      ID( 7 )=LG
772.      ID( 8 )=LH
773.      ID( 9 )=LJ
774.      ID( 10 )=LK
775.      ID( 11 )=LL
776.      ID( 12 )=LM
777.      ID( 13 )=LN
778.      ID( 14 )=LO
779.      RETURN
780.      END
781.      C
782.      C
783.      C THIS SUBROUTINE REPLACES A PREY ITEM WHICH HAS BEEN LOST
784.      C FROM THE SYSTEM DUE TO ENCOUNTER
785.      C
786.      SUBROUTINE REPL (IPRX,IPRY,IPRZ,I,IJ,ID)
787.      DIMENSION IPRX(14),IPRY(14),IPRZ(14),ID(14)
788.      DATA K1,L1,M1, ID1/297,119,247,1/
789.      DATA K2,L2,M2, ID2/331,321,348,2/
790.      DATA K3,L3,M3, ID3/295,359,348,3/
791.      DATA K4,L4,M4, ID4/190,87,369,4/
792.      DATA K5,L5,M5, ID5/207,421,395,1/
793.      IF (IJ.EQ.1) GO TO 10
794.      IF (IJ.EQ.2) GO TO 20
795.      IF (IJ.EQ.3) GO TO 30
796.      IF (IJ.EQ.4) GO TO 40
797.      IF (IJ.EQ.5) GO TO 50
798.      10   IPRX(I)=K1
799.      IPY(I)=L1
800.      IPRZ(I)=M1
801.      ID(I)=ID1
802.      GO TO 60
803.      20   IPRX(I)=K2
804.      IPY(I)=L2
805.      IPRZ(I)=M2
806.      ID(I)=ID2
807.      GO TO 60
808.      30   IPRX(I)=K3
809.      IPY(I)=L3
810.      IPRZ(I)=M3
811.      ID(I)=ID3
812.      GO TO 60
813.      40   IPRX(I)=K4
814.      IPY(I)=L4
815.      IPRZ(I)=M4
816.      ID(I)=ID4
817.      GO TO 60
818.      50   IPRX(I)=K5
819.      IPY(I)=L5
820.      IPRZ(I)=M5
821.      ID(I)=ID5
822.      IJ=0
823.      60   IJ=IJ+1
824.      RETURN
825.      END
826.      //$/DATA

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**APPENDIX E**

**Listing of Computer Program Used  
in Model PREY3**

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1. //PREY3 JOB (S61B,001A,S9B,1BB,HA),'SMITH'
2. /*LEVEL
3. //STEP EXEC WATFIV,REGION=126K
4. //SYSIN DD DATA
5. //OPTIONS
6.      DIMENSION IPRX(14),IPRY(14),IPRZ(14),IDE (14)
7.      INTEGER H,HH,HHH
8.      DOUBLE PRECISION DSEED
9.      DATA IDE/0,0,0,0,0,0,0,0,0,0,0,0,0,0/
10.     IN=1
11.     IM=300
12.     IJ=1
13.     HHH=0
14. C
15. C
16. C      THIS PART OF THE PROGRAM 'SEEDS' THE RANDOM NUMBER GENERATOR
