Age-related foraging efficiency of the American Oystercatcher (*Haematopus palliatus*).

by

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c. Michael D. Cadman 1980

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Table of Contents

ACKNOWLEDGMENTS i

LIST OF TABLES ii

LIST OF FIGURES v

LIST OF PLATES vii

1 INTRODUCTION 1

2 THE STUDY AREA 10

3 METHODS 15

3.1 Observation periods 15

3.2 Use of the study area by oystercatchers 15

3.3 Aging American Oystercatchers 18

3.4 Energetic requirements 19

3.4.1 Body weight 19

3.4.2 Metabolic Rate 20

3.4.3 Energy expenditure 21

3.5 Age variation in bony characters of bill and skull ... 21

3.6 Prey characteristics 22

3.6.1 Density 22

3.6.2 Oyster height and volume 24

3.6.3 Specific gravity of oysters 24

3.6.4 Calorific content of oysters 25

3.7 Collection of foraging data 25

3.7.1 Measurement of tactical parameters of foraging .. 26

3.7.2 Description of oyster-opening techniques 30

3.8 Rate of gain of calories (RGC) 31

3.9 Prey choice 32

3.10 Data analysis 32

4 RESULTS 33

4.1 Use of the study area by American Oystercatchers 33

4.1.1 Daily pattern of activity 35

4.1.2 Effects of weather 36

4.1.3 Tidal pattern of use of oyster beds 37

4.1.4 Available time spent feeding 43

4.2 Comparison of foraging apparatus 44

4.3 Density and size of oysters on the oyster beds 60

4.4 Searching behaviour 62

4.4.1 Step rate 66

4.4.2 Peck rate 66

4.4.3 Search time 70

4.5 Oyster-opening technique 73

4.5.1 Disabling the Oyster 74

4.5.2 Extracting the flesh 77

4.5.3 Sequencing of techniques 79

4.6 Oyster-opening efficiency 80

4.6.1 Giving Up 80

4.6.2 Disabling time 82

4.6.3 Handling time and prey size 85

4.6.4 Number of bites taken by adults and immatures ... 95

4.6.5 Handling time and number of bites 95

4.6.6 Rate of gain of calories (RGC) 99

4.6.7 Choice among prey sizes 102

4.6.8 Relationship between E and RGC 110

4.7 Scavenging 115

4.8 Kleptoparasitism 117

4.9 Ingestion rate 121

4.10 Daily food intake and daily energy requirements 124

5 DISCUSSION 126

5.1 Age-related foraging efficiency 126

5.2 Implications of superior adult foraging proficiency .. 137

6 SUMMARY 144

7 LITERATURE CITED 147

LIST OF TABLES

Table Page

1. Mean percentage of available time spent feeding by first-year, second-year and adult American Oystercatchers.....17
2. Categorization of estimated bite sizes.....28
3. Mean dorso-ventral height of the bill tips of first-year, second-year and adult American Oystercatchers.....47
4. Density and size of oysters in the three microhabitats.....61
5. Step rates for adult and immature American Oystercatchers in each foraging situation.....67
6. Peck rates for adult and immature American Oystercatchers in each foraging situation.....69
7. Search time for adult and immature American Oystercatchers in each foraging situation.....72
8. Giving-up time for each age class.....81
9. Time taken by adult and immature American Oystercatchers to disable oysters of each size class.....83
10. Time taken by adult and immature American Oystercatchers to disable oysters in each foraging situation.....84

11. Handling times of first- and second-year American Oystercatchers for each size class of oyster.....86
12. Handling time of each size class of oyster by adult and immature American Oystercatchers.....87
13. Effect of oyster density on handling time of adult and immature American Oystercatchers.....90
14. Effect of state of exposure on handling time of adult and immature American Oystercatchers.....92
15. The number of bites taken to eat small oysters on wet and dry oyster bars.....94
16. Number of bites taken to eat each oyster size class by adult and immature American Oystercatchers.....96
17. Handling times for adult and immature American Oystercatchers when eating oysters in various numbers of bites.....98
18. Effect of state of exposure on rate of gain of calories (RGC) for adult and immature American Oystercatchers for each oyster size class.....100
19. Effect of oyster density on rate of gain of calories (RGC) for adult and immature American Oystercatchers for

each size class.....101

20. Rate of gain of calories (RGC) for adult and immature American Oystercatchers for each oyster size.....103

21. Mean oyster size taken by adult and immature American Oystercatchers in each foraging situation.....104

22. Electivity indices for adult and immature American Oystercatchers for each foraging situation.....108

23. The frequency of scavenging by first-year and older American Oystercatchers.....116

24. The frequency of stealing from each age class by adult and immature American Oystercatchers.....118

25. Frequency of intraspecific kleptoparasitism by adult and immature American Oystercatchers.....120

26. Ingestion rate of first-year, second-year and adult American Oystercatchers..... 122

27. Number of oysters eaten in 5 min by first-year, second-year and adult American Oystercatchers.....123

28. Daily energy requirements and daily food intake of American Oystercatchers at $0^{o}C$.....125

LIST OF FIGURES

Figure Page

1. Map of the Eastern Shore of Virginia showing the location of the study area.....11
2. The study area.....12
3. Map of the oyster bed at which all foraging data were collected.....13
4. Diagrammatic cross-section through an oyster bar.....14
5. American Oyster after the removal of the right valve.....23
6. Mean percentage of birds feeding at hourly intervals throughout the tidal cycle.....40
7. Percentage of birds feeding at hourly intervals throughout the tidal cycle with low tide occurring at different times of day.....42
8. Diagram of the skull of an American Oystercatcher.....49
9. Correlation of peck rate with the number of oysters eaten in 5 min.....71
10. Percentage composition of the diet of first- and second-year, adult and immature American Oystercatchers.....89
11. Comparison of the percentage composition of diets of American Oystercatchers with

that of the oyster population in microhabitats with high and low oyster densities.....106

12. Comparison of the percentage composition of diets of American Oystercatchers with that of the oyster population on the wet and dry oyster bars.....107

13. Relationship between RGC and E for all prey sizes and foraging situations.....109

14. Relationship between RGC and E for oysters in the 0.5, 2 and 4 ml size classes.....112

15. Effect of foraging situation on the relationship between RGC and E for oysters in the 0.5, 2 and 4 ml size classes.....114

LISI OF PLAIES

Plate Page

1. Ihe high water roost.....38
2. Rhamphothecae of (A) adult, (B) second-year and (C) first-year American Oystercatchers.....46
3. Dorsal view of the skulls of (A) first-year, (B) second-year and (C) adult American Oystercatchers.....50
4. X-rays of the skulls of (A) adult and (B) first-year American Oystercatchers from the dorsal aspect.....51
5. X-rays of the skull of a second-year American Oystercatcher from the dorsal aspect.....52
6. X-rays of the skulls of (A) adult and (B) first-year American Oystercatchers from the lateral aspect.....54
7. X-rays of the skull of a second-year American Oystercatcher from the lateral aspect.....55
8. X-rays of the lower mandible of (A) adult and (B) first-year American Oystercatchers from the dorsal aspect.....56
9. X-rays of the lower mandible of a second-year American Oystercatcher from the

lateral aspect.....57

10. X-rays of the lower mandible of (A) adult and (B) first-year American Oystercatchers from the lateral aspect.....58

11. X-rays of the lower mandible of a second-year American Oystercatcher from the lateral aspect.....59

12. Foraging pose of an American Oystercatcher.....63

13. Oystercatcher disabling an oyster.....65

1 INTRODUCTION

Learning is important in the development of foraging techniques in many species of homeotherms (e.g. Turner 1965, Weigl and Hanson 1980). Recent studies of the ontogeny of foraging proficiency of birds have been stimulated largely by the hypothesis that deferred breeding is the result of the inadequate foraging ability of young birds, as proposed by Ashmole (1963). Some workers (e.g. Buckley and Buckley 1974, Groves 1978) have compared tactical capabilities (handling time, capture success) between ages as a means of testing the hypothesis; they have ignored foraging strategy (prey choice). Conversely, a number of studies concerning foraging strategy and "optimal foraging" have been undertaken recently (see Pyke et al. 1977 for references). Studies of optimal foraging have endeavoured to determine if predators select prey to maximize their rate of food intake (e.g. Krebs et al. 1977, Elner and Hughes 1978). None of this research, however, has investigated the ontogeny of foraging strategy.

