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THE ECOLOGY OF CARRION  
COMMUNITIES IN MARITIME-  
TERRESTRIAL HABITATS: AN INSULAR  
STUDY OF GULL, SEAL, AND RODENT  
DECOMPOSITION ON THE ISLES OF  
SHOALS (NEW HAMPSHIRE)

WAYNE DYSON LORD

*University of New Hampshire, Durham*

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THE ECOLOGY OF CARRION COMMUNITIES IN MARITIME-TERRESTRIAL  
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*University of New Hampshire*

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AN INSULAR STUDY OF GULL, SEAL, AND RODENT DECOMPOSITION  
ON THE ISLES OF SHOALS

BY

Wayne D. Lord  
B.S., Eastern College, 1976  
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DISSERTATION

Submitted to the University of New Hampshire  
in Partial Fulfillment of  
the Requirements for the Degree of

Doctor of Philosophy  
in  
Zoology

December, 1982

This dissertation has been examined and approved.



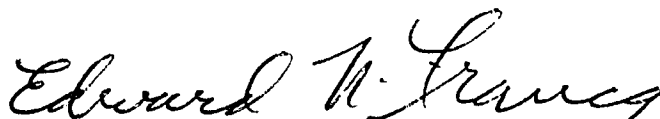
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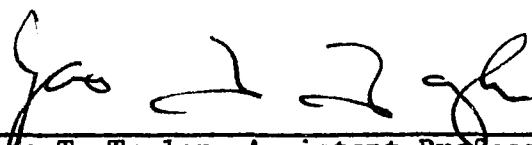
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December 8, 1982  
Date

To Dr. Wilbur Lewis Bullock  
Professor, Distinguished Colleague, and Friend



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ABSTRACT

THE ECOLOGY OF CARRION COMMUNITIES IN MARITIME-TERRESTRIAL HABITATS:  
AN INSULAR STUDY OF GULL, SEAL, AND RODENT DECOMPOSITION  
ON THE ISLES OF SHOALS

by

WAYNE D. LORD

University of New Hampshire, December, 1982

During 1979-1982 I investigated aspects of the ecology of Herring Gull (Larus argentatus) and Great Black-backed Gull (Larus marinus), Harbor seal (Phoca vitulina), and rodent (Rattus norvegicus, Cricetus aurata, Mus musculus) carrion communities on the Isles of Shoals, a group of nine small islands located 10 km SW of Portsmouth, New Hampshire (42°59'N, 70°37'W).

Carcasses passed through a series of predictable decompositional stages (fresh, bloat, active, advanced, and dry) defined by characteristics of carrion appearance and faunal associates.

Of the numerous species of invertebrates collected from coastal carrion, few played a major role in decomposition. Blow fly larvae and dermestid beetles were the primary carrion consumers. Spiders, ants, and staphylinid and histerid beetles were the major predators. The importance of carrion frequenting insects in the decomposition of vertebrate carrion located in habitats with strong maritime influences was indicated.



Carrion community members were divided into 5 trophic guilds: (i) Necrophages, (ii) Necrophiles, (iii) Predators, (iv) Necrophages/Predators, (v) Parasites. Necrophages partition carrion spatially, temporally, and by extent of desiccation. Predators selected prey by location, size, and life stage. Carcasses located in "less exposed" areas characteristically supported a greater variety of species and decomposed at a slower rate. Seasonal variations in carrion abundance, availability to necrophagous arthropods, and community composition were evident on the Isles of Shoals.

Small carcasses supported statistically fewer arthropod species than large; and carrion located at greater distances from source of colonists were also less species rich. The successional process, characteristics of early and late colonists, and the effects of carrion size and distance from source of colonists suggest a process of colonization and community development consistent with geographical and less ephemeral biological island systems.

## INTRODUCTION

The postmortem decomposition of animals, while being of limited aesthetic appeal, is a fascinating process of ecological and medico-legal importance. Assemblages of unique carrion-feeding consumers, and the predators and parasites they in turn support, form communities which enhance the recycling of carrion components through the environment. Predictable changes in species abundance, age, and composition, that occur as the decay process progresses, provide a template for examining concepts of community development, temporal and seasonal succession, and the role of biotic and abiotic regulators.

Similarly, the small size, comparatively simple structure, and insular nature of carrion microcosms may afford a model for predicting the structure and function of larger biological and geographical islands, and continental systems as well.

Understanding the ecology of carrion communities is particularly important in habitats where large assemblages of colonial animals occur. Within such habitats high mortality rates, especially among young individuals, result in an extremely abundant carrion resource. A knowledge of the organisms and processes involved in the redistribution of this resource is fundamental to an understanding of the ecology of the larger community within which the carrion occurs.

### Historical Perspectives

Relatively few studies of carrion ecology exist in the literature, reflecting the limited appeal of this research area. During the last 50 years, however, several important contributions have been published.

Illingworth (1926) listed the arthropods attracted to carrion in southern California. Fuller (1934) studied insect inhabitants of carrion in Australia, stressing the importance of blowflies as primary consumers in decomposition and noting the impact of arthropod predators on their immature stages.

Howden (1950) listed 14 species of beetles from carcasses in North Carolina. She emphasized the role of both predation and necrophagy, and described the general succession.

Reed (1958) examined dog carcass communities in Tennessee. Carcasses placed in pasture supported smaller insect populations, but decayed faster than those in wooded areas, due to higher temperature.

Walker (1957) also studied the arthropod inhabitants of carrion in Tennessee. He emphasized the importance of habitat microclimate in influencing the decay process.

Bornemissza (1957), in Australia, reported dramatic changes in species composition of soil beneath carcasses at various stages of decay.

Payne (1965) demonstrated the importance of arthropods to decay of carrion in South Carolina. Insect-free carrion decomposed remarkably slowly, retaining its form for months, whereas insect infested carrion completely decayed within a week. Payne and Crossley (1966) compiled an extensive list of the arthropods associated with pig carrion. Payne and King (1972) conducted the first study of the fauna associated with floating carcasses in a freshwater pond.

Microseral and seasonal variations in small mammal carrion communities existed in a mixed hardwood forest in Illinois (Johnson 1975). He reported marked seasonal variations in species composition

and decompositional rates and emphasized the presence of predictable microseral stages.

Denno and Cothran (1975) stressed the importance of competitive interactions between species of carrion inhabiting flies, and demonstrated partitioning of carrion resources along seasonal, successional and size gradients.

McKinnerney (1978) investigated roles of both vertebrate and invertebrate components of carrion microcommunities in the Chihuahuan desert of Texas and New Mexico. Utilizing measures of diversity and dominance, she described the successional process of decay. She suggested that correlations between removal efficiency of vertebrates and invertebrate colonization patterns were indicators of the selective pressures molding arthropod adaptations.

Coe (1978), in a study of elephant carcasses in Tsavo National Park, Kenya, emphasized the importance of calcium immobilized in large mammal bones in the process of mineral recycling.

Carrion research has importance to the forensic sciences, as documented by Motter (1898) and more recently by LeClerq (1969), Easton and Smith (1970), Smith (1973), Adelson (1974), Nuorteva (1974), Lane (1975), and Eckert (1980). Nuorteva (1977) compiled a comprehensive review of the medico-legal applications of carrion community data.

#### Research Objectives

Of the the carrion research published to date, the vast majority has been conducted in tropical, semi-tropical, and southern temperate regions. Investigations from colder, northern temperate areas in general and the northeastern United States in particular are lacking. Similarly, carrion research largely has been restricted to classical,

terrestrial habitats such as pasture, woodland, and desert. Coastal and maritime-terrestrial ecotypes have been neglected.

Nearly all carrion studies are based on carcasses of domestic mammals; few investigations have examined communities associated with major forms of naturally occurring carrion.

The following thesis is designed to enhance the understanding of the ecology of carrion communities which occur in maritime-terrestrial habitats characteristic of coastal regions of northern New England.

The thesis is presented in the form of three separate manuscripts, each centering upon a different aspect of coastal carrion ecology. The first describes the invertebrate and vertebrate components of Herring Gull (Larus argentatus) and Great Black-backed Gull (Larus marinus) carrion communities, focusing on community structure, seasonality, and succession. Herring and Great Black-backed Gulls are the most conspicuous components of the vertebrate fauna in northern coastal regions (Kadlec and Drury 1968). The second manuscript, in a similar manner, describes the communities associated with corpses of the Harbor Seal (Phoca vitulina), the largest, non-anthropoid vertebrate inhabiting these coastal areas. The third manuscript discusses insular carrion communities as biological islands and examines their role as models for the assessment of biogeographic theory.

Specifically, the research presented in the following pages addresses these questions:

- 1) What organisms characterize the major vertebrate carrion communities naturally occurring in maritime-terrestrial habitats located in northern New England (community structure)?

- 2) What changes occur within these communities as the decay process progresses (seral succession)?
- 3) Do differences in carrion species assemblages occur during different times of the year (seasonality)?
- 4) Do the patterns of colonization and community development observed during the decompositional process support the theories proposed by McArthur and Wilson (1967) for insular systems (biogeography)?

### Description of Study Site

#### Setting

The research facilities of the University of New Hampshire/Cornell University co-sponsored Shoals Marine Laboratory, located on the Isles of Shoals in the Gulf of Maine, provided an ideal setting for my research. A variety of coastal habitat types, isolated from human disturbance, offered protected settings for field research. The high incidence of naturally occurring mortality in gull and, in 1980, Harbor Seal populations, produced an ample supply of carrion. The facilities of the Shoals Marine Laboratory offered adequate laboratory and living accommodations in close proximity to study areas, enhancing research productivity at a reasonable cost.

The Isles of Shoals are a group of small islands located nine nautical miles southeast of Portsmouth, New Hampshire ( $42^{\circ}59'N$ ,  $70^{\circ}37'W$ ) on the Maine-New Hampshire state line (Figure 1). They are the sole archipelago along an 80 kilometer stretch of New England coast between Cape Ann, Massachusetts and Casco Bay, Maine. These nine islands have a total land area of 75.4 hectares, a maximum height of 21 meters above mean high water, and lie within an area 3 miles north-south by 1.5 miles

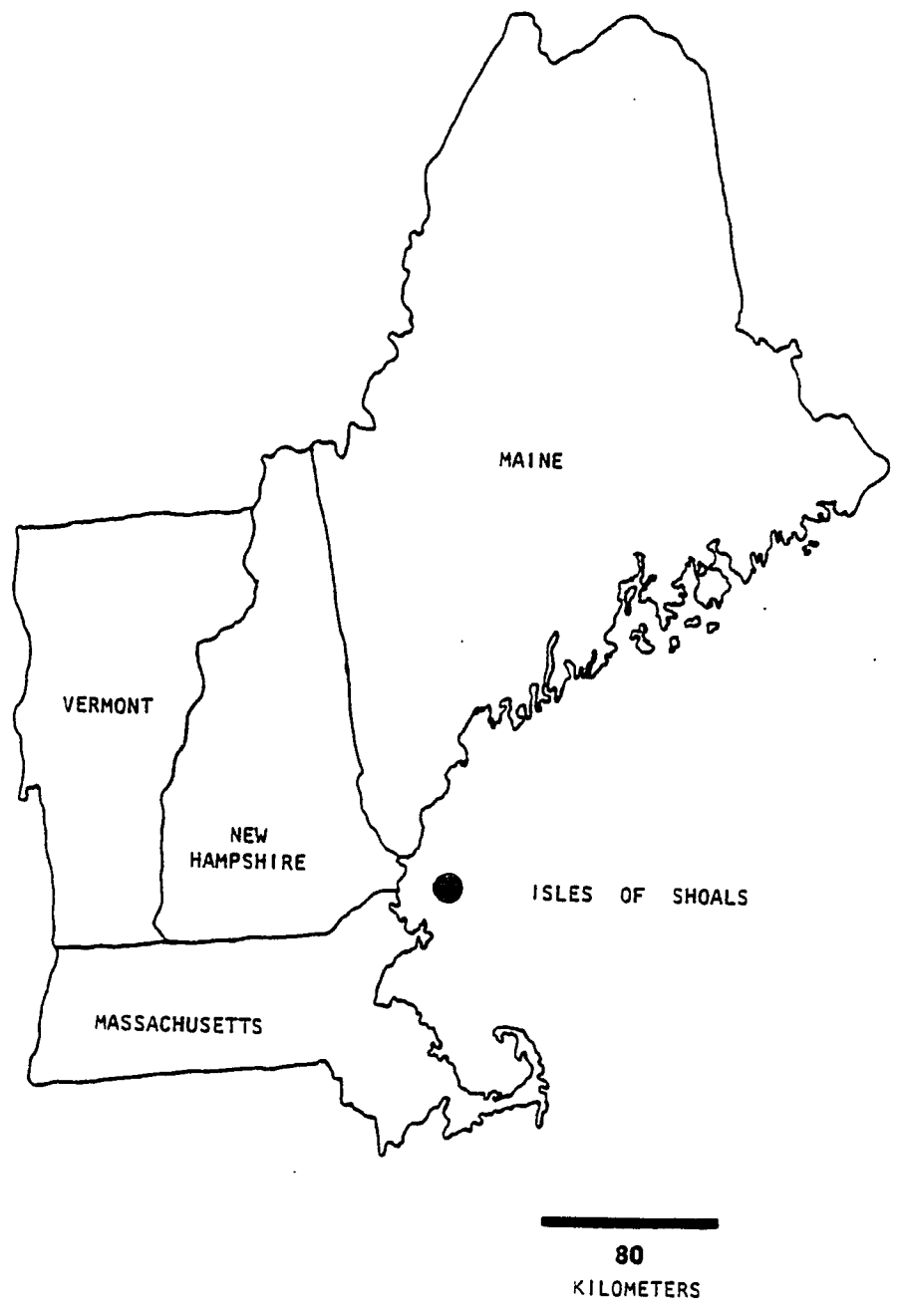


Figure 1. Location of the Isles of Shoals along the New England coast

east-west (Figure 2.). All are surrounded by deep water, 35 to 45 meters in depth. Of the nine islands, Appledore is the largest, with an approximate land area of 33.6 hectares.

Descriptions of the physical and biological characteristics of the Isles of Shoals have been published by Bloomshield (1975), Boden (1977), Borrer (1980), Fowler-Billings (1959), Kingsbury (1976), McGill (1977), and Novak (1971). The following summary is derived from these sources.

### Geology

Appledore Island is a roche montonee island, whose topography resulted from glacial activity during the Wisconsin glacial advance. On the northwest side, which faced the advancing ice, the bedrock is smooth and worn. On the southeastern side stand ragged cliffs. Generally the topography is characterized by rocky internal ridges and valleys, and by peripheral cliffs and cobble beaches. Ridges and cliffs are composed of exposed bedrock, with granite (quarzo-feldsparic gneiss) being the most abundant rock. Dikes of igneous basalt transect these rocks and play a role in the formation of coves and crevices. The shoreline structure varies from abrupt cliffs to sloping cobble beaches composed of till ranging from several centimeters to more than a meter in diameter.

The cover of soil on Appledore varies considerably with location. Soil depth ranges from approximately 70 centimeters, in the more central valleys to a superficial covering on ridge tops.

### Tides

A semi-diurnal cycle underlies the tidal patterns of the Isles of Shoals. Mean tidal range is 2.6 meters, with spring ranging 3 meters.



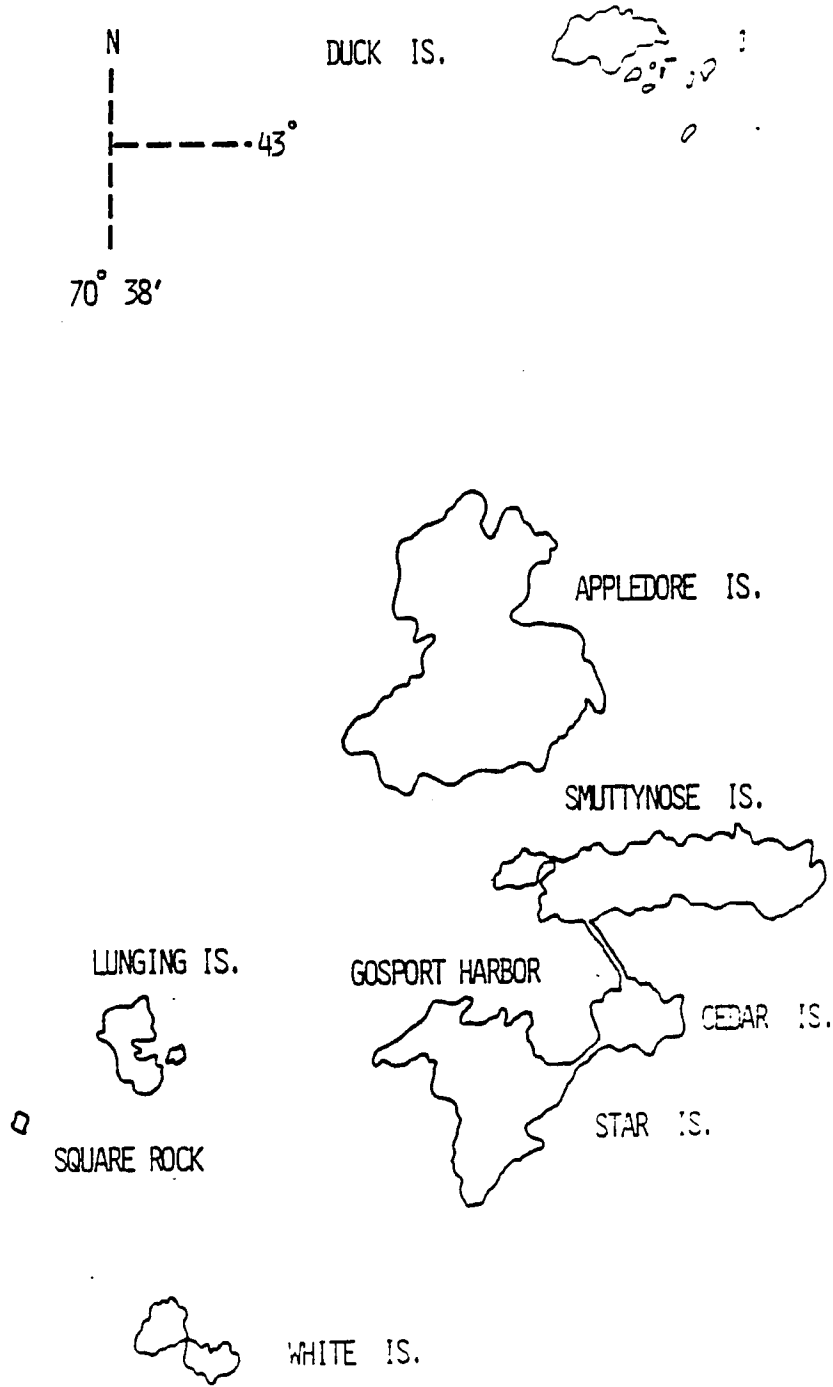


Figure 2. Map of the islands of the Isles of Shoals

Storms with strong, sustained winds periodically build waves which wash normally dry beaches and low lying areas.

### Climate

Weather patterns at the Isles of Shoals are similar to those typical of coastal New England. Seasonal temperatures, however, are moderated by oceanic influences. January and February are the coldest and stormiest months, July and August the warmest (Figure 3). The prevailing winds vary seasonally, with winter months dominated by westerly, northwesterly and northerly components, and summer by a southerly or southwesterly flow. Weather systems associated with passage of low pressure centers typically display winds from a north-easterly direction.