17. C      THE 'SEEDS' USED IN THIS SET OF SIMULATIONS INCLUDE:
18. C      220724543.0 561770.0 937557032.0 8275366.0 930594.0
19. C
20. C      DSEED=220724543.D0
21. C      WRITE (6,999)
22. C      WRITE (6,1005) DSEED
23. C
24. C
25. C      THIS PART OF THE PROGRAM PUTS THE PREY IN THEIR ORIGINAL
26. C      POSITIONS
27. C
28. C      CALL ORIG (IPRX,IPRY,IPRZ)
29. C      WRITE (6,1003)
30. C      WRITE (6,1008)
31. C      DO 2 IK=1,14
32. C      WRITE (6,1004) IPRX(IK),IPRY(IK),IPRZ(IK),HHH
33. C      2 CONTINUE
34. C
35. C
36. C      THIS PART OF THE PROGRAM BEGINS THE 4-HOUR SIMULATION
37. C
38. C      DO 105 LI=1,14400
39. C      I=1
40. C      DO 100 LJ=1,14
41. C      IF (IDE(I).GT.0) GO TO 14
42. C
43. C
44. C      THIS PART OF THE PROGRAM DETERMINES THE DIRECTION OF PREY
45. C      MOVEMENT STOCHASTICALLY IN THE X-Y PLANE
46. C
47. 11 Y=GGUBFS(DSEED)
48. J=IFIX(Y*10)
49. IF (J.EQ.0) GO TO 11
50. C
51. C
52. C      THIS PART OF THE PROGRAM DETERMINES THE MAGNITUDE OF THE PREY
53. C      "HOP" STOCHASTICALLY
54. C
55. 4 Y=GGUBFS(DSEED)
56. H=IFIX(Y*10)
57. IF (H.EQ.0) GO TO 4
58. HH=H
59. LL=H
60. C
61. C
62. C      THIS PART OF THE PROGRAM DETERMINES THE LENGTH OF TIME THE
63. C      PREY SPENDS "SINKING"
64. C
65. 12 Y=GGUBFS(DSEED)
66. L=IFIX(Y*10)
67. IF (L.EQ.0) GO TO 12
68. 14 IF (((IPRX(I).LT.210).OR.(IPRX(I).GT.290)) GO TO 5
69. IF (((IPRY(I).LT.210).OR.(IPRY(I).GT.290)) GO TO 5
70. IF (((IPRZ(I).GT.190).AND.(IPRZ(I).LT.300)) GO TO 45

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71. C
72. C
73. C      IF THE PREY ITEM IS OUTSIDE THE "IMMEDIATE" VICINITY OF THE
74. C      PREDATOR, THIS PART OF THE PROGRAM MOVES THE PREY TO ITS
75. C      NEW LOCATION
76. C
77. 5 IF ( IDE(I).GT.0) GO TO 200
78. IDE(I)=L
79. IF (J.EQ.1) GO TO 10
80. IF (J.EQ.3) GO TO 15
81. IF (J.EQ.5) GO TO 20
82. IF (J.EQ.7) GO TO 25
83. IF (J.EQ.2) GO TO 30
84. IF (J.EQ.4) GO TO 35
85. IF (J.EQ.6) GO TO 40
86. IF (J.EQ.8) GO TO 43
87. IF ((IPRZ(I)-LL).LT.1) GO TO 7
88. IPRZ(I)=IPRZ(I)-LL
89. GO TO 99