Optimal foraging theory assumes that birds inherit the ability to gauge prey value and hence are capable of choosing the appropriate prey items to maximize their energy intake (Krebs 1978). Whereas learning is of paramount importance in the development of foraging techniques, it is not, according to optimal foraging theory, of any direct importance in the development of foraging strategy. This assumption remains untested.

As suggested by Hartwick (1976), the choice of subject species is of paramount importance when testing hypotheses in the field. Oystercatchers are well suited to a study of this type. They show deferred breeding (Harris 1967) and first-year, second-year and adults are

separable in the field by plumage and other somatic characteristics (Bent 1929, Witherby et al. 1941, Baker 1974a). They are large, easily observable birds which eat shellfish - a prey type requiring considerable handling, dexterity and coordination. The non-mobile nature of their prey is of additional value, in that it simplifies quantification of prey and reduces the number of foraging parameters that must be measured (Pulliam 1975).

The flocking of oystercatchers in winter facilitates the comparison of foraging parameters between age classes. Additionally, their world-wide distribution (Baker 1969) and economic importance as pests of the British shellfish industry has made several species of the family the subject of considerable scientific study to date. The bulk of the work has been devoted to feeding ecology (Dewar 1908, 1910, 1913, 1915, 1920, 1922, 1940, Dircksen 1932, Drinnan 1957, 1958a, 1958b, Tinbergen and Norton-Griffiths 1964, Lind 1965, Dare 1966, Davidson 1967, Safriel 1968, Norton-Griffiths 1967, 1969, Baker 1969, 1974a, 1974b, 1975, Hulscher 1964, 1974, Brown and O'Connor 1974, Heppleston 1970, 1971, Horwood and Goss-Custard 1977, Goss-Custard 1977a, Goss-Custard et al. 1977a, 1977b, O'Connor and Brown, 1977). However, to date the American Oystercatcher has been largely overlooked (but see Tomkins 1947, Burger et al. 1977); most work has concentrated on the European Oystercatcher (Haematopus ostralegus).

This study was carried out in Chincoteague, Virginia, which is the northern extreme of the winter range of the American Oystercatcher (Haematopus palliatus palliatus Temminck), the location where efficient foraging strategy is presumably most necessary. The population under

investigation fed entirely upon commercial, intertidal oysterbeds during the winter. Moreover, they fed on an oysterbed which was accessible by car, thus simplifying the logistics of the study. The birds fed almost entirely upon oysters. Monophagy is unusual in predators and is extremely advantageous in a foraging study. When "choosing a currency" (Schoener 1971) which must be optimized, the predator needs to consider only the energetic value of the prey and, hence, simply chooses between various prey sizes. Nutrient content of various prey species need not be of concern to the monophagic predator.

Studies of age-related foraging ability have concentrated wholly upon the tactical aspects of prey acquisition (Orians 1969, Recher and Recher 1969, Dunn 1972, Buckley and Buckley 1974, Groves 1978, Morrison et al. 1978, Burger 1980) in testing Ashmole's hypothesis that deferred breeding is the result of the inadequate foraging ability of young birds. This investigation of the foraging strategy of young birds makes possible an additional test of the hypothesis. Birds that can feed with high tactical proficiency but are unable to choose types and sizes of prey which maximize their energy intake are less likely to be successful in breeding.

The gradual development of foraging ability has been demonstrated in several groups of birds that have evolved relatively difficult methods of acquiring food. Orians (1969) found that Brown Pelicans (Pelicanus occidentalis) improve their fish-catching ability until at least 2 years of age. Similar results have been found in Little Blue Herons (Florida caerulea) by Recher and Recher (1969), Glaucous-winged Gulls (Larus glaucescens) by Searcy (1978), Herring Gulls (Larus argen-

tatus) by Ingolfsson and Estrella (1978), Ring-billed Gulls (Larus delawarensis) by Burger and Gochfeld (1979), Royal Terns (Sterna maxima) by Buckley and Buckley (1974), Sandwich Terns (S. sandvicensis) by Dunn (1972), Ruddy Turnstones (Arenaria interpres) by Groves (1978), and in Olivaceous Cormorants (Phalacracorax olivaceous) by Morrison et al. (1978). It seems clear that these young birds are learning at least some portion of their foraging ability, and that long periods of time can be involved in attaining adult proficiency.

One of the basic assumptions of optimal foraging theory is that there is heritable variation in foraging ability (Pyke et al. 1977). Oystercatchers have been shown to inherit some of the tactical aspects of foraging. Dewar (1920), Lind (1965), and Norton-Griffiths (1967) have shown that European Oystercatchers inherit several motor patterns which are generally applicable to the acquisition of all prey items in their diet. The young birds perfect the orientation, coordination and sequencing of these basic motor patterns by trial-and-error learning and with assistance from their parents (Dewar 1920, Lind 1965, Norton-Griffiths 1967). The gradual improvement in foraging techniques of the European Oystercatcher has been described by Norton-Griffiths (1967), though his work concentrates on the first year of life. Nevertheless, he provides evidence which suggests that some tactical aspects of oystercatcher foraging may improve until at least their third winter.

In addition to the inheritance of the essential motor patterns, oystercatchers may also inherit the ability to ascertain the energetic value of each prey item, rank them and thus select the diet which maximizes energy intake - the "optimal diet" (Krebs 1978). If this is so,

and different age classes have different prey handling abilities, then they might be expected to select prey of different sizes, but each age class should always choose prey sizes which maximize their energy intake. Recent studies in the laboratory (Werner and Hall 1974, Elner and Hughes 1978) and in the field (Goss-Custard 1977b, Hartwick 1976, Davies 1977a) have shown that adult predators are capable of selecting prey items which maximize their energy intake, but there are no studies of the foraging strategy of young predators. The high rate of mortality among young European Oystercatchers (Heppleston 1971, Boyd 1962, Harris 1967) indicates clearly that there is a strong selective advantage to young birds possessing both well developed tactical and strategical proficiency.

Some proof of the ability of young birds to gauge energy intake and rank opposing strategies is provided by Davies (1977b). Davies determined that young Spotted Flycatchers (Muscicapa striata) remain with their parents, begging for food, until they are able to gain energy at a higher rate by feeding themselves. In some species, young birds have been found to take prey which is different from that selected by their parents. Young finches (Fringillinae) choose smaller seeds than adults (this might be a function of skull ossification (Kear 1962)). Young Reed Warblers (Acrocephalus scirpaceus) tend to glean prey rather than use the "flycatch" method preferred by older birds (Davies and Green 1976). No tests have been undertaken to determine whether these young birds are selecting the most appropriate strategy of prey choice.

If the ability to select appropriate prey is learned, adults can be expected to be most adept at selecting appropriate prey. Young birds, in contrast, might tend to select prey which yield relatively little reward, avoid prey which provide the highest calorific return or some combination of these two possibilities. In determining the value of a prey item, most studies to date have used only energetic intake and have ignored the costs of foraging (Krebs 1978). Therefore, to avoid this important shortcoming, in this study I have used rate of gain of calories (RGC), which is a function of both energy intake and the energetic expense of foraging (see Methods). Additionally, I have used the Electivity Index (Ivlev 1961) to indicate prey choice. An efficient predator should select prey which yield greater energetic return, so that higher electivity (E) values should be found for oyster sizes which provide the predator with a high RGC.