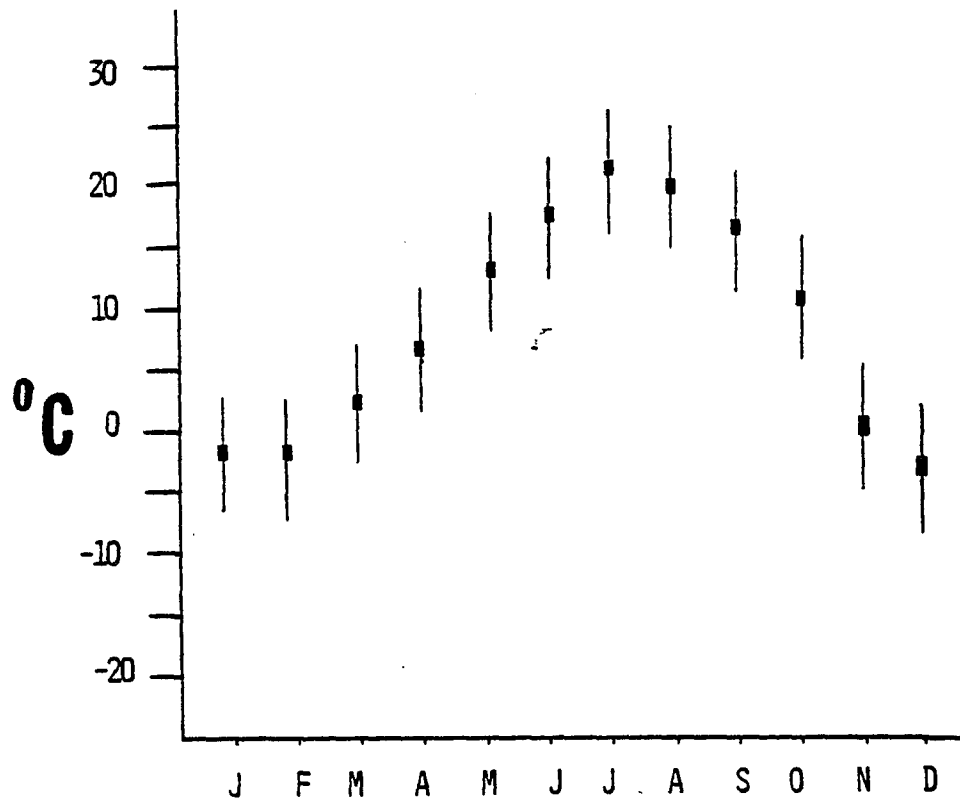
Annual rainfall averages approximately 100 centimeters (Table 1). January and April are generally the wettest months, August the driest. Heavy fog is common during spring and early summer. Catastrophic storms with sustained winds of hurricane force recur approximately every ten years. The most recent occurred in 1978.

### Flora

Boden (1977) published a detailed description of the species composition and distribution of the vascular plants of Appledore Island. There are five major zones of vegetation; dry and moist shrub thicket, granite ridges, cobble beach, and disturbed areas. Of these, two were used in carrion research.

Granite ridge habitats occur on the unprotected cliff tops of the northeastern, eastern, and southeastern sides of the island. Here, large numbers of nesting gulls modify the vegetational structure by

## Mean monthly temperatures (54 years' data)



(adapted from McGill, 1977)

Figure 3. Approximate climatological data, Isles of Shoals

Table 1. Approximate climatological date - Isles of Shoals

Mean Monthly Precipitation (54 years' data)						
Jan.	Feb.	Mar.	Apr.	May	June	July
10.1	8.6	9.3	9.7	7.8	7.8	8.6
	Aug.	Sept.	Oct.	Nov.	Dec.	
	7.6	8.6	7.8	9.7	9.3	centimeters

(adapted from McGill, 1977)

uprooting and trampling during nesting activities and aggressive interactions. The resulting vegetation consists of lawns of short grasses and peripheral shrub borders approximately 1.5 m high. Rumex acetosella, Rumex crispus, Potentilla simplex, Potentilla gracilis, Potentilla norvegica, Spergulariaa rubra, Coclopleurum lucidum, Lepidium ruderale, Matricaria matricarioides, Sagina procumens, Trifolium repens, Bromus tectorum, Bromus marginatus, Polygonum aviculare, Lychnis alba, Argopyron repens, Festuca capillata, Convolvulus speium, Achillea millefolium, Ambrosia artemisifolia, and Heracleum maximum are found in these areas.

Cobble beach areas are also inhabited by large gull populations and are modified by their activities. A few sparsely distributed herbs, including Solidago sempervirens, Galinsoga ciliata, Teucrium canadense, Nepta cataria, and Anagallis arvensis, characterized this habitats.

### Fauna

The Isles of Shoals possess a rich diversity of terrestrial and marine vertebrates and invertebrates (Borrer 1982). Among the terrestrial mammals inhabiting the islands are muskrats (Ondatra zibethicus), Norway rats (Rattus nowegicus), and white-footed mice (Peromyscus leucopus). Harbor seals (Phoca vitulina) occur from November till June on Duck Island. Duck Island is thought to be the southern most pupping site of these animals.

Only two species of reptiles, the Smooth Green Snake (Opheodrys vernalis) and Dekay's Snake (Storeria dekayi) have been found on Appledore. No amphibians are known to occur there.

One hundred and twenty species of birds are sighted annually on Appledore Island. Among the more numerous nesting species are Snowy Egrets (Egretta thula), Black-crowned Night Herons (Nycticorax nycticorax), and Glossy Ibis (Plegadis falcinellus). A wide variety of less numerous species are also known to nest on Appledore.

By far the most numerous of the nesting birds of the Isles of Shoals are Herring (Larus argentatus) and Great Black-backed (Larus marinus) Gulls. During 1979, 3735 and 1552 pairs of Herring and Great Black-backs, respectively, were reported as nesting upon the islands (Borrer 1980). The gulls nest primarily upon the cliffs, ridge tops, and cobble beaches. During the breeding season high mortality rates among adults and particularly among juveniles cause the major colonies to be littered with carrion. One needs only to wander through such an area to appreciate the importance of carrion as a resource.

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CHAPTER I

HERRING GULLS (Larus argentatus)  
AND GREAT BLACK-BACKED GULLS (Larus marinus)

## INTRODUCTION

Herring Gulls (Larus argentatus) and Great Black-backed Gulls (Larus marinus) are conspicuous inhabitants of the New England coast. After suffering nearly complete annihilation at the hands of the millinery industry during the late 1800's, large populations now colonize insular and coastal regions (Drury 1973). Borrer (1980) reported the occurrence of 3735 and 1552 breeding pairs, respectively, on the islands of the Isles of Shoals, Maine alone. Protection from human predation has helped to enhance population growth and range expansion.

Kadlec and Drury (1968) documented a high incidence of naturally occurring mortality within the expanding New England gull population. Factors contributing to non-human gull mortality are climatic conditions (Kadlec and Drury 1968), cannibalism (Parsons 1971), predation (Davis and Dunn 1976, Parsons 1976, and Weaver 1970), and interspecific aggression (McGill 1977). When coupled with population growth, natural mortality produces an abundant carrion resource.

Carrion is a significant component of biological communities, providing food and shelter for numerous organisms (Johnson 1975). A knowledge of the organisms and processes involved in the redistribution of this resource is important for understanding the ecology of larger communities within which carrion occurs (Odum 1971). Carrion ecology is important to medico-legal authorities as a tool useful in determining time of death (Nuorteva 1977).

This paper describes the structure, succession, and seasonality of gull carrion communities studied on islands in the Gulf of Maine during 1980-82. Special attention is given to the carrion frequenting Arthropoda. Payne (1965) demonstrated the dominant role that arthropods play in the decompositional process. Although several authors, including Illingworth (1926), Fuller (1934), Howden (1950), Bornemissza (1957), Reed (1958), Denno and Cothran (1975), and McKinnerney (1978), have examined carrion community ecology no studies published to date deal with carrion communities occurring in temperate coastal regions of North America.

## MATERIALS AND METHODS

We conducted field work from May 1980 through February 1982 on the Isles of Shoals, a group of small islands located 10 km SE of Portsmouth, New Hampshire on the Maine-New Hampshire state line ( $49^{\circ}59'N$ ,  $70^{\circ}37'W$ ). The Isles of Shoals constitute the sole archipelago along an 80 km stretch of New England coast between Cape Ann, Massachusetts and Casco Bay, Maine (Fig. 1). Their topography includes rocky internal ridges and valleys, peripheral cliffs, and cobble beaches, resulting from glacial activity during the Wisconsin glacial advance. Of the nine islands Appledore is the largest with an approximate land area of 36.6 ha. Appledore Island houses facilities of the Cornell University/University of New Hampshire sponsored Shoals Marine Laboratory, where research facilities are located.

The islands offer a variety of coastal habitats protected from human disturbance. Large colonies of Herring and Great Black-backed Gulls insure an ample supply of carrion. Detailed descriptions of physical and biological characteristics of the Isles of Shoals are published in Bloomshield (1975), Boden (1977), Borrer (1980), Fowler-Billings (1959), and Kingsbury (1976).

We utilized 60 adult gull and 24 chick carcasses during the study. Approximately 120 additional specimens were also examined but not routinely sampled.

Each month we placed 3 adult carcasses in each of two habitats, granite ridge, and cobble beach, the habitats most commonly colonized by gulls (McGill 1977). Granite ridges occur as internal and peripheral

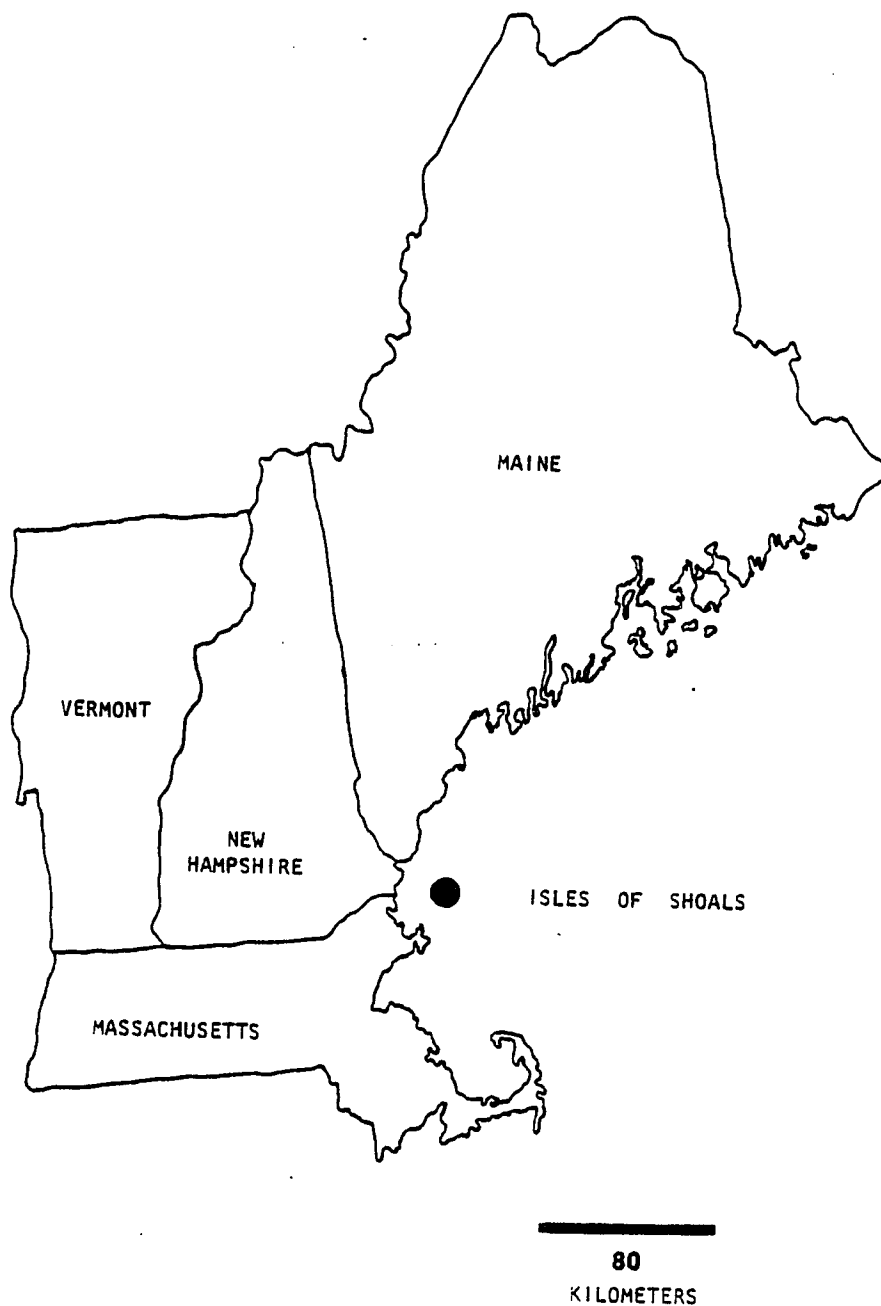


Figure 1. Location of the Isles of Shoals along the New England Coast

cliff tops on the easterly and central portions of the islands. Here lawns of short grass and shrub borders (1.5 meters) high predominate and soil 2 - 7 cm deep is present. Cobble beaches predominate along the shoreline in protected areas and are composed of till, ranging from several centimeters to over a meter in diameter. A few sparsely distributed herbs are the only plants. Boden (1977) provides a detailed description of the vascular flora of Appledore.

We placed adult carcasses beneath metal milk crates (30x30x26 cm) spaced a minimum of 10 m apart to protect them from predation and removal by vertebrate scavengers in sites where natural mortality is common. We used sick or injured gulls and sacrificed them just prior to field placement. Carcasses on beaches were located in nesting zones approximately 3 m above maximum high tide and were never inundated by seawater.

Carcass arthropods were sampled daily for the first 5 days and every 2-3 days thereafter. Considerably longer periods between samples occurred during late fall, winter, and early spring when carrion abundance and activity was minimal. We designed sampling and replicate regimes to insure collection of organisms representative of all successional stages and seasons.

Invertebrates occurring on the upper surface, inside, and beneath carcasses were counted and behavior noted. Representative collections were made using standard entomological equipment (aspirators, forceps, nets, etc.). Only reference specimens were removed to minimize carrion community disturbance. We preserved collections by standard techniques (Peterson 1966) and returned them to the laboratory for identification. Specimens of larval Diptera were reared to adults on beef liver. We

measured carrion mass on a triple beam balance and made photographic records of carrion appearance during each sampling period.

Climatological data including air, ground, and internal carcass temperature, precipitation, and wind speed and direction were also collected.

Two replicates of 12 adult gull and 12 chick carcasses were exposed to vertebrate predation. Visual observations of vertebrate scavenging behavior (0800 - 2000) were recorded.

We calculated the Shannon-Weaver index of general diversity ( $H'$ ) for each successional stage:

$$H' = - \sum_{i=1}^s P_i \ln P_i$$

where:  $s$  is the number of taxa listed for the successional stage and  $P_i$  is the proportion of the total number of individuals in the  $i$ th taxon (Southwood 1978). Evenness ( $J$ ) was also calculated for each successional stage (Pielou 1969):

$$J = H' / H'_{\max}$$

where:  $H'$  is the observed diversity and  $H'_{\max}$  is the maximum possible diversity for a community with the same number of species.

Similar techniques of carrion sampling and/or analysis have been utilized by Johnson (1975), Payne (1965), Payne and Crossley (1966), McKinnerney (1978), and Reed (1958).



## RESULTS AND DISCUSSION

### Community Structure

We collected 65 species, representing 46 families of invertebrates, during the study. All but 2 species (Gastropoda) were arthropods. Dominance of arthropods in carrion communities is well documented (Putnam 1978). Three orders of insects, Diptera, Coleoptera, and Hymenoptera accounted for 75% of the species collected. Payne (1965) found these groups to represent 78% of the invertebrates frequenting pig carrion in South Carolina.

We collected 59 species from granite ridge habitats and 41 from cobble beaches. Ridges were found to have a significantly greater diversity ( $P < .05$ , t-test) in all but the earliest decay stage and significantly greater evenness ( $P < .01$ , t-test) in the later stages of decomposition (Table I). Complete decomposition required less time ( $x = 31$  days) on cobble beaches than on ridges ( $x = 39$  days). Most species collected were common associates of carrion throughout the eastern United States (Payne 1965). Others were typical of wrack communities along the New England coast (Behbehani 1978, Glennon 1979). Descriptions of the major carrion frequenting arthropods encountered during the study are given below.

Five ecological guilds were evident within gull carrion: (i) Necrophages - species feeding directly on carrion or the products of decay, (ii) Necrophiles - species using carrion for shelter or occurring accidentally, (iii) Predators - those preying on carrion community members, (iv) Necrophages/Predators - species feeding on invertebrates

Table I. Duration, diversity, and evenness of gull carrion successional stages

	Duration (x days)		Diversity - H' (x ± SE)		Evenness - J (x ± SE)	
	GR	CB	GR	CB	GR	CB
Fresh	3	3	.63 ±.14	.20 ±.20	.50 ±.05	.18 ±.18
Active	10	10	.96 ±.19	.42* ±.11	.41 ±.07	.29 ±.09
Advanced	12	8	1.72 ±.03	1.34* ±.08	.76 ±.01	.68** ±.02
Dry	14	10	1.27 ±.17	.65** ±.11	.77 ±.03	.46*** ±.04

GR = Granite Ridge; CB = Cobble Beach  
Significance levels (Students t-test)

\*P<.05

\*\*P<.01

\*\*\*P<.001

decaying materials as well, (v) Parasites - parasites of carrion inhabitants. Figures 2 and 3 illustrate the generalized trophic relationships between guilds for ridges and beaches respectively. Similar classifications have been proposed by Morley (1907) and McKinnerney (1978).

#### Necrophagous Group

We collected 26 species of necrophagous arthropods, 22 on granite ridges and 17 on cobble beaches. In each habitat representatives of 2 families, Calliphoridae and Dermestidae, predominate. Blow flies (Calliphoridae) dominated the early stages of decay. Adults usually occurred at carcasses within 10 minutes after field placement. Oviposition was restricted to the first 3 days, but adults continued to occur sporadically throughout decomposition feeding on the fluids of putrefaction. Blow fly larvae were the primary carrion consumers, feeding for 8-10 days before migrating into the substrate to pupate. Up to 90% of carrion mass was lost during larval calliphorid feeding. Four species, Calliphora vicina (Robineau-Desvoidy), Cynomyopsis cadaverina (Robineau-Desvoidy), Lucilia illustrus (Meigen), and Phormia regina (Meigen) frequented both cobble beaches and granite ridges. An additional species, Cochliomyia macellaria (Fabricius) occurred rarely on ridges alone.