90. 7 IDE(I)=IDE(I)+(LL-1)
91. IPRZ(I)=IPRZ(I)+1
92. GO TO 99
93. 10 IF ((IPRZ(I)-LL).LT.1) GO TO 13
94. IF ((IPRX(I)+H).GT.500) H=-H
95. IPRX(I)=IPRX(I)+H
96. IPRZ(I)=IPRZ(I)-LL
97. GO TO 99
98. 13 IDE(I)=IDE(I)+(LL-1)
99. IPRZ(I)=IPRZ(I)+1
100. GO TO 99
101. 15 IF ((IPRZ(I)-LL).LT.1) GO TO 18
102. IF ((IPRY(I)+H).GT.500) H=-H
103. IPRY(I)=IPRY(I)+H
104. IPRZ(I)=IPRZ(I)-LL
105. GO TO 99
106. 18 IDE(I)=IDE(I)+(LL-1)
107. IPRZ(I)=IPRZ(I)+1
108. GO TO 99
109. 20 IF ((IPRZ(I)-LL).LT.1) GO TO 23
110. IF ((IPRX(I)-H).LT.1) H=-H
111. IPRX(I)=IPRX(I)-H
112. IPRZ(I)=IPRZ(I)-LL
113. GO TO 99
114. 23 IDE(I)=IDE(I)+(LL-1)
115. IPRZ(I)=IPRZ(I)+1
116. GO TO 99
117. 25 IF ((IPRZ(I)-LL).LT.1) GO TO 28
118. IF ((IPRY(I)-H).LT.1) H=-H
119. IPRY(I)=IPRY(I)-H
120. IPRZ(I)=IPRZ(I)-LL
121. GO TO 99
122. 28 IDE(I)=IDE(I)+(LL-1)
123. IPRZ(I)=IPRZ(I)+1
124. GO TO 99
125. 30 IF ((IPRZ(I)-LL).LT.1) GO TO 33
126. IF ((IPRX(I)+H).GT.500) H=-H
127. IPRX(I)=IPRX(I)+H
128. IF ((IPRY(I)+HH).GT.500) HH=-HH
129. IPRY(I)=IPRY(I)+HH
130. IPRZ(I)=IPRZ(I)-LL
131. GO TO 99
132. 33 IDE(I)=IDE(I)+(LL-1)
133. IPRZ(I)=IPRZ(I)+1
134. GO TO 99
135. 35 IF ((IPRZ(I)-LL).LT.1) GO TO 38
136. IF ((IPRX(I)-H).LT.1) H=-H
137. IPRX(I)=IPRX(I)-H
138. IF ((IPRY(I)+HH).GT.500) HH=-HH
139. IPRY(I)=IPRY(I)+HH
140. IPRZ(I)=IPRZ(I)-LL

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141.      GO TO 99
142.      38 IDE(I)=IDE(I)+(LL-1)
143.      IPRZ(I)=IPRZ(I)+1
144.      GO TO 99
145.      48 IF ((IPRZ(I)-LL).LT.1) GO TO 42
146.      IF ((IPRX(I)-H).LT.1) H=-H
147.      IPRX(I)=IPRX(I)-H
148.      IF ((IPRY(I)-HH).LT.1) HH=-HH
149.      IPY(I)=IPRY(I)-HH
150.      IPRZ(I)=IPRZ(I)-LL
151.      GO TO 99
152.      42 IDE(I)=IDE(I)+(LL-1)
153.      IPRZ(I)=IPRZ(I)+1
154.      GO TO 99
155.      43 IF ((IPRZ(I)-LL).LT.1) GO TO 44
156.      IF ((IPRX(I)-H).GT.500) H=-H
157.      IPRX(I)=IPRX(I)+H
158.      IF ((IPRY(I)-HH).LT.1) HH=-HH
159.      IPY(I)=IPRY(I)-HH
160.      IPRZ(I)=IPRZ(I)-LL
161.      GO TO 99
162.      44 IDE(I)=IDE(I)+(LL-1)