If oystercatchers inherit the ability to gauge prey quality and, hence, to maximize energy intake, both adults and immatures should exhibit a positive correlation between E and RGC. Should the ability be a learned one, however, young birds can be expected to show an irregular pattern of prey choice that is unrelated to the energetic value of the prey because they cannot accurately gauge this value. Conversely, a non-significant correlation might indicate that birds are actually able to determine prey value, but do not follow the criteria of energy maximization proposed in the model. It seems probable that this simple model of foraging strategy does not take into consideration all of the foraging parameters which potentially influence prey choice. In this study I have investigated how it might be modified by factors such as the functional morphology and strength of the foraging apparatus. Other than

the early work of Kear (1962), bill and skull morphology has not been considered to be of enough importance to warrant investigation in studies of age-related foraging. To some extent, oystercatchers and finches may be unusual in that strength as well as technique is important to the foraging behaviour of these birds. Nevertheless, it is possible that the inferior prey handling ability of young birds demonstrated by several species (Morrison et al. 1978, Buckley and Buckley 1974, Verbeek 1977a, 1977b) is related to morphological development of their foraging structures.

Ashmole (1963) has hypothesized and Lack (1954, 1966, 1968) has suggested indirectly that deferred breeding has evolved because young birds of certain species have difficulty in obtaining enough food to enable them to succesfully withstand the rigorous demands of breeding. For example, Carrick and Ingham (1967, quoted in Fisher (1975)) have proposed that only through an extended period of up to 10 years of learning in the Wandering Albatross (Diomedia exulans) can the bird acquire the foraging skills necessary to provide adequate food for itself and its offspring.

The evidence for delayed breeding of birds as a result of inadequate foraging proficiency is indirect. For example, clutch size and fledging success have been shown to increase with age in some birds (e.g. Coulson and White (1956,1958), Richdale (1949), Ryder (1975)). Additionally Ainley and Schlatter (1972) have shown that Adelie Penguins (Pygoscelis adelidae) raise more chicks per pair as they age; they note that previous breeding experience does not change breeding success. Ainley and Schlatter suggested that improvement in foraging ability up

to 8 years of age can explain their results. Blus and Keahey (1978) proposed that the lower breeding success of immature plumage Brown Pelicans may be due to lower fishing success (as shown by Orians (1969)).

European Oystercatchers occasionally breed in their third year, though they usually wait until their fourth or fifth year (Harris 1967). If Ashmole's and Lack's hypothesis of deferred breeding is correct, then European Oystercatchers in their third year should exhibit the same foraging proficiency as older birds, or at least be more proficient than younger birds. Norton-Griffiths (1967) has presented evidence which suggests that oystercatcher foraging "efficiency" might increase until their third winter. Further evidence for relatively poor feeding by young European Oystercatchers is provided by Dare (1977), who found that while adults gain weight throughout the winter months, immatures are unable to maintain their weight after December and gradually lose weight for the remainder of the winter. Dare suggests that superior foraging ability of the adults explains the observed trends. Heppleston (1971) provided further indirect evidence for poor feeding ability in young birds when he determined that during particularly cold weather, 77% of mortality consisted of first year birds that had apparently starved to death.

Higher mortality of younger birds has often been attributed to poor feeding capability (see, for example, Lack 1954, Kahl 1963, Heppleston 1971). Prolonged parental care is a means of avoiding high post-fledging mortality in species with difficult foraging techniques, and has been described in several species (Ashmole and Iovar 1968), including oystercatchers (Dewar 1920, Lind 1965 and Norton-Griffiths

1967).

The objectives of this study are thus to investigate tactical and strategical aspects of age-related foraging efficiency in the American Oystercatcher, and its possible link with deferred breeding in this species.

2 THE STUDY AREA

The study area is located 5 km West of Chincoteague, Virginia (see Fig. 1 and 2) at latitude 37° 56'N and longitude 75° 28'W. It is characterized by areas of salt marsh, channels, bays, oyster beds and mudflats and is bisected by a road (see Fig. 2). Salt marshes of the Chincoteague area are broadly classified as coastal plain marshes and have developed on fine grey sands and muds (Chapman 1960). Regularly flooded, low lying salt marsh is dominated by Smooth Cordgrass (Spartina alterniflora) while seldom flooded areas are dominated by Salt Hay (Spartina patens) and Saltwort (Salicornia sp.).

The oyster bed upon which observations were made (Fig. 3) is man-made. It is situated at the North end of a large shallow bay (Shelly Bay). Because of its location, the bed is protected from heavy wave action unless the wind is from a southerly direction. The predominant winds during the winter on the study area were from the WNW.

The beds are uncovered on a falling tide and are covered by water again as the tide rises. The tops of the oyster bars are elevated such that a neap tide does not quite cover them (see Fig. 4). The tide range is approximately 1.0 m in Shelly Bay on a spring tide and 0.7 m on a neap tide. At low water for spring tides, the oyster bed is drained so that areas are uncovered which are not usually available to foraging oystercatchers.

The average ambient temperature in January was 2°C and in February, the average temperature was -2°C. The high and low temperatures in January were 16°C and -12°C, and for February 15°C and -14°C.

Figure 1. Map of the Eastern Shore of Virginia showing the location of the study area. The study area is indicated by the black square. It lies between the mainland and the off-shore barrier islands, an area consisting of extensive salt marsh. Chincoteague is represented by the black circle.

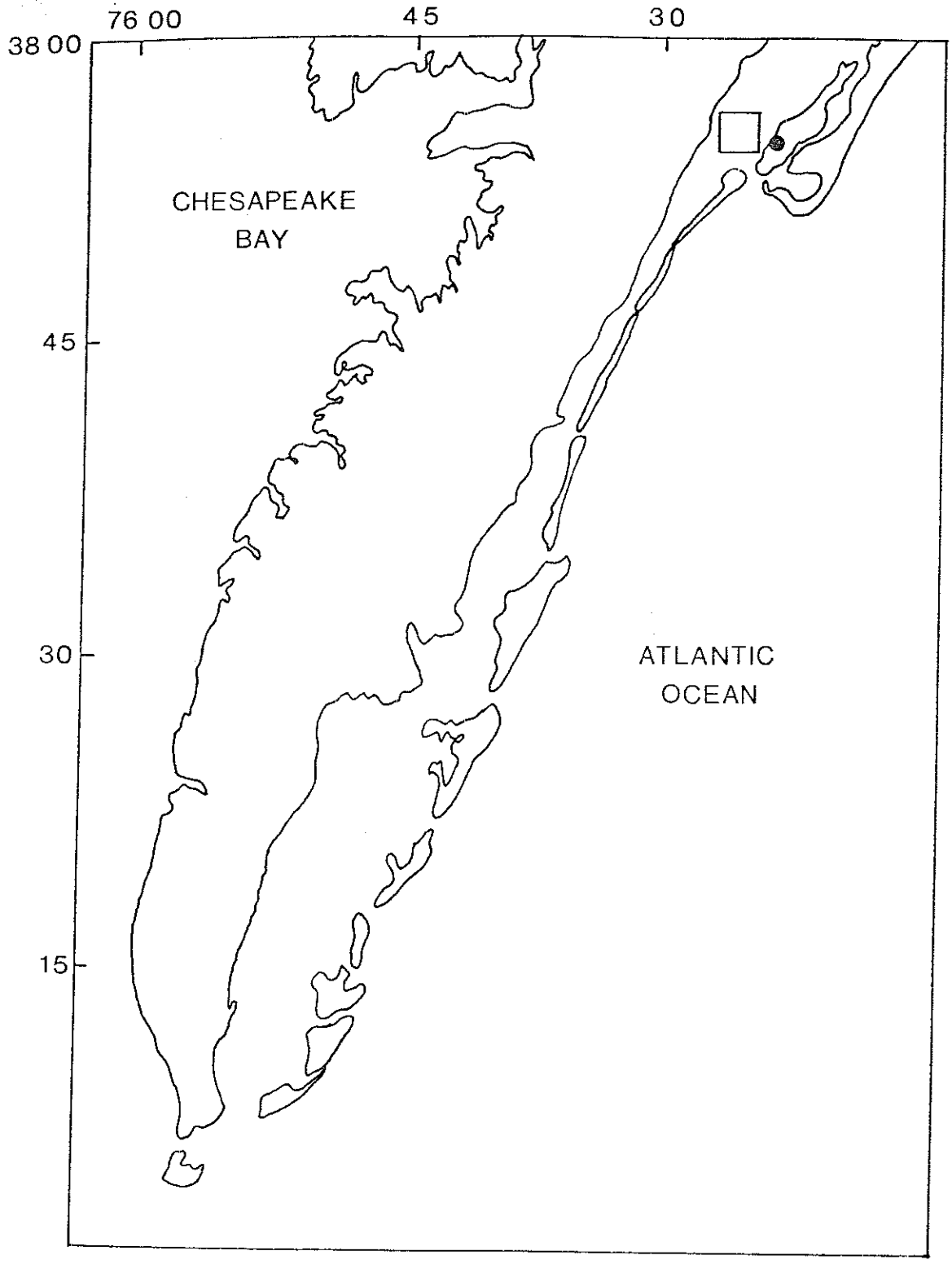

76 00
45
30
38 00
45
30
15
CHESAPEAKE
BAY
ATLANTIC
OCEAN

Figure 2. The study area.