Two species of Dermestidae, Dermestes caninus (Germar) and Dermestes vulpinus (Fabricius), colonize gull carrion. While individuals were present during the entire decay process, most (86%) were associated with later decompositional stages, following blow fly larval migration. Significantly greater numbers of both species ( $P < .05$ ,

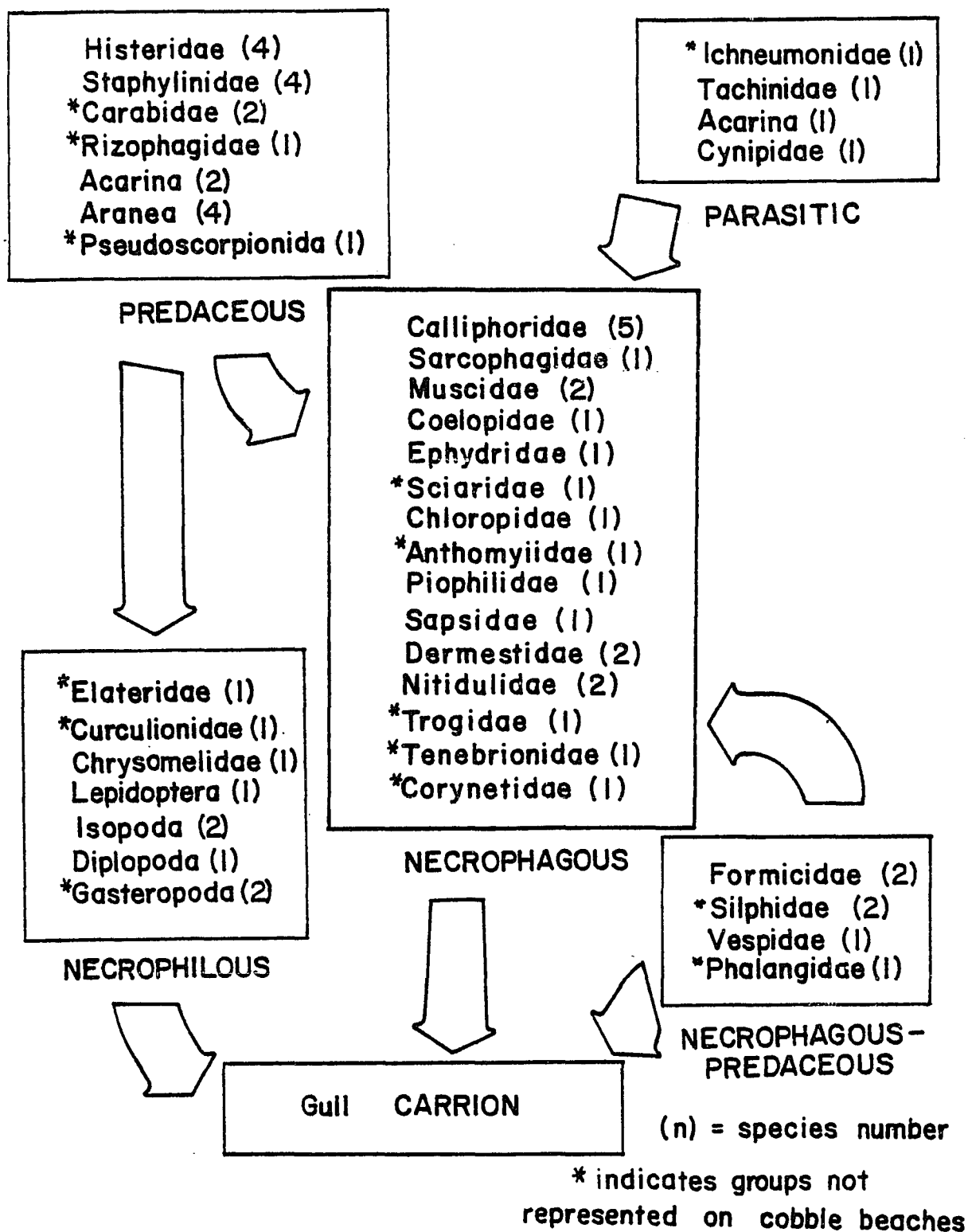
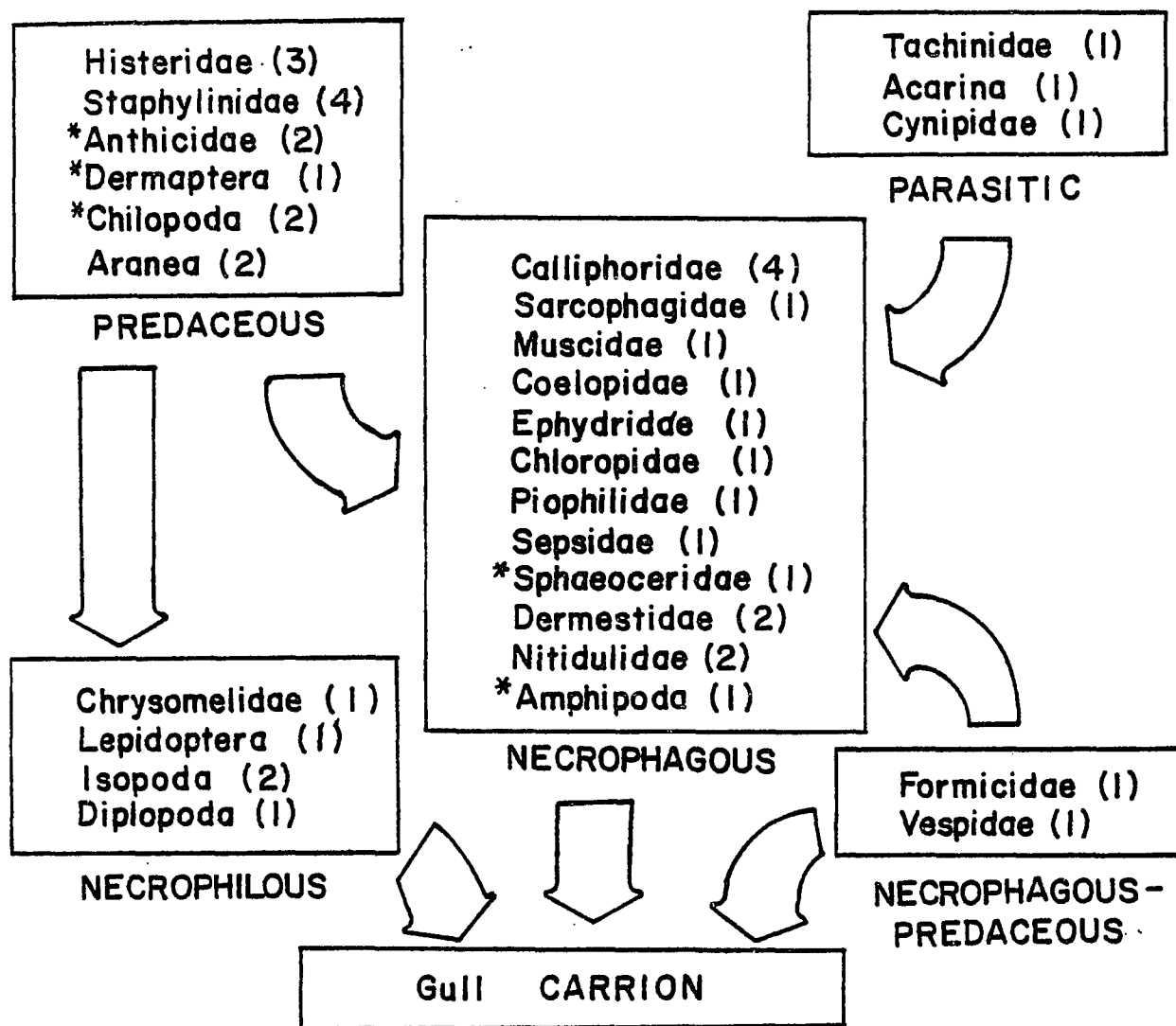


Fig. 2 GENERALIZED TROPHIC RELATIONSHIPS OF  
GULL CARRION ARTHROPODS - GRANITE RIDGE



\*indicates groups not represented on granite ridges

Fig. 3 GENERALIZED TROPHIC RELATIONSHIPS OF GULL CARRION ARTHROPODS - COBBLE BEACH

Table II. Relative abundance of the major necrophages beetles and predatory ants frequenting gull carrion

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	Fresh		Active		Advanced		Dry	
	GR	CB	GR	CB	GR	CB	GR	CB
<b>Dermestidae</b>								
x	0.0	1.00*	14.0	51.20***	47.50	72.25*	39.29	91.75***
SE	0.0	.34	3.21	6.52	9.80	6.62	6.62	7.49
<b>Formicidae</b>								
x	116.0	0.0***	112.1	.33***	62.67	.67***	31.00	0.0***
SE	14.5	0.0	14.15	.26	2.76	.29		

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Dermestidae = Dermestes caninus and Dermestes vulpinus

Formicidae = Tetramorium caespitum and Monomorium minimum

Significance levels (Students t-test)

\*p<.05

\*\*p<.01

\*\*\*p<.001

x = (mean/carcass/day)

t-test) were observed on cobble beaches (Table II). Dermestids feed on dried animal tissues (Dillon and Dillon 1972).

The sap beetle, Stelidota germinata (Say) (Nitidulidae), was also present in substantial numbers on carcasses in both habitats (Figs. 6 and 7), and fed on the liquified products of decay. The small size and feeding habits of this beetle limit its importance in gull decomposition.

The remaining necrophagous species occurred in low abundance (Figs. 6 and 7) and had a minor impact on decompositional rate. Among these were several common carrion inhabitants: Sarcophaga bullata (Park) (Sarcophagidae), Fannia canicularis (Desvoidy) (Fanniidae), Piophilalata latipes (Meigen) (Piophilidae), Sepsis punctum (Fabricius) (Sepsidae), Trox variolatus (Melsheimer) (Trogidae), and Necrophorus tomentosus (Weber) and Silpha noveboracensis (Forster) (Silphidae). Further consideration is given to species of minor importance in the discussion of succession.

#### Predaceous Group

Twenty-three predatory species colonize gull carrion, 18 on ridge carrion and 14 on cobble beaches. Representatives of 2 families of beetles, Histeridae and Staphylinidae, were common to both areas. Three staphylinids, Aleocara lata (Gravenhorst), Creophilus maxillosus (Linne), and Philonthus politus (Curtis), were abundant. A fourth species, Staphylinus violaceus (Gravenhorst), occurred rarely and only on ridges. Three histerids, Pachylopus fraternus (Say), Saprinus conformis (LeConte), and Saprinus assimilis (Paykull) were common in both habitats. We collected Saprinus pennsylvanicus (Paykull) only on beaches. Staphylinids and histerids were commonly observed feeding on larval diptera and coleoptera.

An intertidal earwig, Anisolabis maritima (Gene) (Dermaptera), was common on cobble beach carrion and also preys on invertebrates inhabiting decaying seaweed (Glennon 1979). Several minor predators, including Anthicus cinctus (Say) (Anthicidae), Salticus scenicus (Clerck) and Pardosa lapicina (Emerton) (Aranea), and Arenophilus sp. (Chilopoda) were restricted to beaches as well.

The most abundant predator frequenting ridge carrion was the ant Tetramorium caespitum (Linne) (Formicidae). Significantly greater numbers of individuals ( $P < .001$ , t-test) occurred on granite ridges throughout the decay process (Table II), preying upon large numbers of eggs and larvae of necrophagous species. The predatory influence of these ants was an important factor decreasing the decompositional rate of carrion on ridges. Several less numerous predators, including Monotoma picipes (Hbst.) (Rhizophagidae), Lebia viridis (Say) and Poecilus lucubladus (Say) (Carabidae), and Agelenopsis potteri (Blackwall) (Aranea), occurred solely upon ridges as well.

#### Necrophilous Group

Terrestrial isopods were the most abundant necrophilous group in both habitats. Porcellio rathkei (Brandt) and Philoscia vittata (Say) occurred only on granite ridges and cobble beaches respectively. Porcellio scaber (Latreille) was common to both areas. The millipede Nacerus americanus (Linne) was also present in both habitats, although only in small numbers. Two species of terrestrial snails, Vallonia pulchella (Mueller) and Polygyra sp., were encountered rarely. These snails represent the only non-arthropod invertebrates collected during the study, and were found on ridges only. Other necrophilous species were accidentals and represented approximately one individual per carcass.



### Parasitic Group

A single species of mite, Poecilochirus sp., was the only common parasite encountered on gull carrion. Individuals parasitized a variety of predatory beetles, including species of Histeridae, Staphylinidae, and Silphidae. Other parasites (Cynipidae, Ichneumonidae, and Tachinidae) were rarely collected or successfully reared from larval dipteran hosts.

Many species of insect collected from gull carrion, Coelopa frigida (Fabricius) (Coelopidae), Ephydra riparia (Fallen) (Ephydriidae), Fannia canicularis (Desvoidy) (Muscidae), Arenophilus sp. (Chilopoda), Trombidium sp. (Aracarina), Pardosa lapidicina (Aranea), and the amphipod Orchestria platensis (Kroyer), typically inhabit coastal wrack communities. These species, however, played only a minor role in gull decomposition. Only one insect species, Anisolabis maritima (Dermaptera), was found to be a significant part of both wrack and gull carrion communities. The importance of carrion specializing insects in the decomposition of carcasses located in habitats with strong marine influences is evident.

The importance of climatic influences on carrion community structure have been emphasized by Jacques (1915), Walsh (1931) Kaufman (1937), Walker (1957), and Reed (1958). Carcasses located in "less exposed" areas characteristically support a greater variety of species and decompose at slower rates. We observed similar patterns on Appledore. Carcasses located on ridges supported a greater diversity of inhabitants and decomposed more slowly than those on cobble beaches. Lower temperatures on ridges, particularly during later decay (Table III), reduced wind velocity at heights less than 1 m (Table IV), greater

Table III. Air, ground, and carcass temperature measurements for successional stages of gull carrion

	Air		Ground		Carcass	
	Em	CB	EM	CB	EM	CB
Fresh	4.06	3.56	7.17	6.11	3.83	4.72
	1.29	.43	1.01	.69	.97	1.35
Active	6.39	8.28*	9.11	8.17	7.00	7.00
	.91	.57	.74	1.40	1.01	.66
Advanced	.94	5.22	4.56	8.28*	2.44	4.11*
	.27	2.24	.72	1.63	.29	.85
Dry	10.83	11.50	9.28	14.28*	8.72	12.95*
	.92	1.23	1.38	1.74	1.38	1.81

Significance levels: \* (.01 < P < .05) (Students t-test)

All values =  $\bar{x} \pm SE$

Table IV. Windspeed (m/sec) measurements for granite ridge and cobble beach areas (Isles of Shoals)

Height	Granite Ridges		Cobble Beaches	
	x	SE	x	SE
2.0 m	3.10	.48	2.98	.55
1.0 m	1.46	.29	1.28	.07
.5 m	.70	.30	1.31	.15*
.08 m	.20	.18	.70	.13*

\*Significance Level:  $P < .05$  (Students t-test)

shading by vegetation (McGill 1977), and presence of organic soils (Boden 1977), all characteristic of ridges, enhanced arthropod colonization and survival. Increased ridge community complexity resulted in consistently greater proportions of predators and fewer primary carrion consumers (Fig. 4), thus moderating decay rate.

Drier conditions on cobble beaches resulting from higher temperatures, greater wind speed, and lack of vegetation increased the rate of carcass dehydration. Drier tissues, during the later stages of decay, supported significantly greater populations of dermestid beetles (Table II), enhancing decomposition.

No significant differences in community structure were found between gull species. The larger Black-backed Gulls (x 1575.0 g BBG, vs x 1132.0 g HG) supported consistently larger numbers of individuals, but differences were not statistically different.

#### Succession

As carrion decomposes it passes through a series of predictable physical changes (Johnson 1975). Although decomposition is continuous, investigators have divided the process into various stages based on physical appearance and characteristic faunal associates (McKinnerney 1978). We recognized four decompositional stages - fresh, active decay, advanced decay, and dry - occurring in gull carrion. This classification approximates that of McKinnerney (1978) proposed for rabbit carcasses in deserts. Our classification is based on characteristics of physical appearance, decompositional chemistry, faunal assemblages, and patterns of diversity and similarity. Figure 5 illustrates the successional stages of gull carcass decomposition for granite ridges and cobble beaches as indicated by patterns of general diversity ( $H'$ ). A similar

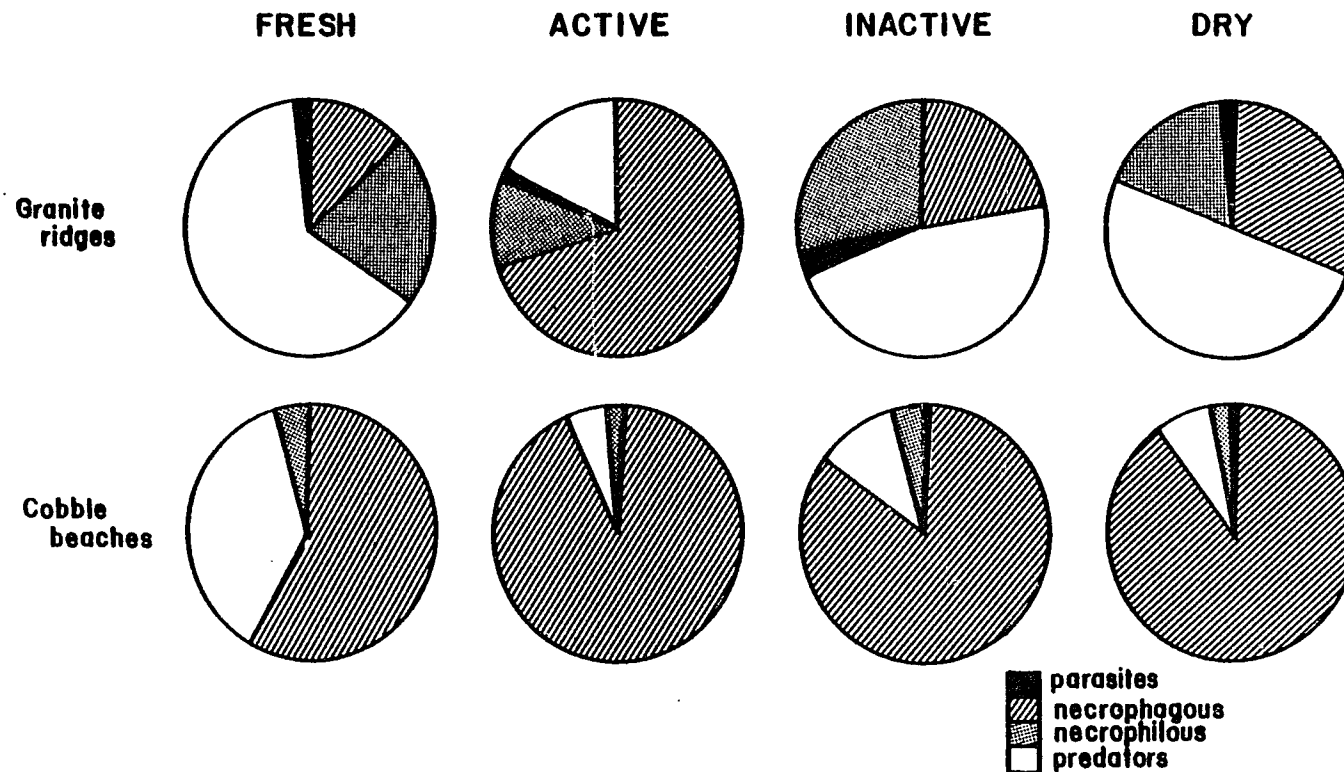


Fig.4 PERCENT COMPOSITION OF NECROPHAGOUS, PREDATORY, AND PARASITIC SPECIES FOR SUCCESSIONAL STAGES OF GULL CARRION (ISLES OF SHOALS)