163.      IPRZ(I)=IPRZ(I)+1
164.      GO TO 99
165.      200 IF ((IPRZ(I)+1).EQ.500) IDE(I)=1
166.      IPRZ(I)=IPRZ(I)+1
167.      IDE(I)=IDE(I)-1
168.      GO TO 99
169.      C
170.      C
171.      C      IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
172.      C      THIS PART OF THE PROGRAM MOVES THE PREY IN THE X-DIRECTION
173.      C      AND/OR Y-DIRECTION ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS
174.      C      MOVED THE PRE-DETERMINED MAGNITUDE
175.      C
176.      45 IDE2=1
177.      IF (IDE(I).GT.0) H=1
178.      IF (IDE(I).GT.0) IDE2=2
179.      DO 86 LA=1,H
180.          IF (IDE(I).GT.0) GO TO 300
181.          IF (J.EQ.1) IPRX(I)=IPRX(I)+1
182.          IF (J.EQ.3) IPY(I)=IPY(I)+1
183.          IF (J.EQ.5) IPRX(I)=IPRX(I)-1
184.          IF (J.EQ.7) IPY(I)=IPY(I)-1
185.          IF (J.NE.2) GO TO 46
186.          IPRX(I)=IPRX(I)+1
187.          IPY(I)=IPY(I)+1
188.      46 IF (J.NE.4) GO TO 47
189.          IPRX(I)=IPRX(I)-1
190.          IPY(I)=IPY(I)+1
191.      47 IF (J.NE.6) GO TO 48
192.          IPRX(I)=IPRX(I)-1
193.          IPY(I)=IPY(I)-1
194.      48 IF (J.NE.8) GO TO 49
195.          IPRX(I)=IPRX(I)+1
196.          IPY(I)=IPY(I)-1
197.      C
198.      C
199.      C      IF THE PREY ITEM IS IN THE "IMMEDIATE" VICINITY OF THE PRED.
200.      C      THIS PART OF THE PROGRAM MOVES THE PREY IN THE Z-DIRECTION
201.      C      ONE UNIT AT A TIME UNTIL THE PREY ITEM HAS MOVED THE
202.      C      PRE-DETERMINED MAGNITUDE
203.      C
204.      49 IPRZ(I)=IPRZ(I)-1
205.      GO TO 50
206.      300 IPRZ(I)=IPRZ(I)+1
207.      IDE(I)=IDE(I)-1
208.      C
209.      C
210.      C      THIS PART OF THE PROGRAM TESTS FOR AN ENCOUNTER BETWEEN THE

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211.      C      PREDATOR AND PREY AFTER EACH UNIT MOVED BY THE PREY
212.      C
213.      58    IF (IPRY(I).NE.250) GO TO 55
214.          IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 53
215.          IZ=718-(2*IPRX(I))
216.          DO 51 LK=1,2
217.              IF (IZ.EQ.IPRZ(I)) GO TO 90
218.              IZ=IZ+1
219.          51    CONTINUE
220.          IZ=(2*IPRX(I))-282
221.          DO 52 LK=1,2
222.              IF (IZ.EQ.IPRZ(I)) GO TO 90
223.              IZ=IZ+1
224.          52    CONTINUE
225.          53    IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 56
226.          IZ=727-(2*IPRX(I))
227.          DO 54 LK=1,2
228.              IF (IZ.EQ.IPRZ(I)) GO TO 90
229.              IZ=IZ+1
230.          54    CONTINUE
231.          IZ=(2*IPRX(I))-273
232.          DO 55 LK=1,2
233.              IF (IZ.EQ.IPRZ(I)) GO TO 90
234.              IZ=IZ+1
235.          55    CONTINUE
236.          56    IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 59
237.          IZ=736-(2*IPRX(I))
238.          DO 57 LK=1,2
239.              IF (IZ.EQ.IPRZ(I)) GO TO 90
240.              IZ=IZ+1
241.          57    CONTINUE
242.          IZ=(2*IPRX(I))-264
243.          DO 58 LK=1,2
244.              IF (IZ.EQ.IPRZ(I)) GO TO 90
245.              IZ=IZ+1
246.          58    CONTINUE
247.          59    IF (IPRX(I).NE.250) GO TO 68
248.          IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 62
249.          IZ=718-(2*IPRY(I))