1. The study oyster bed
2. The loafing area
3. The high water roost
4. The night roost

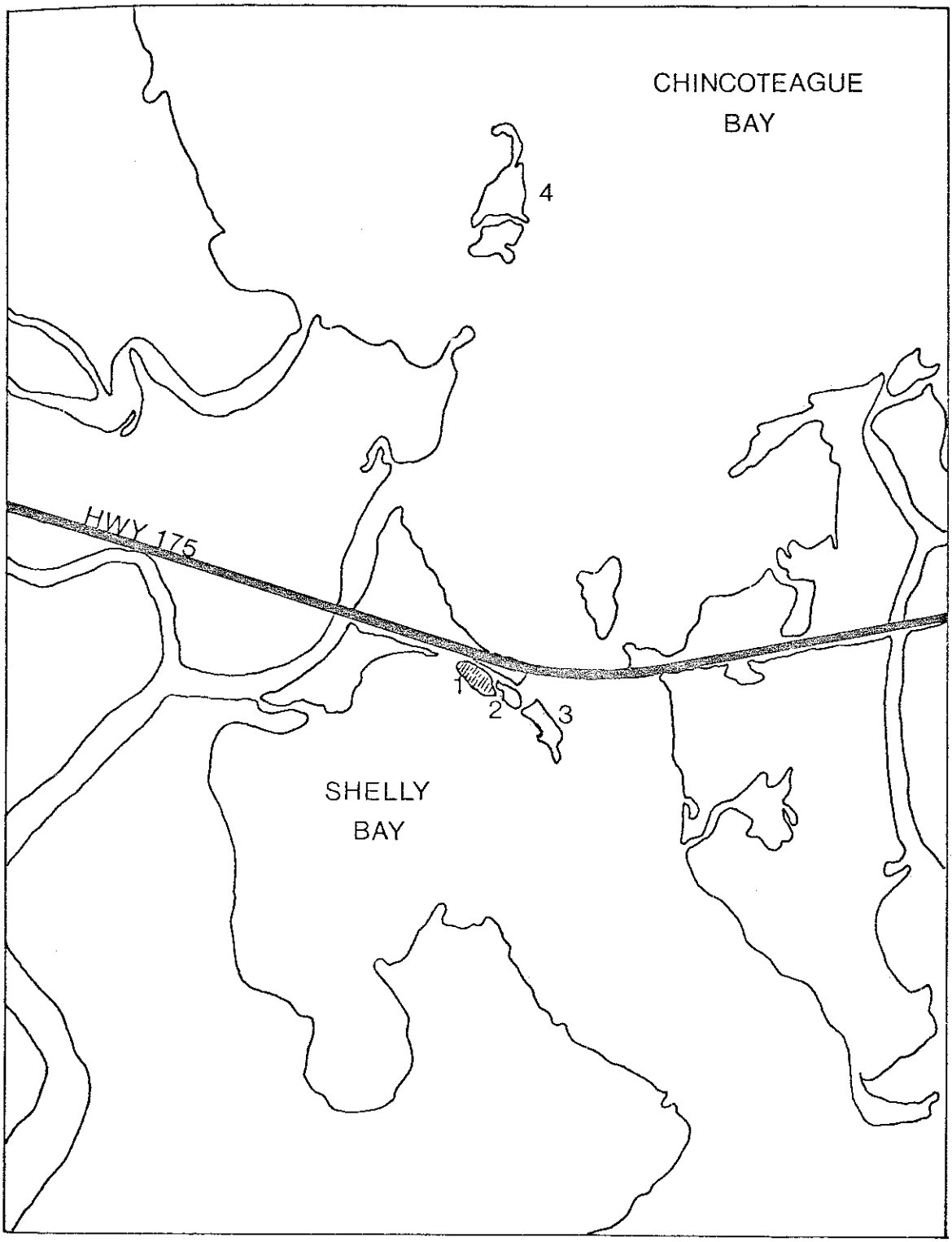

CHINCOTEAGUE
BAY
4
HWY 175
1
2
3
SHELLY
BAY

Figure 3. Map of the oyster bed at which all foraging data were collected. The beds are shown as they would appear at Mean Low Water.