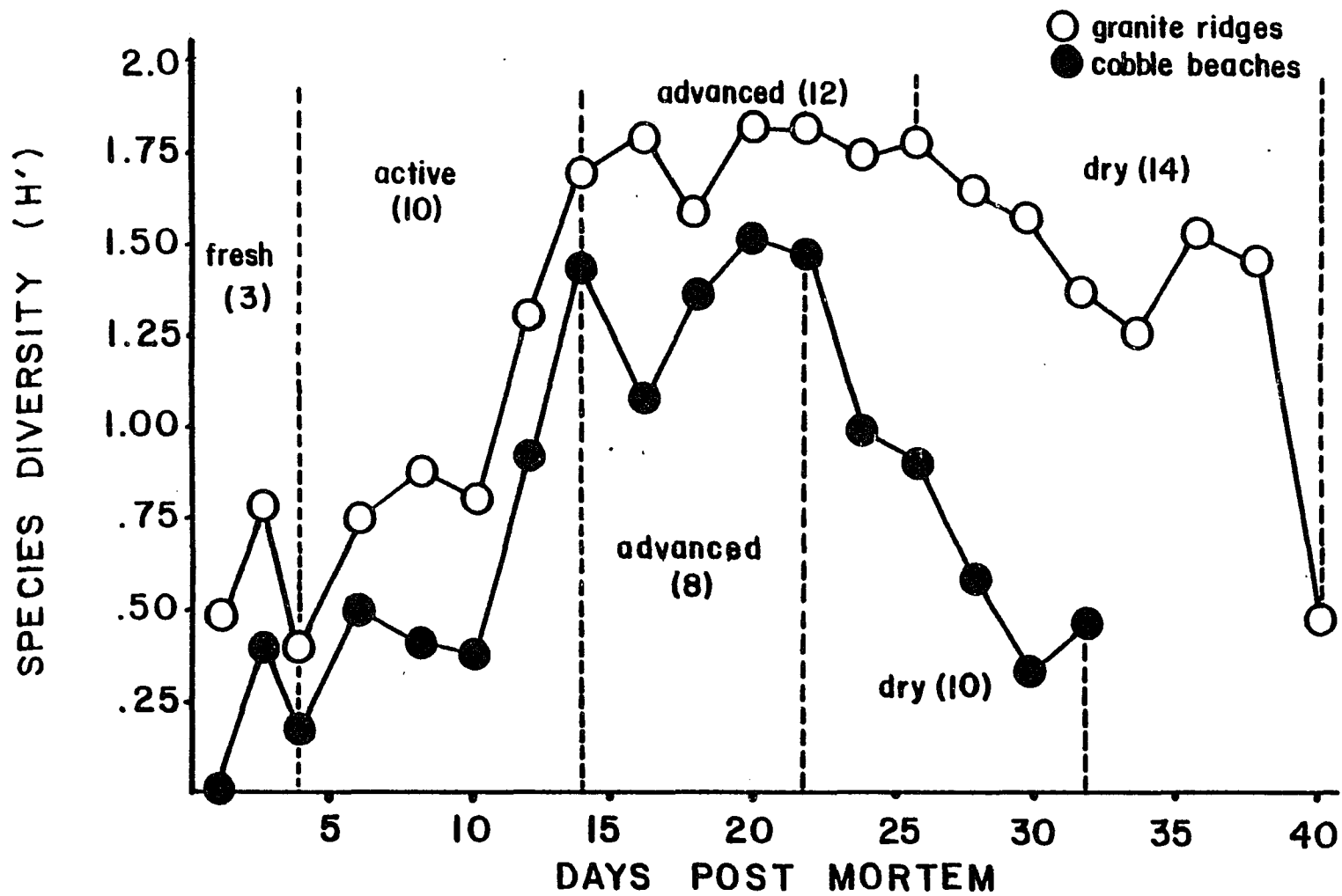


Figure 5. SUCCESSIONAL STAGES OF GULL CARRION AS INDICATED BY CHANGES IN SPECIES DIVERSITY.

successional array was indicated by the Bray-Curtis index. The abundances of taxa (x/carcass/day) associated with each stage are summarized for ridges and beaches in figures 6 and 7 respectively. A description of the characteristics of each stage is given below.

#### Fresh Stage (duration: 3 days)

The fresh stage began with gull death and averaged three days duration. During this time carrion appeared fresh. No odors were noticed and there were no external signs of decay during early phases of anaerobic decomposition (putrification). Adult blow flies (Calliphoridae) were the diagnostic faunal group. Adult flies were commonly observed ovipositing on moist cloacal, ocular, and oral-nasal membranes, and on external lesions when present. Adults also fed on fluids present in these same regions. Calliphora vicina, Cymoniopsis cadaverina, and Lucilia illustrus colonized carcasses on day one. Phormia regina arrived later, usually on day three, along with the flesh fly Sarcophaga bulata. On ridges ants and isopods were also present during this stage. On beaches spiders occurred, preying on adult flies. Species diversity in both habitats was low, similarity high. During the later portion of the fresh stage, minor indications of bloating (Johnson 1975, Payne 1965) were evident. Minor swelling and protrusion of the pericloacal tissues occurred. Bloating was not sufficiently conspicuous in gulls to warrant classification as a separate decompositional stage.

#### Active Decay (duration: 10 days)

The active stage commenced with the onset of aerobic decomposition. By this time body openings emitted fluids and conspicuous odors. Characteristically, larval blow flies (Calliphoridae) and flesh flies

		Postmortem Interval (days)																			
		2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	36	40		
Calliphoridae	12 28	19	27	16	4																
larvae	E L	L	L	L	P	P	P	P	P												
Sarcophagidae	1	1																			
Piophilidae			5	6	5	3	5	2	3			3					1				
Sepsidae							1														
Ephydriidae				9	2																
Staphylinidae			9	22	9	45	28	15	12	8	7	5	5	3	2	2	1				
Histeridae		3	15	2	1	8	7	2	1	3	3	1									
Silphidae									2	1											
Trogidae									1	1	2	2	2	1	1	1					
Dermeestidae			10	8	15	26	11	19	20	23	28	41	26	20	20	20	12	3			
larvae									2	40		25	41	20	29	31	34	34	15		
Carabidae				2	3	1															
Nitidulidae			5	4	27		17	8	6	5	13	10	9	7	6	1	2	1			
Formicidae	104 98	73	81	115	160	127	117	57	63	75	63	56	62	50	41	22	22	11			
Acarina			1	8	10		8	32	31	11	17	23	37	31	18	6					
Isopoda	36	48	93	108	139	84	46	41	44	67	62	63	63	56	50	24	23				
Aranea		1	1	1				1													
	fresh	active					advanced							dry							

E= eggs, L=larvae, P=pupae

All values =  $\bar{X}$ /day

Figure 6. ABUNDANCE OF ARTHROPODS FOR SUCCESSIONAL STAGES OF GULL DECOMPOSITION - GRANITE RIDGES.



	Postmortem Interval ( days )																
	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	
Calliphoridae	4	12	14	8	2												
larvae	E	L	L	L	L	L	P	P	P	P							
Sarcophagidae			1	1													
Piophilidae				1	1												
Coelopidae				1													
Staphylinidae			2	2	9	4	6	1									
Nitidulidae					4	2	16	9	3	6	9	6		1			
Histeridae			1	8	5		1	1									
Corynetidae									1			1					
Dermestidae			2	19	23	25	44	44	22	41	29	27	29	19	19	5	5
larvae				14	21	25	19	38	50	39	43	42	79	87	87	54	12
Aranea		1		5	2	3	1	1	1	1	1	1	1				
Acarina											6	6	1	3			
Diplopoda		5	8	5	6												
Chilopoda										1	1	1					
Amphipoda							5										
Dermoptera			2	32	17	11	11	8	3	9	6	5	3	4	3	3	1
	fresh				active				advanced								dry

E = eggs , L = larvae , P = pupae  
 All values =  $\bar{X}$  / day

Figure 7. ABUNDANCE OF ARTHROPODS FOR SUCCESSIONAL STAGES OF GULL DECOMPOSITION — COBBLE BEACHES .

(Sarcophagidae) fed initially at moist body openings near oviposition sites. They migrated later throughout thoracic and abdominal regions, secreting enzymes, disseminating fungi and bacteria, and aerating tissues, enhancing tissue liquifaction and aerobic decay (Payne 1965). Such activity eventually destroyed internal viscera and ventral integument, producing a dorsal shell of musculature, epithelium, and connective tissue. Caesic (protein) fermentation was evident by the sixth day of active decay, indicated by the arrival of Piophila latipes (Piophilidae). Other flies, including representatives of Sepsidae and Ephydriidae on ridges and Coelopidae on beaches, were attracted to proteinaceous liquids at this time. Two families of necrophagous beetles, Dermestidae and Nitidulidae, also arrived during active decay; dermestid larvae on beaches only. Nitidulids fed on liquids; dermestids on drier peripheral tissues. Various predatory beetles were attracted to the large populations of fly larvae during this period. On ridges Staphylinids, Histerids, Carabids, and Silphids occurred. Staphylinids, Histerids, and numerous Anisolbis maritima (Dermaptera) were present on beaches. Ants were numerous on ridges only. Carcasses supported the greatest numbers of insects during active decay. Diversity during this stage increased sharply and similarity between successive days was highly variable. Termination of active decay was indicated by the migration of larval diptera into the substrate prior to pupariation.

Advanced Decay (duration: 8 days CB, 12 days GR)

During this period carcasses appeared as hollow shells. Muscle, epithelium, and connective tissues were present, particularly associated with bones and appendages. The skeleton remained largely intact and feathers were still attached to the dorsal integument. Tissues remained

moist, with the greatest evidence of desiccation noted peripherally. Necrophagous and predatory beetles were the characteristic fauna. Staphylinids, Silphids, Histerids, Trogids, Nitidulids, and Dermestids, occurred on ridges. Larval dermestids were present for the first time, and with trogids, fed on the drier tissues. Adult and larval dermestids predominated on beaches, with Nitidulids and Corynetids also present. Adult and immature Dermaptera and the centipede, Arenophilus sp., were the most abundant predators. Species diversity remained uniformly high, as did similarity between successive days. Diversity was enhanced by the presence of numerous necrophilous species in both habitats. Termination of the advanced stage was not as clearly delineated as others. Carrion desiccation, skeletal disarticulation, appearance of bare bones, and presence of dry tissue specialists only, were the characteristics utilized. Similar criteria were used by McKinnerney (1978).

Dry Stage (duration: 10 days CB; 14 days GR)

During the dry stage carcasses were reduced to a mass of bare, disarticulated bones and feathers. Dried tissue remnants were removed by dermestid beetles which predominated in both habitats. These beetles were the sole inhabitants on beaches. Populations of Nitidulids, Trogids, Formicids, and Staphylinids persisted on ridges, but numbers of individuals steadily decreased. Diversity also decreased more rapidly on beaches than ridges. Similarity between successive days varied but was generally low. The end of the dry stage was marked by the persistence of bare bones only.

We do know how long gull bones required to decompose on marine islands.

Nuorteva (1977) found similarities between the successional patterns reported for mammal carcasses in Australia, Europe, Japan, and

southern United States. While duration of successional stages observed for gulls on the Isles of Shoals differed somewhat from mammal studies, the characteristic insect groups (families and often genera) dominating each decompositional stage were essentially similar.

#### Seasonality

Seasonal variations in carrion abundance, availability to necrophagous arthropods, and community composition were evident on the Isles of Shoals. These changes result from temporal patterns in gull reproductive and foraging behavior, climatic conditions, and arthropod abundance.

Gulls returned to establish territories on the Isles in February and initiated nesting during March and early April. Adult carcasses were most abundant during this time. Interspecific aggression and environmental stress are suggested as the chief components of adult mortality (McGill 1977). Hatching of young occurred in May and June, and from this time until completion of fledging in early August, juvenile carrion predominated. Gulls vacated the islands for inland wintering sites during August and by September fresh carrion became rare.

Neither Herring nor Great Black-backed Gulls fed on carrion during colonization and nesting. Carcasses found on beaches and ridges frequently had been pecked about the head and neck, but viscera and musculature remained in tact. Experimental animals required no caging during this period. After the onset of hatching, gulls began foraging upon chick carrion. Of 24 chick carcasses tested (12 on ridges and 12 on beaches) during early June, all were consumed by gulls within 4 hours of field placement. Great Black-backed Gulls consumed a greater number

(22) than did Herring Gulls (2). No differences were noted between habitats. Predation and cannibalism are considered major causes of juvenile gull mortality (Davis and Dunn 1976, Parsons 1971, 1976, and Weaver 1970). Few chick carcasses were available to necrophagous arthropods.

As gull chicks grew in size and age, necrophagy by adult gulls expanded to include adult carcasses. Of 24 adult carcasses exposed to gull scavenging during July and August, all were consumed within 36 hours of field placement. Scavenging gulls characteristically removed abdominal viscera and musculature, leaving head, neck, and appendages uneaten. The esophagus and crop also remained. Both Great Black-backed and Herring Gulls were observed scavenging upon adult carcasses, the former more frequently. Increasing demands for food placed upon parents by rapidly growing young may initiate a behavioral change towards carrion utilization. The proximity to nest sites and large size of older juvenile and adult carcasses enhance energetic foraging efficiency. Gulls were the only vertebrates observed feeding on carrion on the Isles. McKinnerney (1978) emphasized the importance of scavenging vertebrates in the regulation of carrion abundance.

Seasonal variations in carrion arthropod composition were also evident. Carcasses examined during February, March, and early April were found to support no invertebrate fauna. Low temperatures characteristic of these months (McGill 1977) are unsuitable for arthropod activity (Johnson 1975). Occasionally, however, on warmer, sunny days adult Calliphora vicina were observed upon sunlit rocks in areas protected from wind. In the absence of arthropods, carcasses remained intact. Repeated freezing and thawing, exposure to wind, and

precipitation eventually resulted in mummification. Dermestid beetles were the major consumers of mummified remains during subsequent months.

From mid-April until September marked seasonal variations in adult and larval fly populations were evident (Fig. 8). During April and early May Calliphora vicina and Cynomyopsis cadaverina were the dominant necrophagous species. Phormia regina also occurred in small numbers. In May and early June Phormia regina was most abundant. During June and early July, both Phormia regina and Lucilia illustris shared dominance, with Lucilia illustris reaching peak abundance in August and early September. Sarcophaga bullata was present in small numbers during July and August. Similar patterns of seasonality among carrion inhabiting blow flies have been reported by Fuller (1934), Johnson (1975), and Payne (1965). Hall (1948) considered temperature to be most significantly correlated with temporal partitioning by blow flies.

No distinct patterns of seasonality were evident among predatory or necrophilous groups. Most of these species occurred consistently from May to September. These data are consistent with those reported by Payne and Crossley (1966).

Among the major species of predatory beetles, however, distinct size differences were noted (Table V). Three significantly different (ANOVA,  $P < .001$ ), species specific size classes of staphylinids and two of histerids (t-test,  $P < .001$ ) were evident. Such differences among predatory guild members suggests partitioning of prey by size (Price 1975).

Gull carrion communities located on maritime islands along the New England coast display patterns of community structure, succession, and seasonality similar to mammal carrion communities studied in a variety

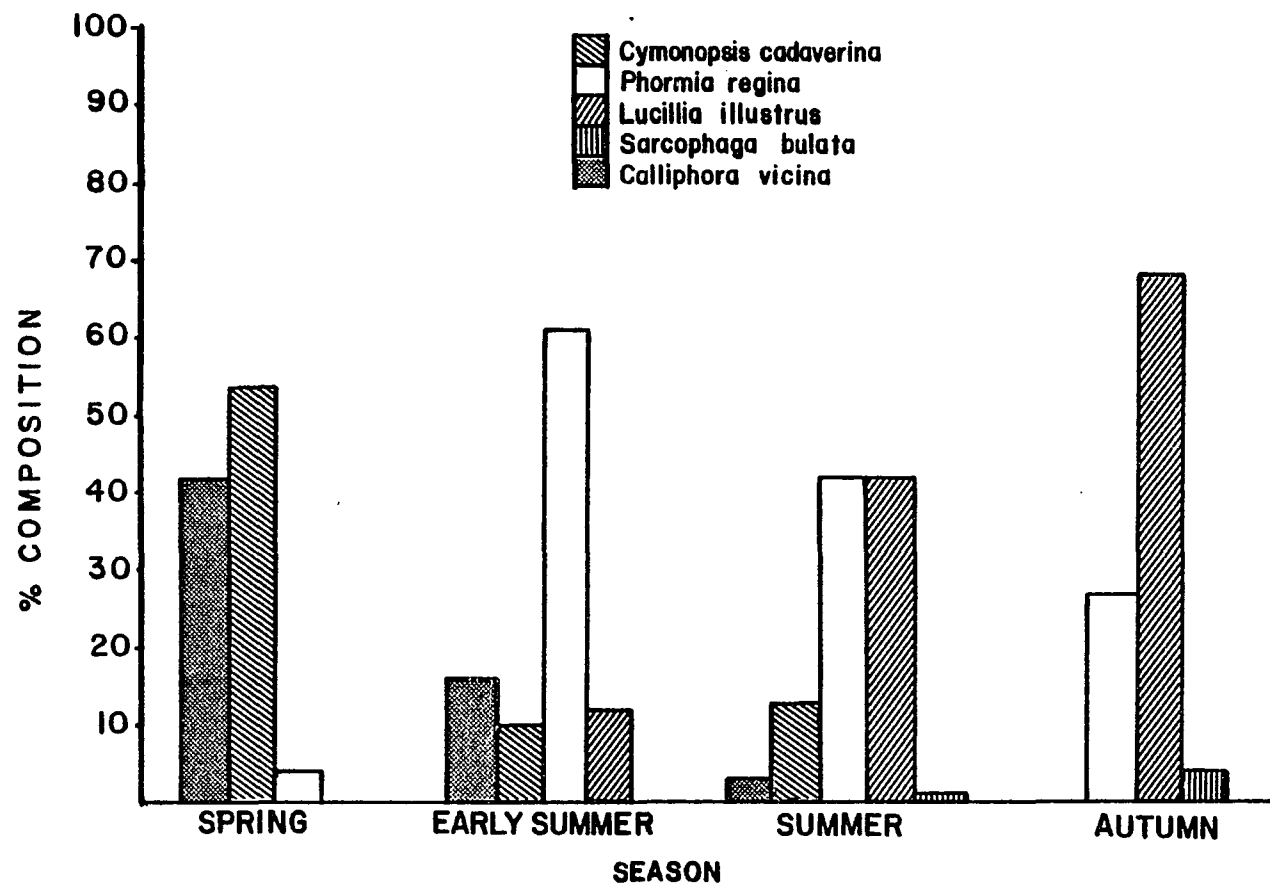


Fig. 8 SEASONAL VARIATION IN CARRION FLY (ADULT) ABUNDANCE (Gulls)

Table V. Lengths (mm) of major species of Predatory beetles frequenting gull carrion<sup>1,2</sup>

	<u>C. maxillosus</u>	<u>P. politus</u>	<u>A. lata</u>
Staphylinidae			
x	19.90	12.60	7.80
SE	.23	.22	.25
	<u>P. fraternus</u>	<u>S. assimilis</u>	
Histeridae			
x	10.00	6.00	
SE	.24	.24	

<sup>1</sup> ANOVA 4, 45; P<.001

<sup>2</sup> Newman-Keuls test ( =.01)



of terrestrial habitats worldwide. Striking similarities with arid regions of Australia and southwestern United States are evident. Our data support the predictability of the vertebrate decompositional process.

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CHAPTER II

HARBOR SEALS (Phoca vitulina)

## INTRODUCTION

Harbor Seals (Phoca vitulina) are the most numerous marine mammals inhabiting the coastal waters of New England. At least 6,000 individuals reside in the Gulf of Maine (Katona et al. 1977). Small herds commonly assemble on nearshore islands and ledges, and in bays, harbors, and estuaries.

From December 1979 until October 1980 an epizootic of acute viral pneumonia spread through the New England seal population (Geraci et al. 1982). More than 400 harbor seals, most of them less than 3 years old, died along the New England coast during this period. The morbidity and mortality associated with this epizootic are attributed to a previously undescribed influenza virus and a mycoplasma. Geraci et al. (1982) estimated that the disease took less than 3 days to develop in an individual, affecting males and females equally, with the most acutely affected seals dying within hours.