250.          DO 60 LK=1,2
251.              IF (IZ.EQ.IPRZ(I)) GO TO 90
252.              IZ=IZ+1
253.          60    CONTINUE
254.          IZ=(2*IPRY(I))-282
255.          DO 61 LK=1,2
256.              IF (IZ.EQ.IPRZ(I)) GO TO 90
257.              IZ=IZ+1
258.          61    CONTINUE
259.          62    IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 65
260.          IZ=727-(2*IPRY(I))
261.          DO 63 LK=1,2
262.              IF (IZ.EQ.IPRZ(I)) GO TO 90
263.              IZ=IZ+1
264.          63    CONTINUE
265.          IZ=(2*IPRY(I))-273
266.          DO 64 LK=1,2
267.              IF (IZ.EQ.IPRZ(I)) GO TO 90
268.              IZ=IZ+1
269.          64    CONTINUE
270.          65    IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 68
271.          IZ=736-(2*IPRY(I))
272.          DO 66 LK=1,2
273.              IF (IZ.EQ.IPRZ(I)) GO TO 90
274.              IZ=IZ+1
275.          66    CONTINUE
276.          IZ=(2*IPRY(I))-264
277.          DO 67 LK=1,2
278.              IF (IZ.EQ.IPRZ(I)) GO TO 90
279.              IZ=IZ+1
280.          67    CONTINUE

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281.      68   IY=500-IPRX(I)
282.      IF (IY.NE.IPRY(I)) GO TO 77
283.      IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 71
284.      IZ=718-(2*IPRX(I))
285.      DO 69 LK=1,2
286.          IF (IZ.EQ.IPRZ(I)) GO TO 90
287.          IZ=IZ+1
288.      69  CONTINUE
289.      IZ=(2*IPRX(I))-282
290.      DO 70 LK=1,2
291.          IF (IZ.EQ.IPRZ(I)) GO TO 90
292.          IZ=IZ+1
293.      70  CONTINUE
294.      71  IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 74
295.      IZ=727-(2*IPRX(I))
296.      DO 72 LK=1,2
297.          IF (IZ.EQ.IPRZ(I)) GO TO 90
298.          IZ=IZ+1
299.      72  CONTINUE
300.      IZ=(2*IPRX(I))-273
301.      DO 73 LK=1,2
302.          IF (IZ.EQ.IPRZ(I)) GO TO 90
303.          IZ=IZ+1
304.      73  CONTINUE
305.      74  IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 77
306.      IZ=736-(2*IPRX(I))
307.      DO 75 LK=1,2
308.          IF (IZ.EQ.IPRZ(I)) GO TO 90
309.          IZ=IZ+1
310.      75  CONTINUE
311.      IZ=(2*IPRX(I))-264
312.      DO 76 LK=1,2
313.          IF (IZ.EQ.IPRZ(I)) GO TO 90
314.          IZ=IZ+1
315.      76  CONTINUE
316.      77  IY=IPRX(I)
317.      IF (IY.NE.IPRY(I)) GO TO 86
318.      IF ((IPRZ(I).LT.218).OR.(IPRZ(I).GT.263)) GO TO 80
319.      IZ=718-(2*IPRX(I))
320.      DO 78 LK=1,2
321.          IF (IZ.EQ.IPRZ(I)) GO TO 90
322.          IZ=IZ+1
323.      78  CONTINUE
324.      IZ=(2*IPRX(I))-282
325.      DO 79 LK=1,2
326.          IF (IZ.EQ.IPRZ(I)) GO TO 90
327.          IZ=IZ+1
328.      79  CONTINUE
329.      80  IF ((IPRZ(I).LT.227).OR.(IPRZ(I).GT.272)) GO TO 83
330.      IZ=727-(2*IPRX(I))
331.      DO 81 LK=1,2
332.          IF (IZ.EQ.IPRZ(I)) GO TO 90
333.          IZ=IZ+1
334.      81  CONTINUE
335.      IZ=(2*IPRX(I))-273
336.      DO 82 LK=1,2
337.          IF (IZ.EQ.IPRZ(I)) GO TO 90
338.          IZ=IZ+1
339.      82  CONTINUE
340.      83  IF ((IPRZ(I).LT.236).OR.(IPRZ(I).GT.281)) GO TO 86
341.      IZ=736-(2*IPRX(I))
342.      DO 84 LK=1,2
343.          IF (IZ.EQ.IPRZ(I)) GO TO 90
344.          IZ=IZ+1
345.      84  CONTINUE