1. The islands
2. The main bars
3. The loafing area
4. Access road from which observations were made
5. Hwy 175

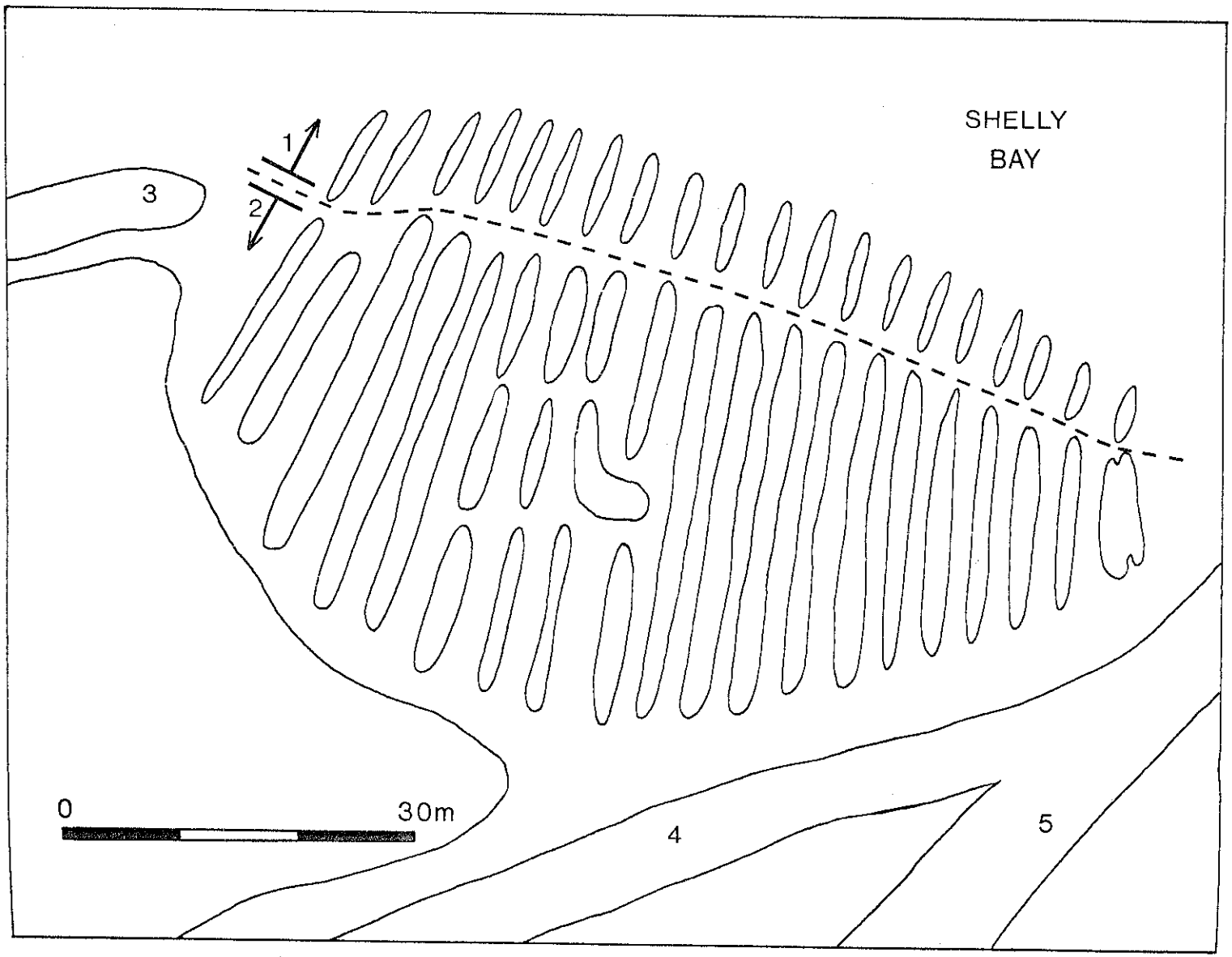
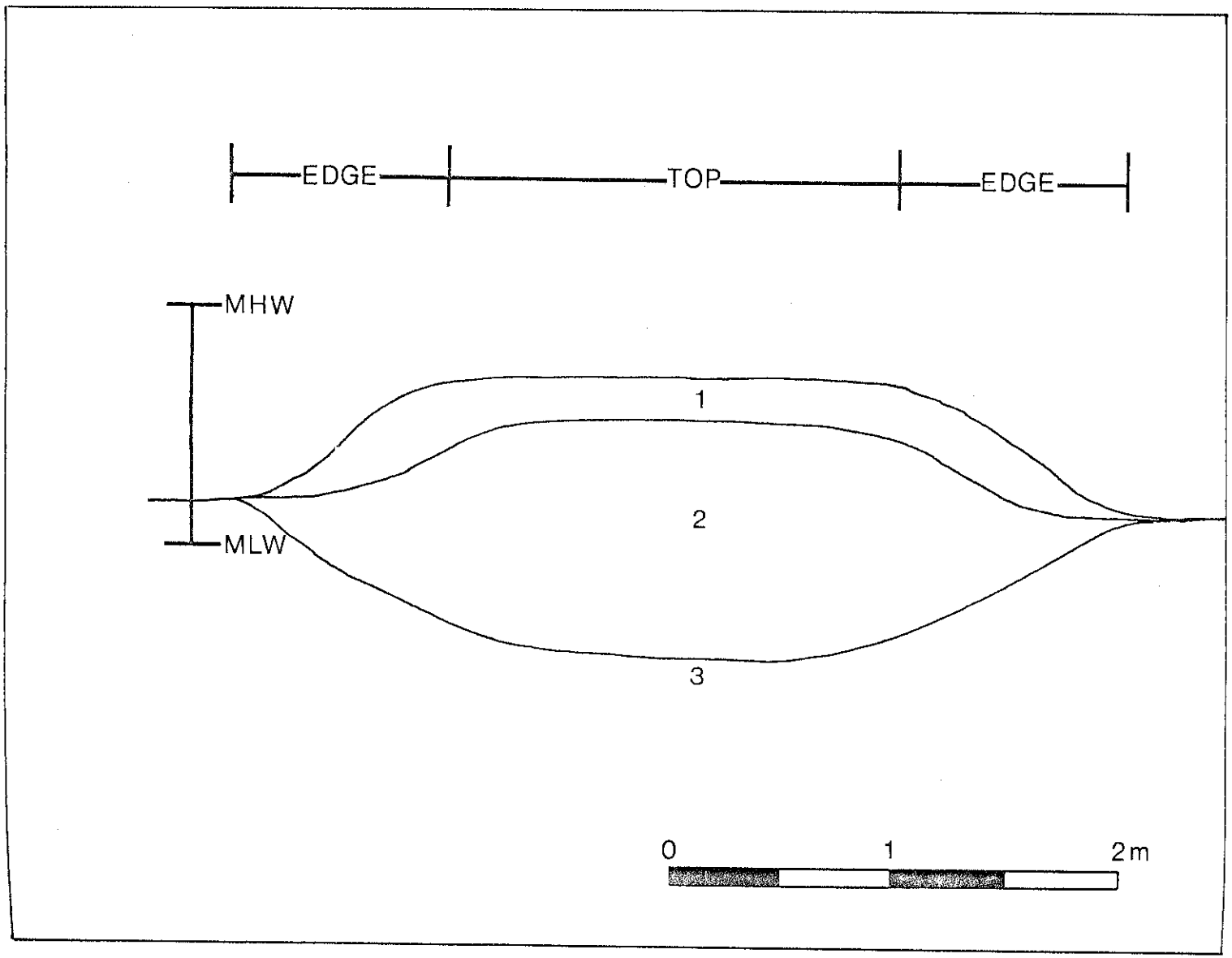

SHELLY
BAY
1
2
3
4
5
0
30m

Figure 4. Diagrammatic section through an oyster bar illustrating construction and location of the top and the edge with respect to tide level (modified from Bahr 1976).

The elevation of individual bars differed such that they were not all fully exposed at Mean Low Water.

1. Oysters and associated fauna
2. Buried shell and mud
3. Mud


EDGE
TOP
EDGE
MHW
MLW
1
2
3
0
1
2m

3 METHODS

3.1 Observation periods

Foraging data used in this study were collected from January 7, 1979 until March 8, 1979. Observations made during one week in February 1978, the breeding season of 1978 and two weeks during December 1978 were used to develop data collection techniques and assess the local area for prime locations for the foraging study.

There were no premeditated patterns to my visits to the oyster beds. Snow, rain and fog occurred frequently during the study period, and observations could not be made under these conditions. Whenever possible I visited the beds for the entire period that they were uncovered and thus available to the oystercatchers for feeding.

3.2 Use of the study area by oystercatchers

Seasonal data were obtained from local birders, Christmas counts published in American Birds and my own observations during the breeding seasons (March-July) of 1978 and 1979. To record the daily pattern of movement of the birds, I made visits to the study area before sunrise both when the beds were exposed and covered by water. I recorded the arrival times and patterns of the birds on the beds (or high water roost if the beds were covered), counting and aging the birds whenever the light permitted. I frequently remained on the study area until after sunset to record the movement from the feeding area or high tide roost to the overnight roost. I recorded the ages and times of departure of the birds as they left for the night.

Predicted times of low and high tide were obtained from the Chincoteague office of the United States Coast Guard. At half hour intervals before and after the predicted low tide level (see Baker 1969, Davidson 1967), I recorded the number of birds on the oyster beds on maps of the area. I recorded the age of each bird on the beds, and the behaviour (either feeding or resting) observed. I then counted the number of birds on the loafing area adjacent to the oyster bed, but was unable to age these birds because of the distance from my observation post. This procedure allowed me to determine the average percentage of birds in the immediate area that were feeding at any time. This average value (50.6%) was then used as the average percentage of each day that an oystercatcher spent feeding. To determine the time spent feeding by each age class another procedure was necessary, because it was impossible to age birds on the loafing area. Each day I determined the maximum number of each age class that I was able to identify at any time. I then calculated the percentage of this maximum that was feeding at each hourly interval, and averaged these values to estimate the percentage of each age class feeding at any time during the day. Unfortunately, because birds tended to leave the study area, these values (Table 1) underestimate the average percentage of birds in the immediate area which were feeding at any particular time (50.6%). Therefore, the average values for each age class were adjusted to 50.6%. This value is obviously only an approximation of the true percentage of the available time spent feeding by each age class.

Table 1. Average percent of available time spent feeding by first-year, second-year and adult American Oystercatchers.