The high mortality rate associated with this disease resulted in an abundance of seal carrion. The availability of harbor seal carcasses on the Isles of Shoals, a group of small islands located 10 km SE of Portsmouth, NH (49°59'N, 70°37'W), enabled us to investigate aspects of the decomposition of these animals. Specifically, we studied the assemblages of insects and other invertebrates involved in the redistribution of seal carrion.

Carrion is a significant component of biological communities providing food and shelter for numerous organisms (Johnson 1975). A knowledge of the organisms and processes involved in the redistribution

of this resource is important for understanding the ecology of the communities within which the carrion occurs (Odum 1971). Carrion ecology is also important to medico-legal authorities as a tool useful in determining the time of death (Nuorteva 1977).

This paper describes the microcommunity structure and succession of invertebrates inhabiting seal carcasses located on islands in the Gulf of Maine. Although several authors have examined carrion community ecology, including Illingworth (1926), Fuller (1934), Howden (1950), Bornemissza (1957), Reed (1958), Denno and Cothran (1975), and McKinnerney (1978), no studies published to date deal with marine mammal carrion.



## MATERIALS AND METHODS

We conducted field work from May until October 1980 on Appledore, Duck, and Lunging Islands, 3 of 9 small islands comprising the Isles of Shoals. The Isles of Shoals is the sole archipelago along an 80 km stretch of New England coastline between Cape Ann, Massachusetts and Casco Bay, Maine ( $49^{\circ}59'N$ ,  $70^{\circ}37'W$ ). Of the 9 islands (Fig. 1) Appledore is the largest with an approximate land area of 36.6 ha. Lunging and Duck Islands have approximate land areas of 2.5 and 3.2 ha, respectively (Borrer 1980). The islands are characterized by rocky ridges and valleys, peripheral cliffs, and cobble beaches, resulting from glacial activity during the Wisconsin glacial advance. Detailed descriptions of physical and biological characteristics of the Isles have been published by Bloomshield (1975), Boden (1977), Borrer (1980), and Kingsbury (1976).

A colony of approximately 120 harbor seals inhabits Duck Island from January until June each year. Duck Island is considered the southernmost pupping ground of this species. During winter and spring individuals frequent the other islands of the Shoals archipelago.

We encountered 5 harbor seal carcasses during May and June 1980 while censusing Shoals seal and seabird populations. We studied all five carcasses in the locations where found. Samples of invertebrates occurring on the upper surface, inside, and beneath carcasses were taken daily for the first 5 days and at 3 day intervals thereafter. We designed sampling regimes to insure collection of organisms representative of all successional stages.

Representative collections were made using standard entomological equipment (aspirators, forceps, nets, etc.). Only reference specimens were removed to minimize carrion disturbance. We preserved specimens by standard techniques (Peterson 1966) and returned them to the laboratory for identification. Specimens of larval Diptera were reared to adults on beef liver. Records of abundance, region of carcass colonized, and behavioral observations were made for each invertebrate species encountered during a sampling period. Photographs of carrion appearance were also taken. Similar techniques of carrion sampling have been utilized by Johnson (1975), Payne (1965), McKinnerney (1978), and Reed (1958).

To assess changes in carrion microcommunity structure and complexity, we calculated the Shannon-Weaver index of general diversity ( $H'$ ) and the index of Evenness ( $J$ ) for each successional stage. Similarity between successional stages was measured by the Bray-Curtis index of similarity ( $S_{jk}$ ). These indices are commonly accepted ecological measures (Pielou 1969, Ricklefs 1973, Southwood 1978, and Wilson and Bossert 1971). Detailed descriptions of the seal decompositional process and invertebrate succession were also studied.

## RESULTS AND DISCUSSION

### Carrion Location

The 5 seal carcasses used in the study were discovered on the western shores of the most westerly islands, Appledore, Duck, and Lunging (Fig. 1). All were situated in the rocky supratidal zone about a meter ( $x = 1.2$  m) above mean high water. The westerly sides of the islands faced advancing ice during the Wisconsin glacial period (Fowler-Billings 1959), and the resulting smooth, sloping topography provides the most suitable haulouts for seals. Westerly shores also offer protection from winter and spring storms that are usually characterized by a northeasterly flow of wind and surf (McGill 1977). Seals are known to seek supratidal refuge when sick or debilitated (Beekman pers. comm.).

Carcasses 2, 3, and 4 were fresh when found with postmortem interval estimated at <24 hours. Carcass 1 was bloated when discovered, death occurring 2-3 days previous to discovery. Carcass 5 was badly decomposed with only bare bones and dorsal integument remaining. Postmortem interval for this animal is unknown. Carcasses 1 through 4 were discovered during the last week of May and the first week of June. Carcass 5 was found during the last week in June. The occurrence of Shoals seal mortality is consistent with the temporal pattern observed by Geraci et al. (1982) elsewhere along the New England coast during the epizootic.

### Decompositional Stages

Although decomposition is a continuous process, investigators have divided it into various stages based upon physical appearance and

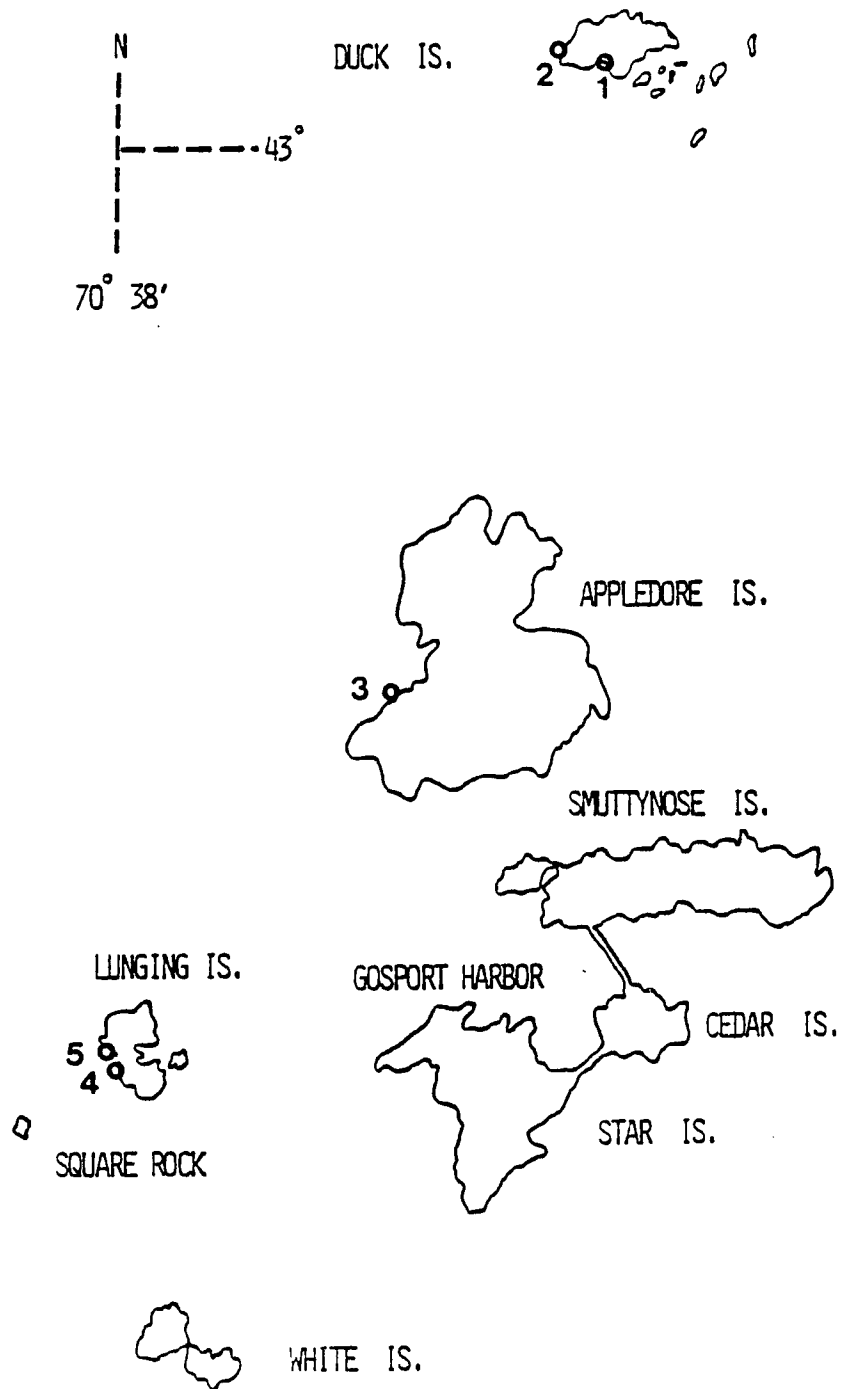


Figure 1. Map of the islands of the Isles of Shoals and location of seal carcasses, June 1980

characteristic faunal associates. Reed (1958) and Johnson (1975) described four decompositional stages. Payne (1965) and McKinnerney (1978) recognized five, while Howden (1950) defined only two based on dipteran life cycles.

Five decompositional stages occurred in seal carrion: fresh, bloat, active decay, advanced decay, and dry. Our classification was based upon carrion appearance, faunal associates, and patterns of diversity. A description of the characteristics of each stage is given below.

Fresh Stage (approx. duration: 1 day)

The fresh stage was initiated with death and continued until bloating. During this period bacteria from the intestines and lungs migrated into local tissues, capillaries, veins, and lymphatic vessels and then into the body tissues generally (Evans 1963). Aerobic organisms rapidly depleted tissue oxygen enhancing the growth of anaerobes. Bacterial flora changed from aerobic groups to anaerobic varieties in which the Clostridia predominated. Externally no signs of decay were evident, and odors of putrefaction were absent.

Adult blow flies were the dominant invertebrates, ovipositing on moist ocular, oral-nasal, and rectal tissues and feeding upon fluids in these regions. The black blow fly, Phormia regina, and the green blow fly, Lucilia illustrus, predominated. Wolf spiders, Pardosa lapidicina, and jumping spiders, Saticus scenicus, occurred rarely. Small green crabs, Carcicus maenas, and amphipods, Ochestia platensis, were present on carcasses dampened by sea spray. Communities reflected low diversity, low evenness, and high similarity.

### Bloat Stage (approx. duration: 4 days)

Bloating results from gaseous production by anaerobic bacteria and tissue decomposition (Evans 1963). The gases produced include carbon dioxide, hydrogen sulfide, ammonia, and methane. During this stage the carcass swelled, eyes bulged, tongue and rectum protruded, and frothy fluids exuded from the natural orifices. A strong odor was present.

Adult blow flies remained the dominant invertebrates. Blow fly egg masses and first and second instar larvae were prevalent externally around body orifices. Other adult Diptera, including the flesh fly, Sarcophaga bullata, and the seaweed fly, Coelopa frigida, were present in small numbers (1-5 per carcass). Sap beetles, Stelidota geminata, rove beetles, Philonthus politus, velvet mites, Trombidium sp., little black ants, Monomorium minimum, and the intertidal earwig, Anisolabis maritima, occurred in similar numbers (1-5 per carcass). Community diversity and evenness were greater than during the fresh stage, similarity lower.

The end of the bloat stage was indicated by carcass deflation. Deflation resulted from release of gases through integumentary perforations created by burrowing blow fly larvae.

### Active Decay (approx. duration: 10 days)

Active decay commenced with the resumption of aerobic decomposition. During this stage second and third instar blow fly larvae burrowed throughout carrion thoracic and abdominal regions, secreting enzymes, disseminating bacteria and fungi, and aerating tissues. Aerobic decay is dependent upon insect activity (Johnson 1975, Payne 1965). Maggots eventually destroyed viscera and ventral integument completely, leaving only a dorsal integumentary shell and skeleton with associated

musculature. The quantity of fly larvae present (8,000-10,000 per carcass) caused the remains and substrate to vibrate with activity. Liquefied products of decay saturated the ground and a strong odor of putrefaction persisted.

Other flies, including a cheese skipper Piophilalata latipes, brine fly Ephydra riparia, a black scavenger fly Sepsis punctum, and the muscid fly Fannia canicularis, were attracted to proteineous liquids during this period. Another muscid, Ophyra leucostoma, whose larvae are predators on larval blow flies, also arrived.

A variety of necrophagous and predatory beetles also colonized carrion during active decay. These included the rove beetles Creophilus maxillosus, Aleochara lata, and Philonthus politus, hister beetles Pachylopus fraternus, Saprinus assimilis, and Saprinus conformis, ant-like beetles Anthicus cinctus and Anthicus cervinus, and dermestid beetles Dermestes caninus and Dermestes vulpinus. Yellowjacket wasps Vespula maculifrons, the parasitic mite Poecilochirus sp., the phalangid Leiobunum politum, and Monomorium minimum and Anisolabis maritima also were present.

Carcasses supported the greatest numbers of invertebrates during the active stage. Diversity increased sharply. Evenness, however, remained low due to the numbers of blow fly larvae characteristic of this stage. Similarity also was low.

Termination of active decay occurred when fly larvae abandoned carrion and migrated into the substrate subsequent to pupariation. Approximately 90% of seal carrion weight was lost during this active decay.

Advanced Decay (approx. duration: 15 days)

During this stage seal carcasses were hollow shells of dorsal integument. Only musculature and connective tissues remained internally, particularly in association with pelvis and appendages. The skeleton was largely intact and the substrate wet with fluids of putrifaction. Externally the integument had a hard, leathery texture, was devoid of hair, and riddled with holes (5-10 mm) created previously by burrowing maggots. Fluid drainage had ceased and carrion odor gradually disappeared.

Necrophagous and predatory beetles were the characteristic fauna. Rove, hister, and sap beetles persisted, but gradually departed as carrion desiccation progressed. Adult and larval dermestid beetles, Dermestes caninus and Dermestes vulpinus, were the dominant species, specializing upon the keratinized remains. Adult and immature earwigs, the centipede Arenophilus sp., terrestrial isopods Philoscia vittata and Porcellio scaber, and an unidentified nematode also occurred during advanced decay.

Large numbers of blow fly pupae were present in the surrounding substrate up to 4 meters from carrion. Emerging adults and pupal parasites (Ichneumonidae and Pteromalidae) periodically aggregated beneath carrion and in the immediate area. Wolf and jumping spiders preyed upon newly emerged blow flies, as did the funnel-web weaver Agelenopsis potteri which constructed funnel nests beneath carcasses.

During advanced decay carrion communities reflected gradually decreasing diversity and evenness; similarity was high. Termination of advanced and initiation of the dry stage was not as clearly delineated as others. Complete carrion desiccation, skeletal disarticulation, appearance of bare bones, and abandonment by all but dried tissue



specialists were the diagnostic criteria. Similar criteria are used by Reed (1958), Payne (1965), Johnson (1975), and McKinnerney (1978).

Dry Stage (approx. duration: 70 days)

Throughout the dry stage carcasses appeared as fragments of dried dorsal integument and disarticulated bones. All distinctive odors were absent and the substrate was marked only by dried fluid stains. Dermestid beetles, particularly Dermestes caninus, predominated initially. Terrestrial isopods eventually occurred in the greatest number. Occasionally individuals of species inhabiting earlier decompositional stages were collected, but only infrequently.

Field study was terminated in mid-October 1980 when an early winter storm washed away all carrion remains. It is not known how long harbor seal bones require to completely decompose.

The process of seal decomposition and faunal succession described above is similar to those reported by Fuller (1934) for sheep carcasses in Australia, Reed (1958) for dogs in Tennessee, Payne (1965) for pigs in South Carolina, Johnson (1975) for small mammals in Illinois, McKinnerney (1978) for rabbits in New Mexico, and Coe (1978) for elephants in Kenya. Insect families and often genera dominating each particular decay stage were essentially the same. Decompositional rates varied, however, with latitude and carcass size. Nuorteva (1977) found distinct similarities between successional patterns of mammal carcasses located in inland regions of Australia, Europe, Japan, and United States. The physical characteristics and faunal associates of harbor seal carcasses located in coastal New England lend further support for the predictability of carrion community succession.

The abundance of the major invertebrates frequenting seal carrion is given for each decompositional stage in Figure 2. Insects specializing on carrion were the chief components of the seal microcommunity. Invertebrates typical of marine intertidal and wrack habitats played only a minor role in the decay process. Payne (1965) and Putnam (1978) stress the importance of a few specialized insect groups, particularly blow flies and necrophagous beetles, in vertebrate decomposition. The importance of these insects in habitats with strong maritime influences is evident.

General diversity ( $H'$ ) and evenness ( $J$ ) values for each stage of decay are given in Figure 3. Initially diversity and evenness were low, reflecting the presence of only a few early colonizers. Diversity increased rapidly during bloating and active decay, as numerous necrophages, predators, and necrophiles were attracted. Evenness remained low due to large numbers of blow fly larvae. During advanced and dry stages, diversity and evenness gradually decreased as remaining tissues were depleted. When adjustments for resource depletion are made, the pattern of community development evident closely resembles that described by Wilson and Simberloff (1969) for mangrove islands in southern Florida. Odum (1971) suggests that isolated biological resources (dung, carrion, etc.) may reflect colonization patterns observed on geographical islands. Further study is needed to substantiate this hypothesis for seal carrion.