346.      IZ=(2*IPRX(I))-264
347.      DO 85 LK=1,2
348.          IF (IZ.EQ.IPRZ(I)) GO TO 90
349.          IZ=IZ+1
350.      85  CONTINUE

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351.      86 CONTINUE
352.      IF (IDE2.EQ.1) IDE(I)=L
353.      GO TO 99
354.      C
355.      C      THIS PART OF THE PROGRAM RECORDS ENCOUNTERS
356.      C
357.      C
358.      98 WRITE (6,1003)
359.      WRITE (6,1000)
360.      WRITE (6,1001)
361.      WRITE (6,1002) IPRX(I),IPRY(I),IPRZ(I)
362.      WRITE (6,1006) LI
363.      WRITE (6,1007) LJ
364.      C
365.      C
366.      C      THIS PART OF THE PROGRAM REPLACES PREY THAT HAVE BEEN
367.      C      ENCOUNTERED
368.      C
369.      CALL REPL (IPRX,IPRY,IPRZ,I,IJ,IDE)
370.      99 I=I+1
371.      100 CONTINUE
372.      IF (LI.NE.IM) GO TO 105
373.      WRITE (6,1003)
374.      DO 101 LK=1,14
375.      WRITE (6,1004) IPRX(LK),IPRY(LK),IPRZ(LK),LI
376.      101 CONTINUE
377.      IN=IN+1
378.      IM=IN*300
379.      C
380.      C
381.      C      THIS PART OF THE PROGRAM BEGINS A NEW SIMULATION SECOND
382.      C
383.      105 CONTINUE
384.      999 FORMAT ('1')
385.      1000 FORMAT (' ',80X,'A PREY ITEM HAS BEEN ENCOUNTERED')
386.      1001 FORMAT (' ',80X,'AT COORDINATES')
387.      1002 FORMAT (89X,13,3X,I3,3X,I3)
388.      1003 FORMAT (' ')
389.      1004 FORMAT (' ',20X,I3,5X,I3,5X,I3,5X,15)
390.      1005 FORMAT (1X,'RANDOM NUMBER GENERATOR SEED IS',F12.1)
391.      1006 FORMAT (' ',80X,'AT TIME',2X,I5,2X,'SECONDS')
392.      1007 FORMAT (' ',80X,'PREY ITEM',2X,I2,2X,'WAS ENCOUNTERED')
393.      1008 FORMAT (' ',21X,'X',7X,'Y',7X,'Z',5X,'TIME SEC')
394.      STOP
395.      END
396.      C
397.      C
398.      C      THIS SUBROUTINE PLACES THE PREY IN THEIR ORIGINAL POSITIONS
399.      C
400.      SUBROUTINE ORIG (IPRX,IPRY,IPRZ)
401.      DIMENSION IPRX(14),IPRY(14),IPRZ(14)
402.      DATA IA,IB,IC,ID,IE,IF,IG,IH,IJ,IK,IL,IM,IN,IO/104,168,
403.      C119,015,495,182,145,103,042,324,227,290,204,464/
404.      DATA JA,JB,JC,JD,JE,JF,JG,JH,JJ,JK,JL,JM,JN,JO/465,061,
405.      C253,051,103,026,047,252,411,072,424,351,145,350/
406.      DATA KA,KB,KC,KD,KE,KF,KG,KH,KJ,KK,KL,KM,KN,KO/226,349,
407.      C179,306,336,312,151,074,341,265,416,205,075,257/
408.      IPRX(1)=IA
409.      IPRX(2)=IB
410.      IPRX(3)=IC
411.      IPRX(4)=ID
412.      IPRX(5)=IE
413.      IPRX(6)=IF
414.      IPRX(7)=IG
415.      IPRX(8)=IH
416.      IPRX(9)=IJ
417.      IPRX(10)=IK
418.      IPRX(11)=IL
419.      IPRX(12)=IM
420.      IPRX(13)=IN

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421.      IPRX(14)=IO
422.      IPRY(1)=JA
423.      IPRY(2)=JB
424.      IPRY(3)=JC
425.      IPRY(4)=JD
426.      IPRY(5)=JE
427.      IPRY(6)=JF
428.      IPRY(7)=JG
429.      IPRY(8)=JH
430.      IPRY(9)=JJ
431.      IPRY(10)=JK
432.      IPRY(11)=JL
433.      IPRY(12)=JM
434.      IPRY(13)=JN
435.      IPRY(14)=JO
436.      IPRZ(1)=KA
437.      IPRZ(2)=KB
438.      IPRZ(3)=KC
439.      IPRZ(4)=KD
440.      IPRZ(5)=KE
441.      IPRZ(6)=KF
442.      IPRZ(7)=KG
443.      IPRZ(8)=KH
444.      IPRZ(9)=KJ
445.      IPRZ(10)=KK
446.      IPRZ(11)=KL
447.      IPRZ(12)=KM
448.      IPRZ(13)=KN
449.      IPRZ(14)=KO
450.      RETURN
451.      END
452.