Age	Percentage of maximum number feeding		Adjusted means
	Mean ± S.E.	n	
First-year+	47.65 ± 3.01	123	54.69
Second-year+	39.73 ± 3.01	123	45.60
Adult+	44.75 ± 3.11	123	51.36

+ Means not significantly different. Means were transformed with an arcsine transformation (Sokal and Rohlf 1969) for testing. ($P = 0.3737$ Duncan's multiple range test).

I also noted the ages of birds which moved to the high water roost when the beds began to cover, and of the birds moving to the beds from the roost as the tide fell. This provided information on whether specific age classes were arriving on the beds first or leaving the beds last. To determine if night feeding occurred on the oyster bed, I made several night visits to the bed and was usually present on the oyster bed before sunrise and after sunset.

3.3 Aging American Oystercatchers

Bent (1929) has published the only information to date on changes in the plumage of the American Oystercatcher with age, and he is somewhat vague. Therefore, I have used supplementary information on aging European Oystercatchers from Witherby et al. (1941) and the South Island Pied Oystercatcher (H. o. finschi) as described by Baker (1974a).

For the purposes of this study I refer to birds in their third-year or older as adults. Although third winter European Oystercatchers can apparently be distinguished from other ages (Dare 1977), I was unable to definitively separate third-year American Oystercatchers in the field. Adult birds can be distinguished by their dark brown dorsal plumage, bright, reddish-orange bill, light pink legs and brilliant chrome yellow irides. Second-year birds have the dark dorsal plumage of the adult, but they have pale lemon irides, greyish legs and their pale orange bill is dusky at the extreme tip. First-year birds are noticeably different from all other age groups. The most apparent difference is the suffusion of buff throughout the dark dorsal plumage, because the tips of the back feathers have buff edges. In addition, they have brown

irides, grey legs and pale orange bills which are dark on the distal half or more.

3.4 Energetic requirements

3.4.1 Body weight

As I was unable to capture any wintering oystercatchers, I have used modified springtime weights to calculate metabolic rates. I used weights of 29 adult oystercatchers from South Carolina collected in March 1977 from the collection of the Royal Ontario Museum. Generally, female oystercatchers are heavier than males (Baker 1975, Dare 1977) in each age class, but as I was unable to sex birds in the field, I have combined the sexes to obtain a single average weight for each age class. Whereas Dare (1977) treated third-year birds as immatures, I have chosen to categorize them as adults, as I was unable to distinguish them in the field.

Dare (1977) calculated the changes in weight undergone by European Oystercatchers throughout the year. Because there are no data available on weight changes of American Oystercatchers, I used Dare's data to calculate the relationship between European Oystercatcher weights in March, and those of early February (the middle of my observation period). I then multiplied the weights of the American Oystercatcher in March by the same proportion to obtain early February weights. As the collection of the Royal Ontario Museum has very few specimens of immature birds, I used Dare's proportion of weights of adults to immature birds to estimate the weight of first- and second-year American Oystercatchers. The

mean weight of adults used in this study is 592.6 g, and for immatures 525.0 g is used.

3.4.2 Metabolic Rate

Basal or standard metabolic rate (SMR) is the energy requirement, usually measured over short periods, of an individual at complete rest and in a postabsorptive state (Kendeigh 1970). SMR is typically measured in the zone of thermal neutrality. Average temperature on the study area during January and February was $0^{o}C$ (January average = $+2^{o}C$, February average = $-2^{o}C$). No data exist to define the thermal-neutral zone of the oystercatcher; therefore, I have assumed from data on other species (Kendeigh 1969) that $0^{o}C$ is below the lower critical temperature, and hence out of the thermal neutral zone. Kendeigh has calculated SMR for non-passerines at $0^{o}C$ by using the equation:

$$\log M = 0.5240 + 0.5257 \log W \pm 0.0845$$

Where M is kcal/day/bird-day

W is weight in grams.

I used estimated weights of adults and immatures from early February in Kendeigh's formula to determine SMR of American Oystercatchers at $0^{o}C$. SMR was calculated to be 95.86 kcal/day (3.327 cal/s) for adults and 89.95 kcal/day (3.120 cal/s) for immatures.

3.4.3 Energy expenditure

I adjusted SMR from Kcal/day to cal/s and with the use of multipliers, converted time budgets to energy budgets (Zach 1978). The rate of expenditure of energy while foraging was estimated as 3xSMR for that period. Similar values have been used for various species by Schartz and Zimmerman (1971), Custer and Pitelka (1972), and Zach (1978). I have followed King (1974) in estimating daily energetic needs as 3xSMR for 24 h.

3.5 Age variation in bony characters of bill and skull

To examine the ontogenetic development of the foraging apparatus of the American Oystercatcher, I compared the skulls and bills of first-year, second-year and adult birds. Unfortunately, only two first-year and three second-year specimens were available, although 21 adults were examined. The skulls were examined visually for obvious morphological changes with age. Measurements of the dorso-ventral thickness of the tips of the rhamphothecae were made with Vernier calipers held approximately 1 - 2 mm from the distal extremity, where the rounded edges of the tip joined the shaft of the rhamphotheca.

Radiographs were taken of the lower mandible and skull of a specimen of first-year, second-year and adult male from both dorsal and lateral aspects. The X-rays were made for stereo viewing. This provides a clearer, three-dimensional picture of the skull, which is useful in pinpointing variation in bone density. The radiographs were taken with a General Electric Rotating Anode X-Ray tube, Model MBN 1.0-2.0. The exposure was set at 0.6 s at 100 ma and 45 KVP.

3.6 Prey characteristics

3.6.1 Density

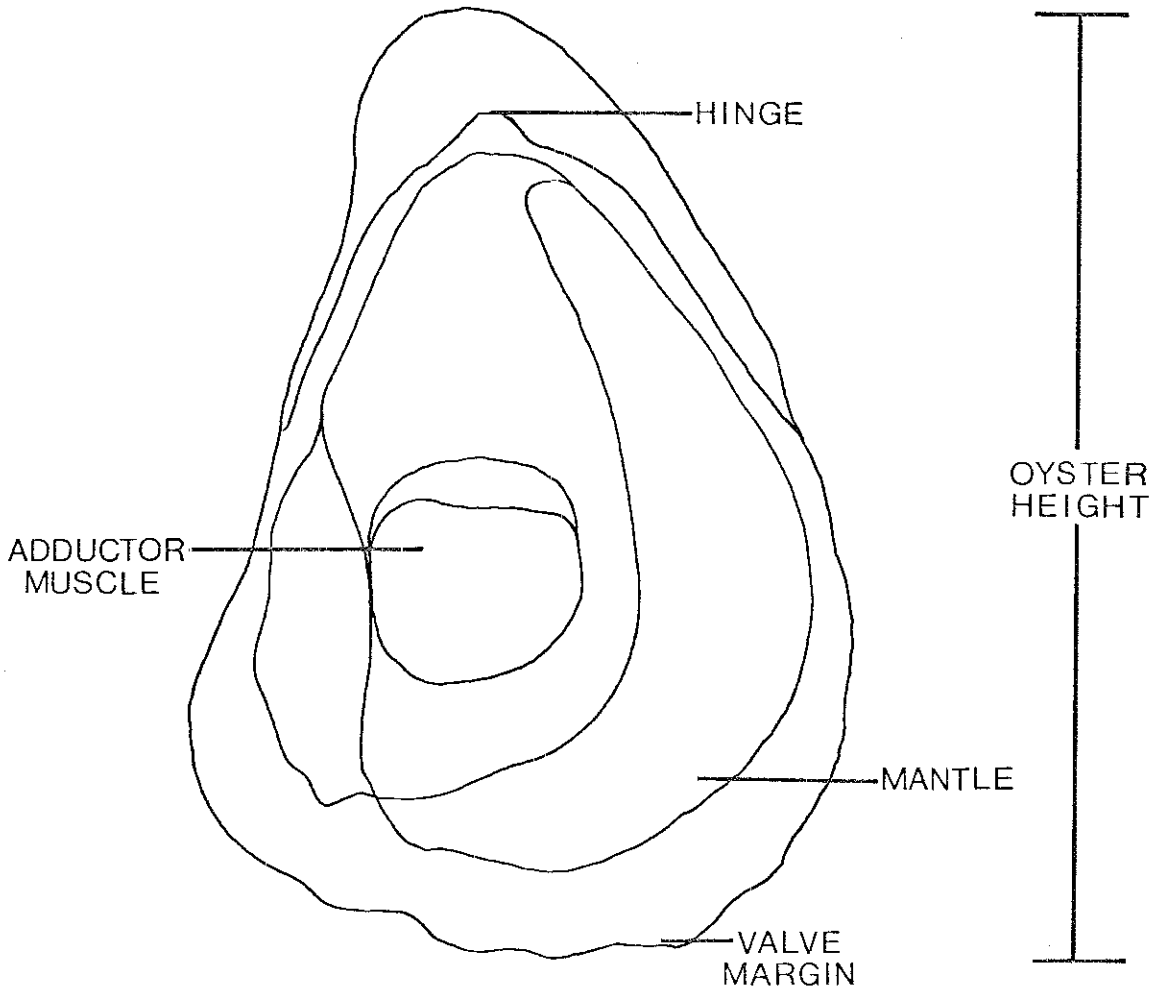
I subdivided the oyster bed into three separate microhabitats, according to location and oyster density (see Figs. 3 and 4). These areas are:

1) the top of the main bars
2) the edge of the main bars
3) the islands

I sampled randomly within each of the microhabitats (top, edge and islands) by tossing a 1/16 m^2 square on the surface, and measuring and counting all the oysters in the square. Oyster shell height (Fig. 5) was measured using a ruler accurate to 1 mm. Iwenty-four samples were taken on each of the top and edge of the oyster bed, and 16 samples were taken on the islands.

Oysters were sampled at the end of the study period, and the early February population was estimated by adding the estimated natural mortality for the month of February (see Dame 1976) to the sampled estimate of density. The number of oysters eaten by the birds per m^2 during the month of February was then added to this total.

Figure 5. American Oyster (Crassostrea virginica) after the removal of the right valve (modified from Galtsoff 1964).


HINGE
ADDUCTOR
MUSCLE
MANTLE
VALVE
MARGIN
OYSTER
HEIGHT

3.6.2 Oyster height and volume

Oysters were allocated to 5 mm size classes according to height. They were then shucked and the volume of their flesh determined by water displacement to ± 0.1 ml. The relationship is described by the expression:

$$\text{Log (height)} = 1.61379 + 0.35757 \text{ (log volume)}$$

which provides a good fit of the data ($r = 0.9417$). Using this equation it was then possible to determine the height of oysters eaten from the volume of flesh ingested.

3.6.3 Specific gravity of oysters

Estimations of food intake on the oyster beds were made by flesh volumes ingested. To calculate calorific content, it was necessary to convert volumes to weights. Twelve large oysters (>5 ml) were used. Shucked oysters were gently dried with tissue paper, then weighed to the nearest 0.001 g on a Mettler balance. Volumes were determined by water displacement to the nearest 0.5 ml, and specific gravities were determined from the expression:

$$\text{Specific gravity} = \text{weight (g)/volume (ml)}$$

The specific gravity of oyster meat was 1.07 ± 0.009 g/ml which is the same value determined by Drinnan (1958b) for cockles (*Cerastoderma* sp).

3.6.4 Calorific content of oysters

Dame (1972a,b) determined that the dry weight of oysters is 16.6% of wet weight, and that oysters contain 5066 cal/g dry weight. His values are used in this study.

3.7 Collection of foraging data

I arbitrarily selected and observed actively hunting birds for 5 min periods with a 20x telescope. If, during the observation period, the bird preened excessively, rested, became sluggish or alert for more than a few seconds, I terminated the observation. Unmarked birds were difficult to follow during observations and observer fatigue became a definite liability beyond the 5 min period. Several colour-banded birds were watched for longer periods (37 to 76 min) to give an indication of the patterns of feeding and resting for individual birds.

During observations, an electronic metronome sounded at 10 s intervals, prompting me to record the relevant behaviour over the previous 10 s with coded symbols. Each bird was aged and the time of observation and the microhabitat in which the bird was feeding was recorded.

3.7.1 Measurement of tactical parameters of foraging

Step rate was defined as the number of steps taken in 10 s and was recorded to the nearest 0.1 s with a stop watch immediately prior to the 5 min observation period.

A peck was defined as the touching of the oyster bed with the tips of the mandibles. At each sounding of the metronome, I recorded the number of pecks occurring in the previous 10 s. Peck rate was later calculated over the entire 5 min period by averaging the number of pecks within 10 s blocks in which no other behaviour was noted.

A stop watch was used to ascertain handling times of prey to the nearest second. Timing commenced with the dart-probe (see p. 74) at a prospective prey item and ended when the bird commenced searching for another oyster. This caused some minor overestimation of handling time, but was necessary because the birds sometimes took long pauses which gave the impression that they were finished with a prey item, only to continue extracting flesh shortly thereafter.

If the bird made an unsuccessful attempt to open an oyster, the "giving-up time" was the time from the initial stab at the oyster until the bird began hunting for another prey item. However, the birds frequently made brief (0-3 s) attempts to open oysters. For ease of data recording, I recorded the giving up time only when a bird made an attempt lasting for a minimum of 3 s.

During the opening and ingestion of an oyster, the birds frequently "paused". A pause consisted of lifting the head and looking briefly around before continuing to either force open the oyster or remove particles of flesh. A pause usually lasted 1-2 s. I defined the disabling time to be the time from the initial dart-probe to the first pause. This is based upon the assumption that the bird did not pause until the oyster was sufficiently incapacitated and was unable to close the valves firmly during the pause.

Usually, unless an oyster was small, it was extracted from the shell in more than one piece, herein referred to as a "bite". By gauging the size of the bite, using the dimensions of the oystercatcher's bill, I allocated all bites into one of the four size categories described in Table 2. In the field, I used additional information to assist in categorizing bite size. The largest bite size (6 ml) was difficult for the birds to swallow. They usually struggled with these large pieces of flesh for several seconds, or were actually forced to drop and re-orient them before swallowing. If I saw a snapping and swallowing motion but was unable to see the prey clearly, I classified it as size category 1 (0.5 ml). Otherwise, I gauged bite size from relative bill dimensions - exposed culmen, bill tip to nares, bill depth and bill width. My capacity to categorize accurately the oyster volume was checked with the help of my field assistant who held pieces of oyster flesh in an oystercatcher bill for 1 - 2 s. Using a 20x telescope at the distance of 25 m, I placed each bite into one of the four categories. I then determined the volume of each piece by water displacement. My accuracy was 89%, with 5% of estimates being too high and 6% too low.

Table 2. Categorization of estimated bite sizes. Mid-point values are used in the text to describe bite sizes.

Category	Estimated Volume (ml)	Mid-point (ml)
1	0 - 0.99	0.5
2	1 - 2.99	2.0
3	3 - 4.99	4.0
4	5+	6.0

Io determine the volume of flesh extracted from each oyster, I added together the sizes of the various bites by using average sizes of 0.5, 2, 4 and 6 ml. I then grouped these volumes into 2 ml prey size classes in an attempt to reduce error (see Goss-Custard 1977b).

Search time is defined as the time taken from the completed consumption of one oyster to the successful attempt at another. Search times were extracted from the data by counting the number of 10 s blocks between prey items. Ihe number of blocks was multiplied by 10 to approximate search time in seconds. If the subsequent oyster was attacked in the same 10 s time block in which the previous oyster was finished, search time was estimated to be 5 s.

Feeding birds were often displaced or chased from prey by other oystercatchers. In such cases, I endeavoured to record the age of the birds involved and the outcome of the interaction.