#### Carrion Guilds

A guild is defined as a group of species exploiting the same environmental resource in a similar manner (Price 1975). Guilds are associated with a wide variety of insect assemblages including collard

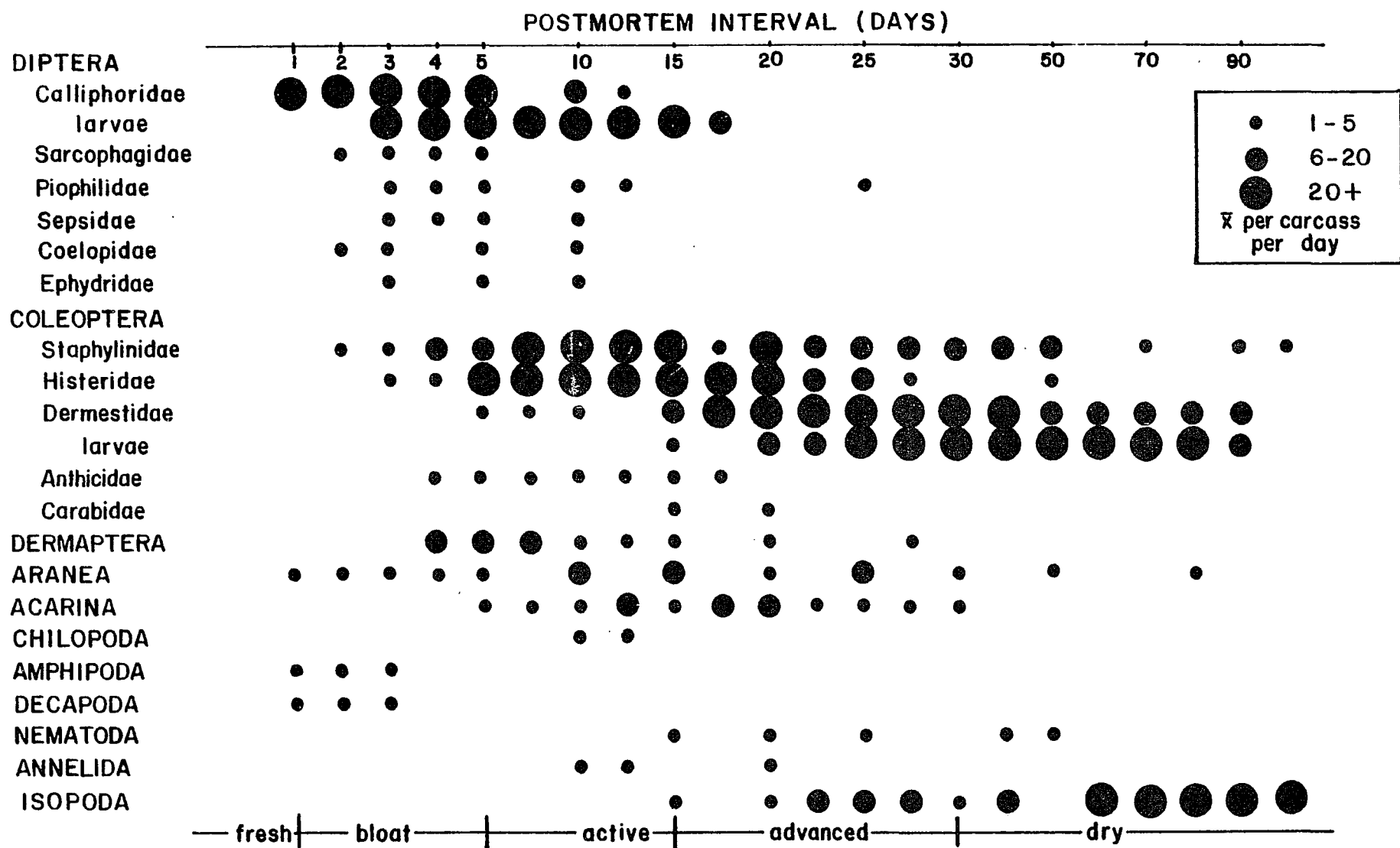
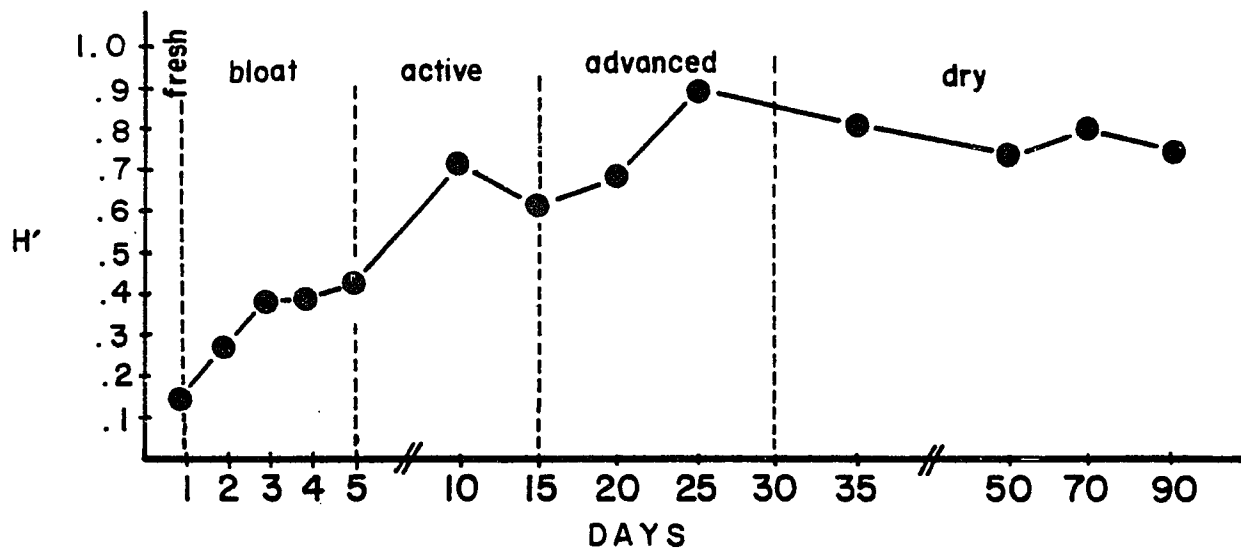
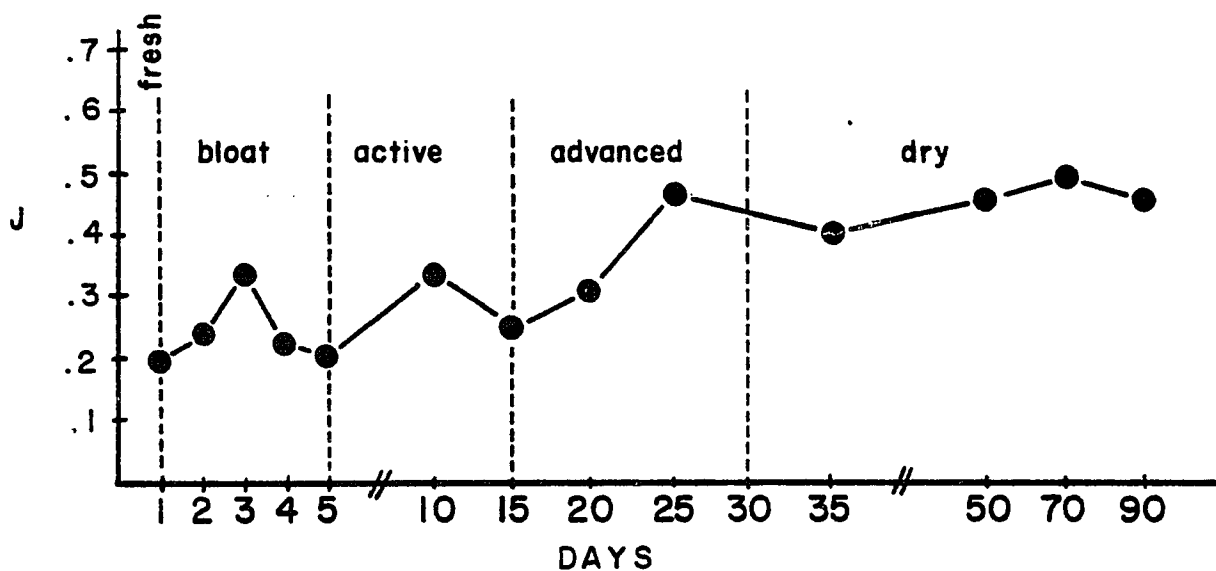


Figure 2. ABUNDANCE OF INVERTEBRATES FREQUENTING SEAL CARRION, ISLES OF SHOALS, 1980.



POSTMORTEM INTERVAL



POSTMORTEM INTERVAL

Fig. 3. GENERAL DIVERSITY AND EVENNESS MEASUREMENTS FOR SEAL CARRION DECOMPOSITIONAL STAGES, ISLES OF SHOALS, 1980.

herbivores (Root 1973), saw fly parasitoids (Price 1971), and carrion flies (Denno and Cothran 1975). We grouped seal carrion inhabitants into 5 ecological guilds based on general trophic habits: (i) Necrophages - species feeding on carrion on decay products, (ii) Necrophiles - species using carrion for shelter or occurring accidentally, (iii) Predators - species preying on carrion community members, (iv) Necrophages/Predators - species preying on invertebrates and feeding on carrion as well, (v) Parasites - parasites of carrion inhabitants. The invertebrates comprising each guild and the trophic relationships between guilds are given in Figure 4.

#### Necrophages

Necrophagous guild members fed directly on the products of putrification in seal tissues. Five species of insects, 2 blow flies, and 3 beetles were the important necrophagous species. Others occurred in small numbers and contributed little to the decay process. Blow flies segregated from beetles by occurring only during fresh, bloat, and active decay stages (Fig. 5). Necrophagous beetles were present primarily during advanced and dry stages. Blow flies partitioned carrion by differences in duration of larval lifestage. Phormia regina, the black blow fly, had a short larval period ( $x = 7.5$  days). Lucilia illustrus, the green blow fly, had a longer interval ( $x = 12$  days). While larger, actively burrowing P. regina larvae fed internally, smaller L. illustrus larvae remained externally. Of the 3 species of necrophagous beetles found, only Dermestes caninus specialized on dry carrion (Dillon and Dillon 1972). Dermestes vulpinus and Stelidota geminata fed upon moist tissues. S. geminata ( $x = 3.50$  mm) was statistically smaller (T-test,  $P < .001$ ) than D. vulpinus ( $x = 9.50$  mm),

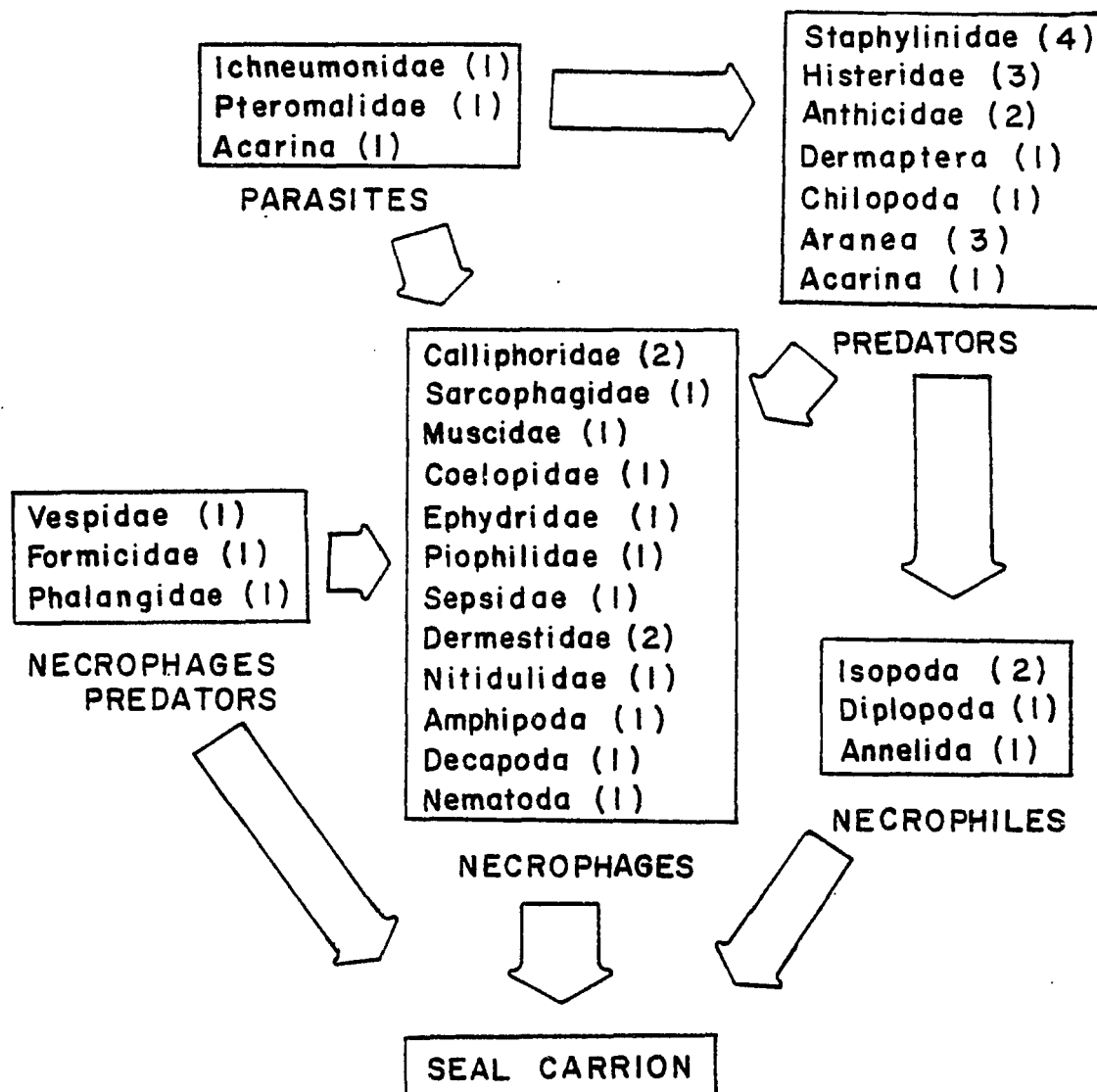


Figure 4. GENERALIZED TROPHIC RELATIONSHIPS BETWEEN GUILDS OF INVERTEBRATES ON SEAL CARRION, ISLES OF SHOALS, 1980.

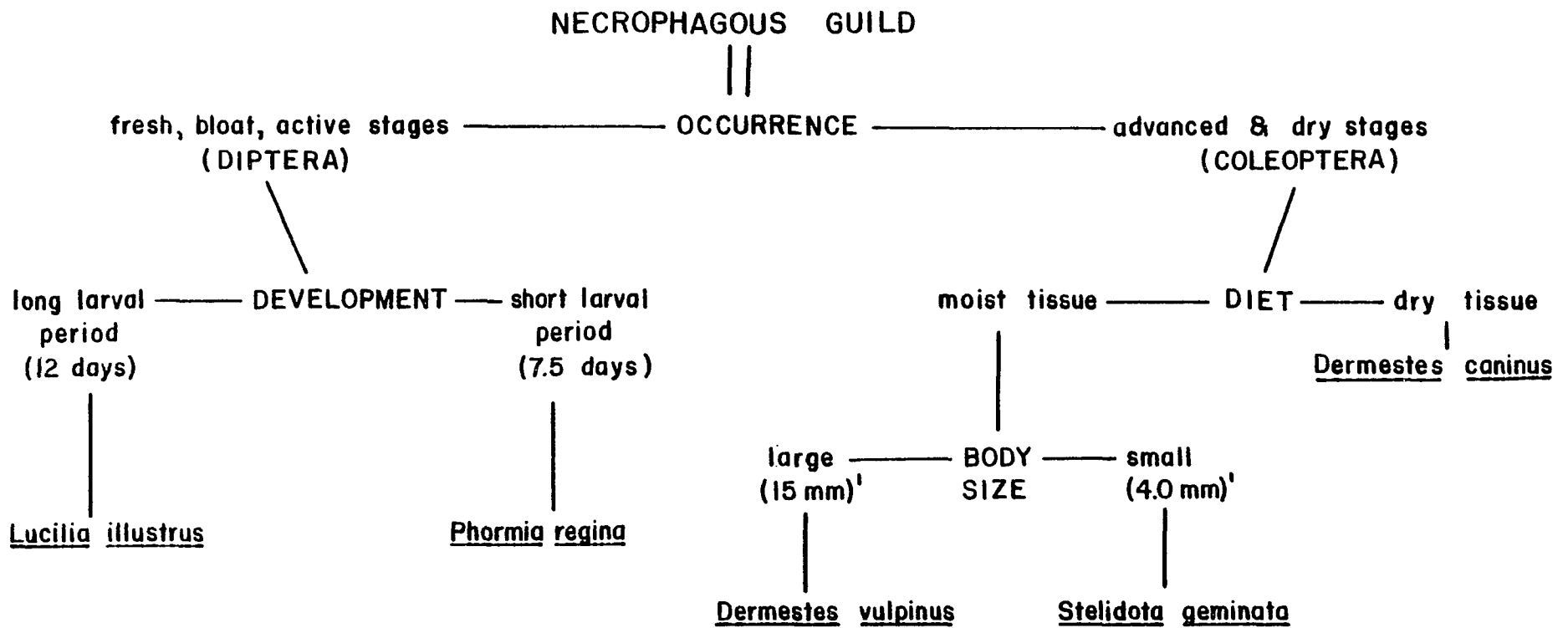


Figure 5. CARRION PARTITIONING BY MAJOR NECROPHAGOUS INSECTS INHABITING HARBOR SEALS, ISLES OF SHOALS, 1980.

<sup>1</sup>Student's T-test,  $P < .001$

reflecting differences in food sites utilized. Necrophages thus partitioned seal carrion spacially, temporally, and by state of desiccation.

### Necrophiles

Two species of terrestrial isopods, Philoscia vittata and Porcellio scaber, were the only invertebrates of consequence using seal carrion for shelter. Both species were most abundant during later decay stages. Mixed aggregations were commonly encountered. No differences in size or distribution were evident.

### Predators

Three species of spiders and 5 of beetles (Histeridae and Staphylinidae) were the chief predators (Fig. 6). Others (Anthicidae, Dermaptera, and Chilopoda) occurred rarely and were never observed with prey. Spiders fed primarily on adult flies and hunted on the dorsal surface and about the periphery of carcasses. Predatory beetles fed upon fly larvae and were located beneath or within seal remains. Among the spiders, Agelenopsis potteri was the sole web builder. Pardosa lapidicina and Salticus scenicus were motile hunters, the former statistically larger (t-test,  $P < .001$ ). Of the 2 families of beetles, the Staphylinidae were elongate and rapid moving, the Histeridae oval and sluggish. All 5 species were in distinct size classes (ANOVA,  $P < .001$ ). Guild members appear to partition prey by location on carrion, life stage, and size.

### Necrophages/Predators

A wasp, Vespula maculifrons; an ant, Monomorium minimum; and a nocturnal phalangid, Lejobunum politum, fed on both fly larvae and



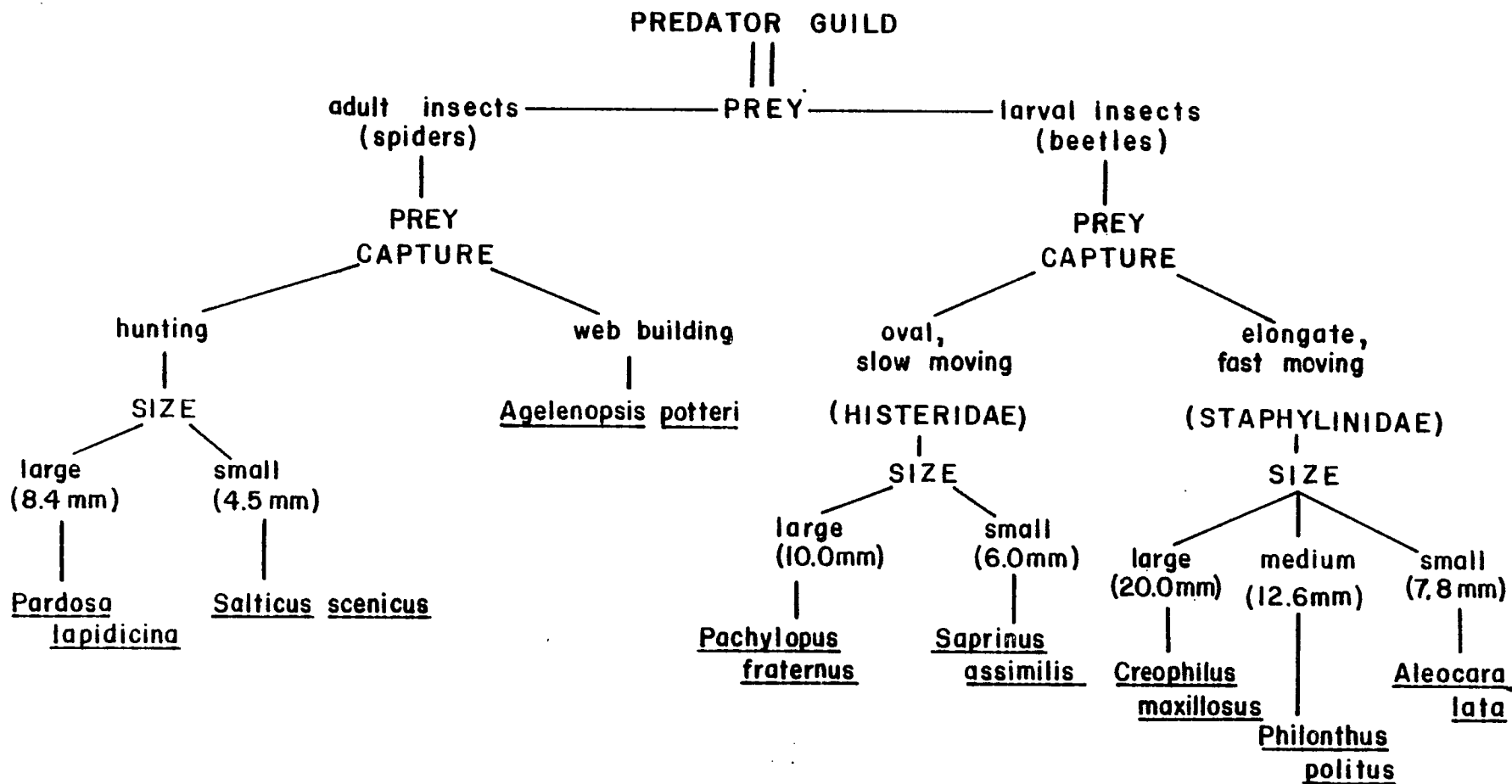


Figure 6. PREY PARTITIONING BY MAJOR PREDACEOUS ARTHROPODS FREQUENTING HARBOR SEAL CARRION, ISLES OF SHOALS, 1980.

carrion. All three occurred in small numbers (1-5 per carcass) and had little impact on decomposition.