453.      C
454.      C THIS SUBROUTINE REPLACES A PREY ITEM WHICH HAS BEEN LOST
455.      C FROM THE SYSTEM DUE TO ENCOUNTER
456.      C
457.      SUBROUTINE REPL (IPRX,IPRY,IPRZ,I,IJ,IDE)
458.      DIMENSION IPRX(14),IPRY(14),IPRZ(14),IDE(14)
459.      DATA K1,L1,M1,IDE1/297,119,247,0/
460.      DATA K2,L2,M2,IDE2/331,321,348,0/
461.      DATA K3,L3,M3,IDE3/295,359,348,0/
462.      DATA K4,L4,M4,IDE4/190,87,369,0/
463.      DATA K5,L5,M5,IDE5/207,421,395,0/
464.      IF (IJ.EQ.1) GO TO 10
465.      IF (IJ.EQ.2) GO TO 20
466.      IF (IJ.EQ.3) GO TO 30
467.      IF (IJ.EQ.4) GO TO 40
468.      IF (IJ.EQ.5) GO TO 50
469.      10 IPRX(I)=K1
470.      IPRY(I)=L1
471.      IPRZ(I)=M1
472.      IDE(I)=IDE1
473.      GO TO 60
474.      20 IPRX(I)=K2
475.      IPRY(I)=L2
476.      IPRZ(I)=M2
477.      IDE(I)=IDE2
478.      GO TO 60
479.      30 IPRX(I)=K3
480.      IPRY(I)=L3
481.      IPRZ(I)=M3
482.      IDE(I)=IDE3
483.      GO TO 60
484.      40 IPRX(I)=K4
485.      IPRY(I)=L4
486.      IPRZ(I)=M4
487.      IDE(I)=IDE4
488.      GO TO 60
489.      50 IPRX(I)=K5
490.      IPRY(I)=L5

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491.      IPRZ( I )=M5
492.      IDE( I )=IDE5
493.      IJ=g
494. 60    IJ=IJ+1
495.      RETURN
496.      END
497. //$/DATA
```

APPENDIX F  
Net-Zooplankton Densities  
in the Gulf of Mexico

After the completion of this dissertation, data was made available to the author concerning copepod densities in the western Gulf of Mexico from the MOCNESS tows taken during the spring, summer and fall Gulf cruises. Cummings (1982) enumerated 97 taxonomic categories (83 species) from the MOCNESS tows. Because of taxonomic uncertainties, he made no attempt to identify the small species of several genera or the cyclopoid species. Combining all 97 taxonomic categories resulted in an average density of approximately 1,600 animals per 100 m<sup>3</sup>.

The following table summarizes the densities of species counted in the seasonal data analysis whose genera were common in the prey used in the foraging experiments of Chapter III.

Table 21. Summary statistics for selected species of copepod enumerated from MOCNESS samples taken on the spring, summer and fall research cruises. Counts have been standardized to #/100 m<sup>3</sup>. Data from Cummings (1982).

Species	Mean No.	Maximum No.
<u>Nannacalanus minor</u>	93.3	971.0
<u>Euchaeta spp. (immatures)</u>	77.7	613.5
<u>Euchaeta marina</u>	57.3	528.5
<u>Scolecithrix danae</u>	48.5	432.5
<u>Eucalanus sewelli</u>	40.7	638.7
<u>Eucalanus hyalinus</u>	30.2	782.8
<u>Candacia spp. (immatures)</u>	18.7	128.2
<u>Scolecithrix bradyi</u>	14.6	157.1
<u>Euchaeta media</u>	10.6	120.5
<u>Candacia longimana</u>	10.6	240.3
<u>Rhincalanus cornutus</u>	10.0	78.2
<u>Eucalanus monachus</u>	9.8	156.4
<u>Candacia varicans</u>	8.3	182.5
<u>Candacia pachydactyla</u>	4.3	65.4

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