### Parasites

Two parasitic wasps, Ichneumonidae and Pteromalidae, were reared from fly pupae. The incidence of pupal parasitism was low (3-5%). A single species of parasitic mite, Poecilochirus sp., was collected from predatory beetles, primarily Staphylinidae.

## GENERAL CONCLUSIONS

Harbor seals pass through a series of predictable decompositional stages defined by characteristics of carrion appearance and faunal associates. Similarities between these stages and those described by other authors for a variety of mammals located worldwide are evident.

Of the numerous species of invertebrates collected from seal carrion few played a major role in decomposition. Blow fly larvae and dermestid beetles were the primary carrion consumers. Spiders and staphylinid and histerid beetles were the major predators. The importance of carrion frequenting insects in the decomposition of vertebrates located in habitats with strong maritime influences is evident.

Carrion community members can be divided into 5 trophic guilds. Necrophages guild members partition carrion spatially, temporally, and by extent of desiccation. Predators select prey by location, size, and life stage.

The patterns of colonization and community development observed in seal carrion suggest those described by Wilson and Simberloff (1969) for geographical islands. Further research is needed, however, to substantiate this hypothesis.

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CHAPTER III

CARCASSES AS ECOLOGICAL ISLANDS

## INTRODUCTION

Islands are ecologically important entities. Their isolated nature and relatively simplistic biota enhance investigations of ecological and evolutionary concepts obscured in less distinct, more complex settings (Simberloff 1974). Classically, oceanic islands have served as templates for such research. Darwin's (1859) observations in the Galapagos Islands and Wallace's (1869) in the Malay Archipelago for example resulted in the theory of evolution by natural selection. Problems in community structure and function (May 1973), speciation (Levins and Heatwole 1973), biological control (Baumhover 1955) and biogeography (Simberloff and Wilson 1969, 1970) have also been elucidated on oceanic islands.

MacArthur and Wilson (1963, 1967) revolutionized biogeography by suggesting that insular biota represent a dynamic equilibrium between immigration of new species and extinction of old. They proposed that: (i) island size and distance from source of colonists determines species number, (ii) species number remains constant over time, and (iii) evolution gradually increases the species equilibrium. Simberloff and Wilson (1969, 1970) tested and confirmed the equilibrium model by investigating arthropod colonization of defaunated mangrove islands in Florida Bay. Since then the equilibrium theory of island biogeography has enjoyed wide acceptance.

Any patch of habitat may be considered an island if it is separated from similar patches by regions of terrain difficult for habitat patch organisms to traverse (Simberloff 1974). Tree trunks (Graham 1925),



cow pats (Mohr 1943), bromeliad containers (Laessle 1961), caves of aquatic (Culver 1970) and terrestrial animals (Vuilleumier 1973, Crowell 1973), and freshwater (Henebry and Cairns (1980) and marine fouling communities (Schoener 1974) have all been viewed as ecological islands. Simberloff (1974) suggests much of the world to be insular, with biotic habitats arranged in a quilt of patches. Any theory of island biology should be valid for small, biological islands as well as for larger geographic ones.

The following paper presents the results of a study I conducted during 1980-81 investigating the insular nature of rodent carrion. Specifically, I tested the effects of carcass size and distance from source of colonists on communities of arthropods frequenting rodent carrion located on small islands in the Gulf of Maine. I conducted this study as part of a larger research program investigating the ecology of carrion communities located in coastal habitats of northern New England. A detailed description of rodent decomposition and comparison of observed colonization patterns with the MacArthur-Wilson Hypothesis are included.

## MATERIALS AND METHODS

I conducted the study on Appledore Island, the largest of 9 small islands (Isles of Shoals) located 10 km SE of Portsmouth, New Hampshire (49°59'N, 70°37'W). The Isles of Shoals is the sole archipelago along an 80 km stretch of New England coast between Cape Ann, Massachusetts and Casco Bay, Maine. Appledore has an approximate land area of 36.6 ha. (Borrer 1980) and is characterized by rocky ridges and valleys, peripheral cliffs, and cobble beaches originating from glacial activity during the Wisconsin glacial advance (Fowler-Billings 1959). Detailed descriptions of biological and physical characteristics of the island are given in Bloomshield (1975), Boden (1977), McGill (1977), and Borrer (1980). Appledore houses the Cornell University/University of New Hampshire sponsored Shoals Marine Laboratory, where research facilities were located.

I tested the island size - species richness relationship for carrion by examining arthropod colonization on 3 size classes of rodents placed in the same (thicket) habitat on Appledore Island. Rodent species used (Table I) differed significantly in size (ANOVA,  $P < .001$ ). Norway rats were statistically larger than golden hamsters, which were significantly larger than mice (Student Newman-Keuls Test,  $\alpha = .05$ ). Three replicates of 9 individuals (3 of each species) were sampled. Predation on mouse carcasses by Herring and Great Black-backed gulls, however, reduced the analyzable data set to 1 replicate. I sacrificed rodents just prior to field placement by cervical dislocation, and

Table I. Size classes of rat, hamster, and mouse carrion, Appledore Island, 1981

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	Rattus <sup>A</sup> <u>norvegicus</u>	Cricetus <sup>B</sup> <u>aurata</u>	Mus <sup>C</sup> <u>musculus</u>
Weight (g)			
x	220.00	55.83	23.83 <sup>1,2</sup>
SE	4.28	3.52	1.74
n	9	9	9

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<sup>1</sup> ANOVA<sub>2,24</sub> (P<.001)

<sup>2</sup> Student Newman-Keuls Test; H<sub>A</sub>>H<sub>B</sub>>H<sub>C</sub> ( =.05)

placed specimens beneath metal milk crates, 30 cm x 30 cm x 30 cm, to prevent removal by vertebrate predators.

I collected samples of arthropods occurring on, in, and beneath carcasses daily for the first 7 days and at 2 day intervals thereafter. Sampling regimes were designed to insure collection of organisms representative of all decompositional stages.

Representative collections were made using standard entomological equipment (aspirators, forceps, nets, etc.). I removed only reference specimens to minimize carrion disturbance. Specimens were preserved by standard techniques (Peterson 1966) and returned to the laboratory for identification. Reference specimens were identified to species. A list of species encountered during the study is given in Lord (1982). Larval Diptera were reared to adults on beef liver. I recorded abundance, region of carcass colonized, and behavioral observations for each arthropod species encountered during a sampling period. Detailed descriptions and photographs of carrion appearance were also made. Similar techniques of carrion sampling have been utilized by Reed (1958), Payne (1965), Johnson (1975), and McKinnerney (1978).

I tested the effects of distance on arthropod colonization of carrion by sampling rodents placed in 3 different habitats on Appledore. Study sites on Appledore were located (i) centrally, (ii) on the western shore, and (iii) on a small accessory island W of Appledore, representing a sequence of increasing distances from the source of carrion colonists (Fig. 1). Individual rodents were separated by a minimum distance of 12 m, and new replicates were initiated monthly during June, July, and August. Lord (1982) demonstrated greater diversity of carrion frequenting insects in centrally located habitats on Appledore. Central

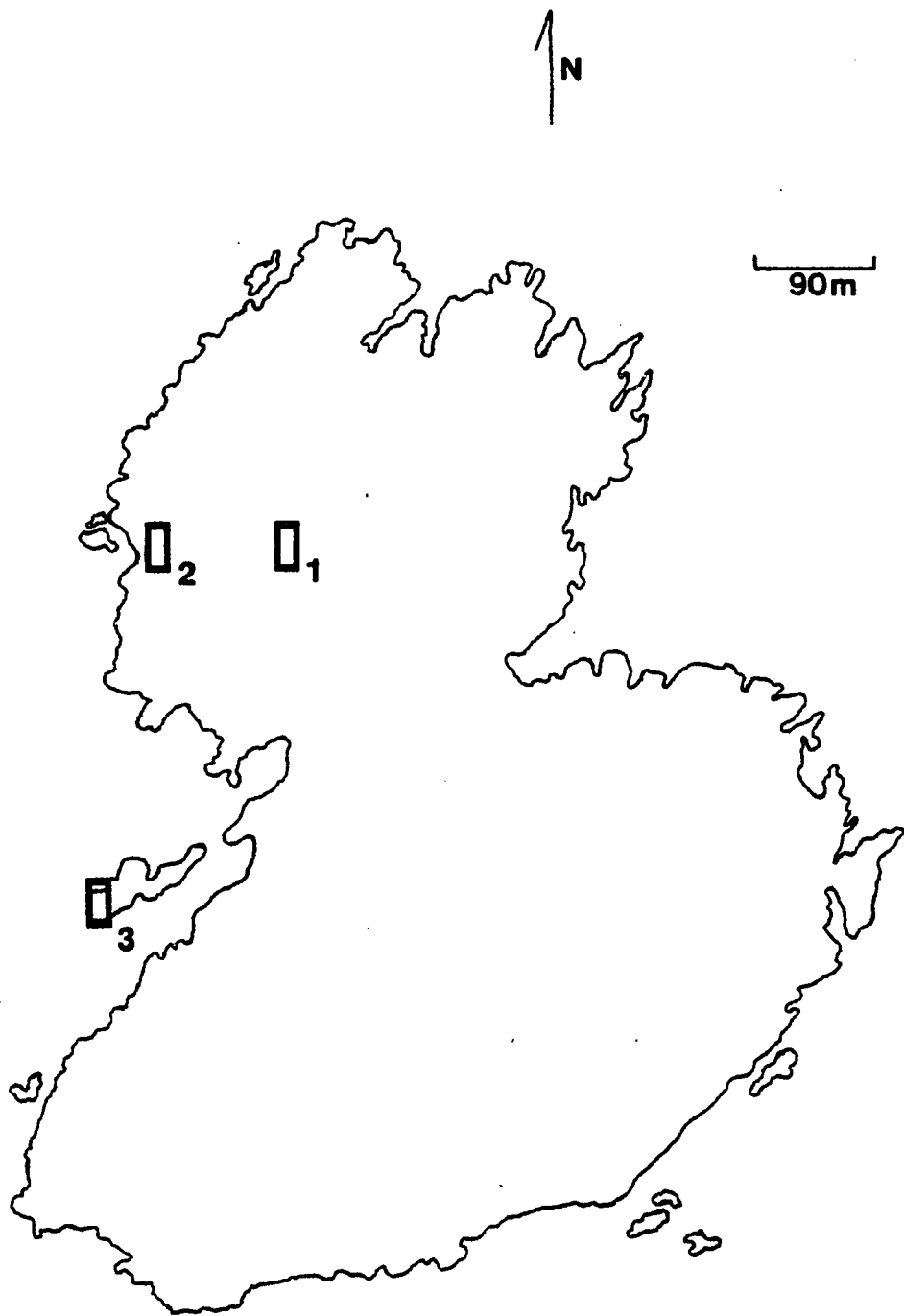


Figure 1. Map of Appledore Island, Isles of Shoals, ME and locations of rodent carrion sampling sites.

areas are considered the source of colonists. Sampling and laboratory procedures used were those described for size effects.

The resulting data were analyzed statistically to assess effects of rodent species (island size) and location (distance from source of colonists) on arthropod species number. In this manner similarities between rodent carrion and geographical islands were examined.

## RESULTS AND DISCUSSION

### Decompositional Stages

While decomposition is a continuous process, investigators have divided it into various stages based on physical appearance and faunal associates. Four decompositional stages were described by Reed (1958) and Johnson (1975), five by Payne (1965) and McKinnerney (1978), and two, based on dipteran life cycles, by Howden (1950). Five decay stages occurred in rodent carrion on the Isles of Shoals: fresh, bloat, active, advanced, and dry.

#### Fresh Stage (approx. duration: 1 day)

The fresh stage began with death and continued until bloating. During this period carrion appeared fresh. No external signs of decomposition were evident and odors of putrefaction were absent. Blow fly (Calliphoridae) adults were the dominant faunal associates, ovipositing on moist ocular, oral-nasal, and rectal tissues and feeding on fluids in these regions. Ants (Formicidae) and spiders (Aranea) occurred in small numbers, feeding on blow fly eggs and adults respectively. Ants also remove moist rodent tissues.

Taxa present: Calliphoridae, Formicidae, Araneae.

#### Bloat Stage (approx. duration: 3 days)

Bloating resulted from gases produced by anaerobic bacteria and tissue decomposition. During this stage carcasses swelled, eyes bulged, tongue and rectum protruded, and frothy fluids exuded from body orifices. A strong, putrid odor prevailed. Blow flies continued to be the dominant

fauna. Adults oviposited and early instar larvae fed in and around body orifices. Numerous additional fly and beetle species were attracted to decompositional fluids during this time. Bloating terminated with carcass deflation, resulting from release of gases through integumentary perforations caused by burrowing fly larvae.

Taxa present: Calliphoridae, Sarcophagidae, Ephydriidae, Coelopidae, Staphylinidae, Nitidulidae, Formicidae, Dermaptera, Araneae, Acarina, Chilopoda.

Active Decay (approx. duration: 5 days)

Active decay commenced with the resumption of aerobic decay. During this stage blow fly larvae burrowed throughout rodent thoracic and abdominal regions, enhancing decay by secreting digestive enzymes, disseminating bacteria, and aerating tissues. Maggots eventually destroyed internal viscera and ventral integument completely. A dorsal integumentary shell, skeleton, and associated musculature were all that remained. Liquified decay products saturated remains and the substrate beneath, and a strong odor of putrefaction persisted. A variety of necrophagous and predatory insects colonized carrion during this stage. Large numbers of insects caused carcasses to vibrate with activity. Termination of active decay occurred when fly larvae abandoned carrion and migrated into the soil prior to pupariation.

Taxa present: Calliphoridae, Sarcophagidae, Muscidae, Coelopidae, Piophilidae, Sepsidae, Sphaeroceridae, Carabidae, Dermestidae, Nitidulidae, Histeridae, Staphylinidae, Trogidae, Silphidae, Formicidae, Vespidae, Araneae, Acarina, Chilopoda, Isopoda, Diplopoda.



Advanced Decay (approx. duration: 10 days)

During advanced decay rodent carcasses appeared as hollow shells of dorsal integument. Externally the integument was hard and leathery, devoid of hair, and riddled with holes created previously by maggot burrowing. Fluid drainage had ceased and carrion odor gradually dissipated. Internally, the skeleton remained intact and the substrate wet with putrified fluids. Necrophagous and predatory beetles were the characteristic fauna. Numerous fly pupae were present, buried in the substrate. Advanced decay was terminated with appearance of skeletal disarticulation, complete carrion desiccation, and abandonment by all but dry tissue specialists.

Taxa present: Piophilidae, Dermestidae, Histeridae, Staphylinidae, Nitidulidae, Carabidae, Silphidae, Formicidae, Vespidae, Araneae, Acarina, Isopoda, Chilopoda.

Dry Stage (approx. duration: 10 days)

Throughout the dry stage carcasses appeared as dry skeletons covered with small fragments of integument, muscle, and connective tissue. Dermestid beetles eventually removed all remaining soft tissues, leaving only disarticulated bones. All distinctive odors were absent, and the substrate marked only with dried fluid stains.

Taxa present: Dermestidae, Nitidulidae, Corynetidae, Staphylinidae, Acarina, Isopoda.

Five arthropod families played a major role in rodent decomposition. Blow flies (Calliphoridae) and dermestid beetles (Dermestidae) were the important necrophages, rove (Staphylinidae), hister (Histeridae), and trogid (Trogidae) beetles the major predators. Payne (1965) and Putman

(1978) stress the importance of a few specialized insect species in vertebrate decay. The significance of such insects in habitats with strong maritime influences is evident. I found similar insects on gull and seal carrion located in supratidal areas of the Isles of Shoals (Lord 1982).

The process of rodent decomposition and faunal succession I observed on the Isles of Shoals is similar to that described by investigators for a variety of mammals and habitats worldwide (Fuller 1934, Reed 1958, Johnson 1975, McKinnerney 1978, and Coe 1978). Insect families and often genera characterizing particular decompositional stages are essentially the same. Decompositional rates, however, vary with habitat and carcass size (Nuroteva 1977). Differences in decay between rodent species are discussed in subsequent sections.

Insects colonizing rodent carcasses early in succession tended to have shorter life histories and shorter colonization periods than those arriving later in decay. Similar successional characteristics have been observed by Mohr (1943) on cow pats, Simberloff and Wilson (1970) on mangrove islands, Schoener (1978) on marine fouling communities, Henebry and Cairns (1980) on protozoan colonies, and by numerous terrestrial ecologists (Ricklefs 1973). The general biological characteristics of early and late successional groups of carrion frequenting insects are thus consistent with those described for a variety of plant and animal colonists.

#### Size Effects

The MacArthur-Wilson model of island biogeography (Fig. 2) predicts that large islands will support greater numbers of species than smaller ones equidistant from source of colonists (MacArthur and Wilson

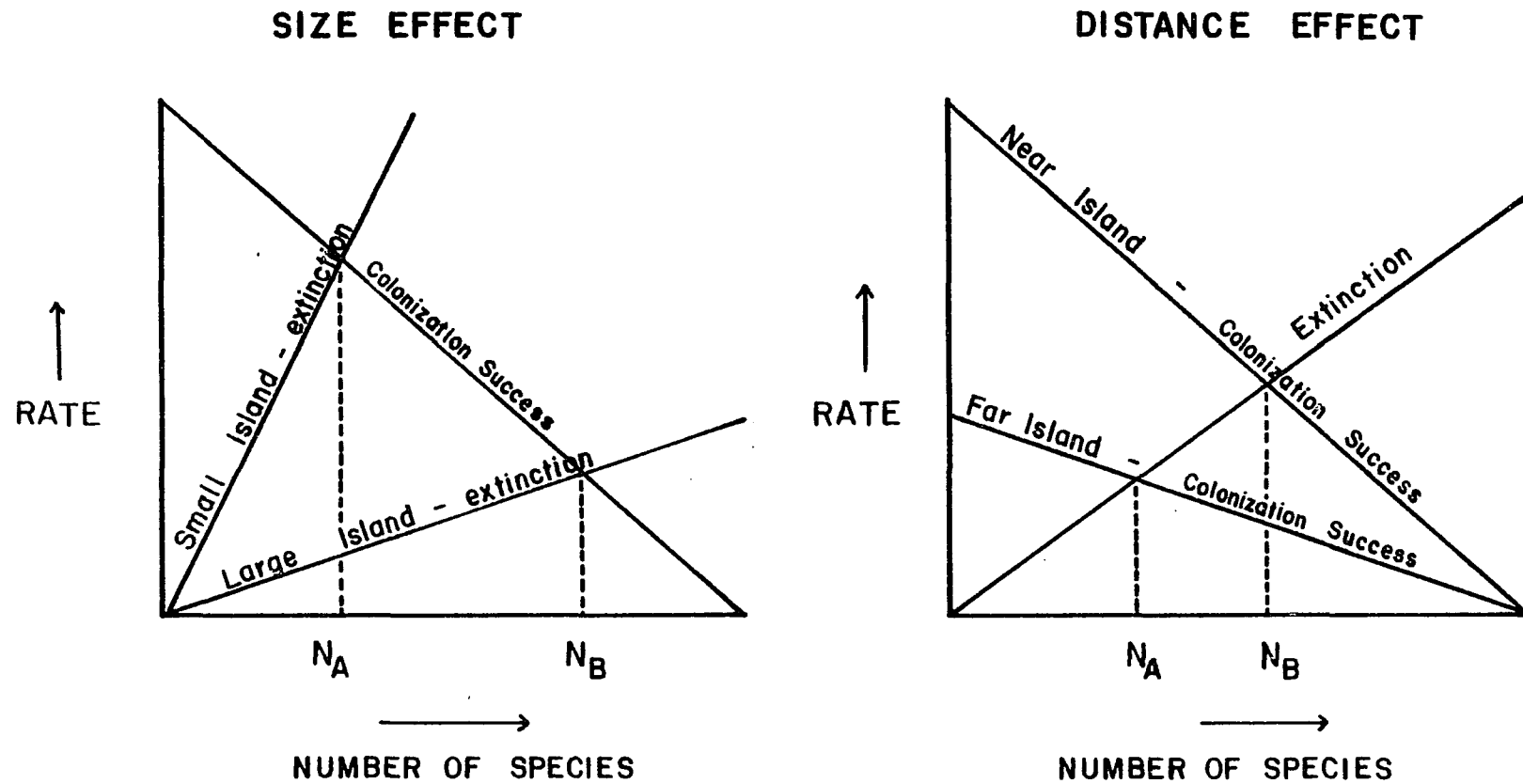


Figure 2. RELATIONSHIPS BETWEEN ISLAND SIZE AND DISTANCE FROM SOURCE OF COLONISTS ON SPECIES RICHNESS AS PREDICTED BY MacARTHUR AND WILSON (1967).

1967). Increased island size reduces competitive exclusion of colonists via greater resource availability and variety increasing species number. Field experiments have confirmed the island size - species richness hypothesis for a variety of island types. Simberloff and Wilson (1970) found greater arthropod species richness on large mangrove islands located in Florida Bay than on smaller ones equidistant from the mainland. Diamond (1973) discovered greater avifaunal variety on the larger islands of the Channel Archipelago. Schoener (1974) found greater numbers of marine invertebrate species on large artificial sponges, and Kuhn and Plafkin (1977) demonstrated greater protozoan species richness on larger freshwater fouling panels. Henebry and Cairns (1980) concluded that colonization of artificial substrates by protozoans in laboratory was consistent with the MacArthur-Wilson hypothesis.

I found arthropod species richness (Table II) to be directly proportional to carrion size (Two-way ANOVA,  $P < .001$ ). Rat carcasses supported the greatest number of arthropod species, hamsters and mice fewer, respectively (Student Newman-Keuls Test,  $\alpha = .01$ ). Regression analysis of species richness and carrion size is given in Figure 3. Ninety-two percent of the variance in species richness between carcasses ( $r = .96$ ) was attributed to island (carrion) size. Lord (1982) found gull carcasses ( $x = 1200$  g) located in similar habitat on Appledore to support 56 arthropod species.

The relationship between island size and species richness evident for carrion communities is consistent with the results obtained by investigators for a variety of geographical and biological islands. Carrion data support the island size - species richness hypothesis of the MacArthur-Wilson model.

Table II. Effect of rat, hamster, and mouse size on carrion arthropod species richness, Appledore Island, 1981.

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	Rattus <sup>A</sup> <u>rattus</u>	Cricetus <sup>B</sup> <u>auratus</u>	Mus <sup>C</sup> <u>musculus</u>
Species number			
x	25.00	15.67	10.67 <sup>1,2</sup>
SE	1.73	.67	.63
n	9	9	9

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<sup>1</sup> Two-way ANOVA<sub>2,24</sub> (F=56.13) (P<.001)

<sup>2</sup> Student Newman-Keuls Test; H<sub>A</sub>>H<sub>B</sub>>H<sub>C</sub> ( =.01)

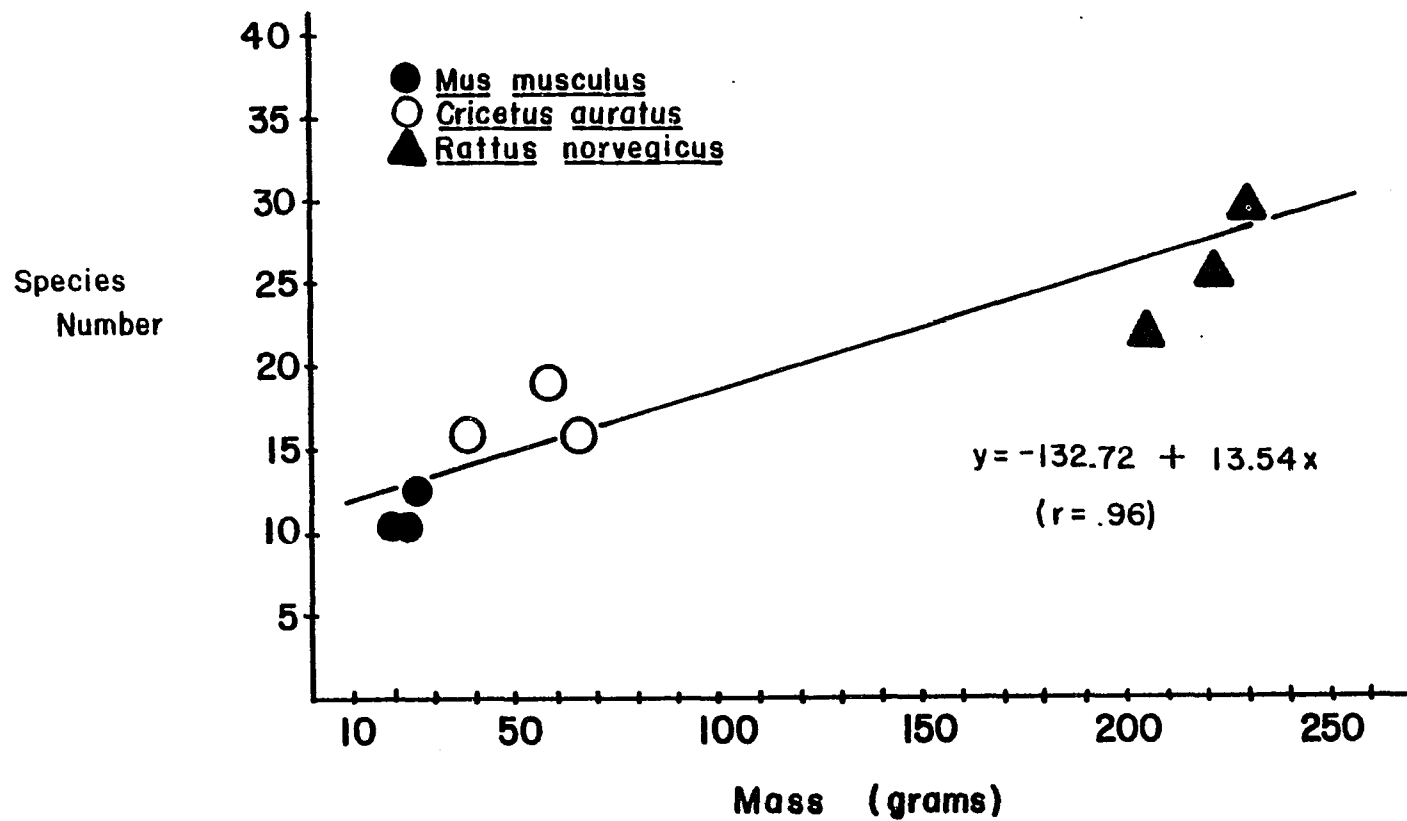


Figure 3. RELATIONSHIP BETWEEN RODENT CARRION SIZE AND ARTHROPOD SPECIES RICHNESS, APPLIEDORE ISLAND, 1981.

It is interesting to note that major species of carrion-specializing insects were present on all rodent carcasses. Less resource specific insects were absent from smaller carcasses. Differences in carrion colonizing capability between insect species may thus determine colonization success when carrion resources are limited.

#### Distance Effects

The MacArthur-Wilson model also predicts that islands located near a source of colonists will support a greater number of species than distant islands of equal size (MacArthur and Wilson 1967). An increase in distance from the source of immigrants reduces the rate of successful colonization, decreasing the species number. Field studies have been less successful in confirming the predicted distance effects than those of island size, due largely to the difficulties of accurately determining the location and composition of colonist pools. Macguire (1963), however, demonstrated decreased species richness in water-filled beakers located at greater distances from a pond. Simberloff and Wilson (1970) document decreased arthropod species numbers on more distant mangrove islands in Florida Bay, and Henebry and Cairns (1980) found fewer protozoan species colonizing artificial substrates as distance from laboratory culture was increased.

All 3 types of rodent carrion studied, rats, hamsters, and mice, supported significantly fewer arthropod species when placed at increasing distances from inland habitat (Two-way ANOVA,  $P < .001$ ) (Table III). Carcasses located on cobble beaches and an accessory island were less species rich, respectively, than those located on central ridges (Student Newman-Keuls Test,  $\alpha = .01$ ). Correlation analysis (Fig. 4) confirmed a significant and negative relationship between arthropod

Table III. Effect of distance from source of colonists on rat, hamster,  
and mouse carrion species richness, Appledore Island, 1981<sup>1,2,3</sup>.

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	<u>Rattus</u> <u>rattus</u>	<u>Cricetus</u> <u>aurantus</u>	<u>Mus</u> <u>musculus</u>
Thicket <sup>A</sup>	25.00 ±1.73	15.67 ±.67	10.67 ±.63
Shore <sup>B</sup>	11.67 ±1.20	7.33 ±.33	7.67 ±.33
Accessory <sup>C</sup> Island	2.67 ±.33	1.33 ±.33	1.00 ±.00

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<sup>1</sup> all values =  $\bar{x} \pm SE$

<sup>2</sup> Two-way ANOVA<sub>2,24</sub> (F=278.47) (P<.001)

<sup>3</sup> Student Newman-Keuls Test;  $H_A > H_B > H_C$  ( =.01)



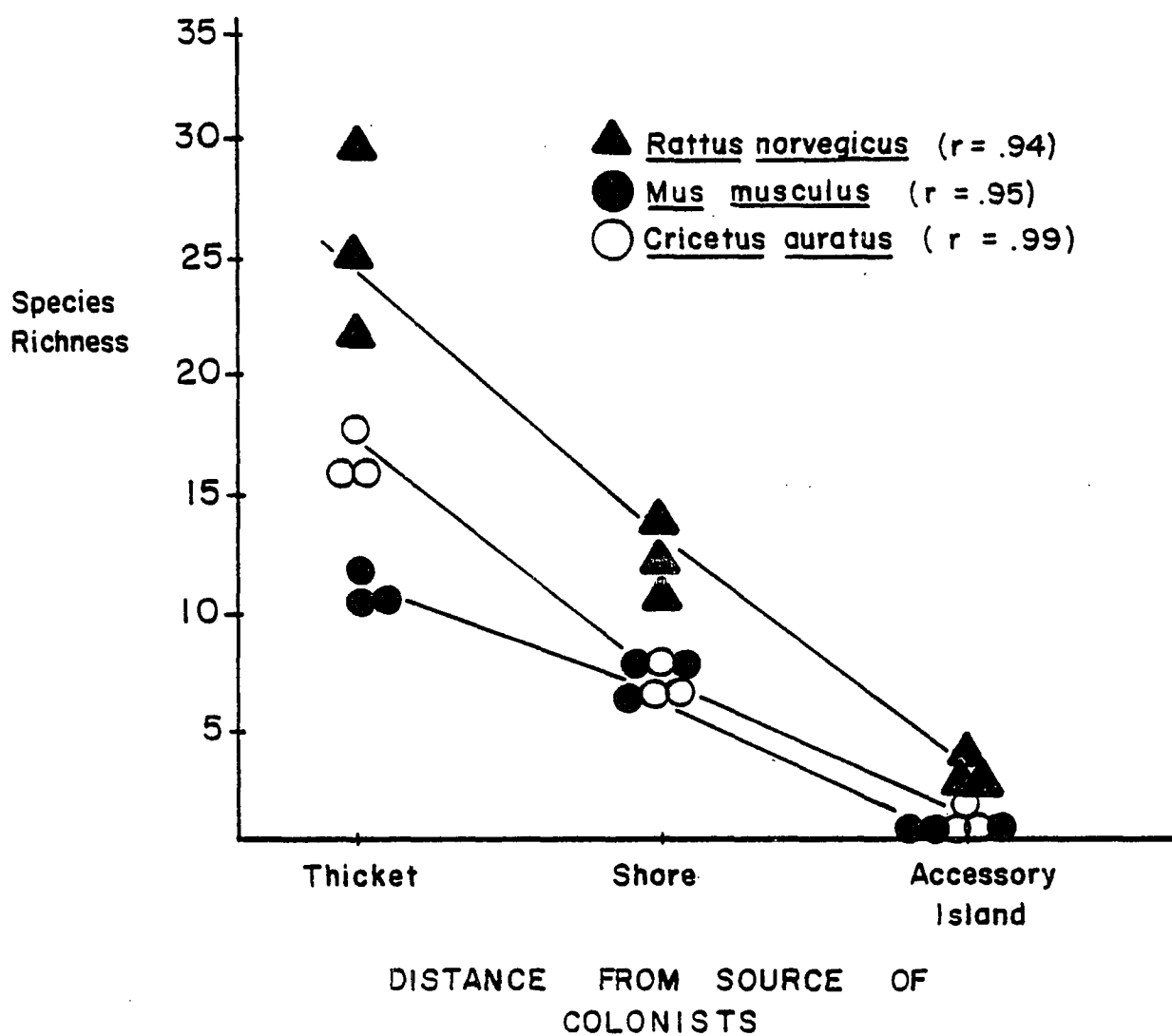


Figure 4. RELATIONSHIPS BETWEEN DISTANCE FROM SOURCE OF COLONISTS AND CARRION ARTHROPOD SPECIES RICHNESS, APPLIEDORE ISLAND, 1981.

species richness and carrion distance from source of colonists. Lord (1982) found gull carcasses on ridges to support 59 species of arthropods and those on cobble beaches 41 species, a significantly (t-test,  $P < .05$ ) smaller number. The results of these experiments support the relationship between island distance from colonists and species richness predicted by the MacArthur-Wilson hypothesis.

Distance effects were substantially greater ( $F = 278.47$ ) than the effects attributed to carrion size ( $F = 56.13$ ). Simberloff and Wilson (1970) found similar relationships between size and distance of mangrove islands in Florida Bay. The dominance of distance effects in rodent carrion communities lends further support to the validity of the MacArthur-Wilson hypothesis and the insular nature of carrion. Interaction between distance and size was also significant ( $P < .01$ ). As distance increases smaller carcasses lose arthropod species at faster rates than do large. These data may reflect limitations of dispersal and searching abilities for carrion frequenting insects.

The results of these experiments demonstrate similarities between aspects of the ecology of carrion communities and geographical islands. The successional process, characteristics of early and late colonists, and the effects of carrion size and distance from source of colonists suggest a process of colonization and community development consistent with those reported for other geographical and biological island systems.

The temporary nature of carrion makes measurement of colonization and extinction rates difficult. The predictive value of the island size-distance hypothesis of MacArthur-Wilson (1967) is confirmed, however, for these ephemeral communities, and the usefulness of carrion as templates for the testing of ecological principles evident.

When coupled with the ecological patterns described for other geographical and biological islands, these data support a uniform process of colonization and community development for both large and small, and ephemeral and permanent resource patches, and the insular nature of biota.

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**APPENDIX**



## APPENDIX I

LIST OF INVERTEBRATE SPECIES COLLECTED FROM CARRION  
ON THE ISLES OF SHOALS (1979-1982)

	Seals	Gulls	Rodents
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DIPTERA			
<u>Cymonyopsis cadaverina</u>	x	x	x
<u>Calliphora vicina</u>	x	x	
<u>Phormia regina</u>	x	x	x
<u>Lucilia illustrus</u>		x	x
<u>Cochliomyia mancellaria</u>		x	
<u>Sarcophaga bullata</u>	x	x	x
<u>Coelopa frigida</u>	x	x	x
<u>Ephydra riparia</u>	x	x	
<u>Chloropisa variceps</u>	x	x	
<u>Piophilata latipes</u>	x	x	x
<u>Sepsis punctum</u>	x	x	
<u>Sciara sp.</u>		x	
<u>Anthomyia sp.</u>		x	
<u>Proboscimyia sp.</u>		x	
<u>Sphaecocera sp.</u>		x	
<u>Chasmatodonotus sp.</u>		x	
<u>Ophyra leucostomata</u>	x	x	
<u>Fannia canicularis</u>	x	x	
COLEOPTERA			
<u>Monotoma picipes</u>		x	
<u>Anaedes brunneus</u>		x	
<u>Dermestes caninus</u>	x	x	x
<u>Dermestes vulpinus</u>	x	x	x
<u>Anthicus cinctus</u>		x	
<u>Anthicus cervinus</u>	x	x	
<u>Creophilus maxillosus</u>	x	x	x
<u>Aleochara lata</u>	x	x	x
<u>Philothus politus</u>	x	x	x
<u>Staphylinus violaceus</u>		x	
<u>Trox variolatus</u>		x	x
<u>Saprinus pennsylvanicus</u>	x	x	x
<u>Saprinus conformis</u>	x	x	x
<u>Saprinus assimilis</u>	x	x	
<u>Pachylopus fraternus</u>		x	
<u>Silpha noveboracensis</u>	x	x	
<u>Necrophorus tomentosus</u>			x
<u>Carpophilus sp.</u>	x	x	x
<u>Stelidota geminata</u>	x	x	x
<u>Necrobia ruficollis</u>		x	x
<u>Haltica chalybea</u>		x	

	Seals	Gulls	Rodents
<u>Amphedus collaris</u>		x	
<u>Poecilus lucoblandus</u>		x	x
HYMENOPTERA			
<u>Tetramorium caespitum</u>		x	x
<u>Monomorium minimum</u>		x	x
<u>Vespula maculifrons</u>	x	x	x
<u>Cynipidae A</u>	x	x	
<u>Ichneumonidae A</u>		x	
DERMAPTERA			
<u>Anisolabis maritima</u>	x	x	x
ACARINA			
<u>Trombidium sp.</u>	x	x	x
<u>Macrocheles sp.</u>	x	x	x
<u>Poecilochirus sp.</u>	x	x	x
ARANEAE			
<u>Pardosa lapidicina</u>	x	x	x
<u>Agelenopsis potteri</u>	x	x	
<u>Salticus scenicus</u>	x	x	
OPILIONES			
<u>Leiobunum politum</u>		x	
ISOPODA			
<u>Porcellio scaber</u>	x	x	x
<u>Porcellio rathkei</u>		x	
<u>Philoscia vittata</u>	x	x	x
AMPHIPODA			
<u>Orchestria platensis</u>	x	x	
DIPLOPODA			
<u>Nacerus americans</u>		x	
CHILOPODA			
<u>Lithobius sp.</u>	x	x	
<u>Arenophilus sp.</u>	x	x	
PSEUDOSCORPIONIDA			
<u>Lamphocherus oblongus</u>		x	
DECAPODA			
<u>Carcinus maenas</u>	x		
GASTROPODA			
<u>Polgyvra sp.</u>		x	
<u>Vallonia pulchella</u>		x	