Oysters become more difficult to open as their gape closes in response to desiccation. Io determine the ability of the birds to open oysters under various conditions, I compared foraging parameters on the tops of the main oyster bars when they were wet and dry. "Wet" oyster bars were either water-covered, partially covered or recently exposed, while "dry" bars had been exposed for some time. The tops of the main oyster bars were somewhat flattened and so were at a nearly uniform state of water coverage. However, because the edge and the islands were sloped, parts of these microhabitats were likely to be at different states of water coverage. Additionally, oysters on the tops are significantly smaller than those on the edge and the islands. Iherefore, the foraging parameters collected on the oyster bar tops are not compared

directly to those on the edge and the islands.

Oystercatchers are expected to vary their foraging technique with oyster density (see Norberg 1977). To compare foraging at various oyster densities, I contrasted feeding on the edge with feeding on the islands. The islands exhibit significantly higher oyster densities than the edge but have roughly the same average size of oyster.

3.7.2 Description of oyster-opening techniques

Casual observation of oyster-opening techniques during the 5 min observation periods was supplemented with more detailed description, which was recorded verbally on a portable tape recorder. A Super 8 movie film of 15 min duration was taken from a blind near the beds to provide further information on foraging behaviour. Oyster-opening behaviours were recorded using the terminology of Norton-Griffiths (1967), which was developed to describe the feeding techniques of the European Oystercatcher.

3.8 Rate of gain of calories (RGC)

The rate of gain of calories from each prey size was calculated for adults and immatures. Ihe RGC takes into consideration the energy expenditure in acquiring prey as well as calorific intake from the prey, thus producing a realistic indication of the value of the prey to the predator. RGC is calculated as follows:

RGC=(calories intake-calories expended)/ handling time

where

calories intake = V * SG * DW * cal/g

calories expended = 3 * SMR * HI

HI = handling time

V = volume oyster flesh

SG = specific gravity of oyster flesh

DW = dry weight = (wet weight * 0.166)

cal/g = calorific content of 1 g dry weight of oyster flesh (= 5066 cal).

SMR = standard metabolic rate of American Oystercatchers at $0^{o}C$ (measured in cal/s)

3.9 Prey choice

Electivity (E) (Ivlev 1961) is used as a gauge of "choice" by a predator, and is calculated as follows:

$$E = r/p$$

where

r = percentage of a particular prey size in the diet

p = percentage of that prey size in the environment

Values of E greater than 1 indicate that the predator was preferentially selecting prey of that size, whereas E values of less than 1 indicate that the predator was avoiding this prey size.

3.10 Data analysis

Analysis of data was carried out using the Statistical Analysis System (SAS Institute, 1979) and Statistical Packages for the Social Sciences (Nie et al. 1975). Unless otherwise indicated, means are given plus or minus their standard errors. Probabilities of less than 5% ($P < 0.05$) are considered significant, and significance levels are designated as follows: $^{*} = P < 0.05$, $^{**} = P < 0.01$, $^{***} = P < 0.001$, n.s. (not significant) = $P > 0.05$.

4 RESULTS

4.1 Use of the study area by American Oystercatchers

At present, Chincoteague is the northern extreme of the wintering range of the American Oystercatcher, although birds are found as far north as Connecticut in the breeding season (Finch 1976). Birds which breed north of Chincoteague move south in winter, and some of these probably winter in the Chincoteague area. Some birds breeding near Chincoteague appear to move south. I colour-banded 35 adults and 8 first-year birds 15 km south of Chincoteague in the summer of 1978, and saw only three of the adults and four of the first-year birds on my winter study area, located west of Chincoteague, during the study period (Jan. - Mar. 1979). The wintering areas of the migrants are unknown. Thus, in winter the Chincoteague oystercatcher population consists of some local birds and some birds which summer north of Chincoteague.

Christmas bird counts over the period 1970-1980, published in American Birds, recorded an average of approximately 200 oystercatchers in the Chincoteague area. In 1978, 197 were reported on the Christmas count, while approximately 50 birds were discovered north of Chincoteague, due to an exceptionally mild autumn. These latter birds apparently arrived in the Chincoteague area in early January, when the weather cooled, as an increase in oystercatcher numbers was noted at that time.

Some families of European Oystercatchers have been found to remain together for up to 43 weeks (Norton-Griffiths 1967). In December 1978, a family of American Oystercatchers was still together on the study area. The two young birds would then be approximately 20-25 weeks old. The young were observed begging for food from their parents but they were not seen to be fed. The family fed and roosted separately from a flock of oystercatchers in the area. By early January, the family appeared to have joined the flock, and no obvious family ties were observed until late February, when pair formation became evident. Therefore, some first-year birds in the population under observation were newly independent.

In late February there was an influx of birds from the south. Birds within the flock began to form pair bonds, and some territorial displays began as pairs started to claim breeding and feeding territories. By early March most of the wintering flock had either dispersed into breeding pairs or had migrated north. Three pairs of birds had claimed most of the oyster bed as feeding territories, and were vigorously defending them against the remaining adults. Immature birds, however, were sometimes tolerated. A group of 8-10 immature birds fed on the oyster bed, but had left the area by the middle of March. In 1978, despite frequent disturbance by breeding birds, two immature birds used the oyster bed and nearby salt marsh to feed until late April, but were not seen after this time. The whereabouts of immature birds during the breeding season is unknown.

4.1.1 Daily pattern of activity

The flock of 200-300 birds which fed on the Queen's Sound and Shelly Bay oyster beds used Egg Marsh Island, a small, salt marsh island to the north of the study area, as a night roost (see Fig. 2). At sunrise, small groups comprised of 1-30 birds arrived on the oyster beds from the night roost. If the beds were covered by the tide, the birds landed on the high water roost (see Fig. 2). They remained there or on the oyster beds until sunset, when they returned to the night roost, again in small groups. A disturbance near sunset was often enough to send the entire flock to the night roost together.

The total number of birds using the study oyster bed varied daily. The largest number of birds to feed at one time was 115 while the average daily maximum number of birds was 47. The number of birds on the oyster beds varied during the day as birds flew across the bay to feed on other oyster beds, and moved because of disturbances. When disturbed, all of the birds feeding on and around Shelly Bay took flight in a loose flock and circled the Bay before breaking up and returning to each oyster bed. I do not know if the birds returned to the beds from which they had flown, although the total number of birds using the beds before and after disturbances tended to remain approximately constant. By recording observations of colour-marked birds, I determined that individual birds do not use the same oyster bed every day.

The birds do not appear to feed at night. The diurnal pattern of movement to and from the beds at the beginning and end of each day indicates that they are not utilized in the dark. Five night visits to the beds (three in January and two in February) were made to discover if

night feeding was occurring. I could neither hear nor see any activity on the oyster bed on any of these visits. It seems unlikely that oystercatchers would forage on mudflats or salt marsh during the night, as they ignored these habitats during the day and fed entirely on intertidal oyster beds. Therefore, I conclude that American Oystercatchers wintering in Shelly Bay obtained their entire daily food intake during daylight from intertidal oyster beds.

4.1.2 Effects of weather

The birds avoided strong winds by feeding predominantly on the leeward side of each oyster bar which provided a good windbreak when the tide was low. At higher tide levels, wind created waves on the usually calm Bay, which delayed the arrival of the birds onto the oyster bed from the high tide roost. The birds were unable to land on the top of the oyster bars while large waves were moving across them. As the water level dropped, the broken, uneven surface of the oyster bars disturbed wave action and made the water over the oyster bed calmer than the surrounding areas. This allowed the birds to feed.

From February 11 - 14, 1979, each oyster bar was fringed with ice, forcing the birds to feed on the tops of the bars, which were not ice-covered. From February 14 - 18, the beds were completely frozen over with the exception of a patch of mud and oyster bar, measuring approximately 5 m x 10 m. When the low tide permitted, a few birds at a time fed in this patch, while the remainder of the flock roosted nearby. A group of up to 40 Ring-billed and Herring gulls waited at the edge of the patch, and stole the majority of prey items from the oystercatchers

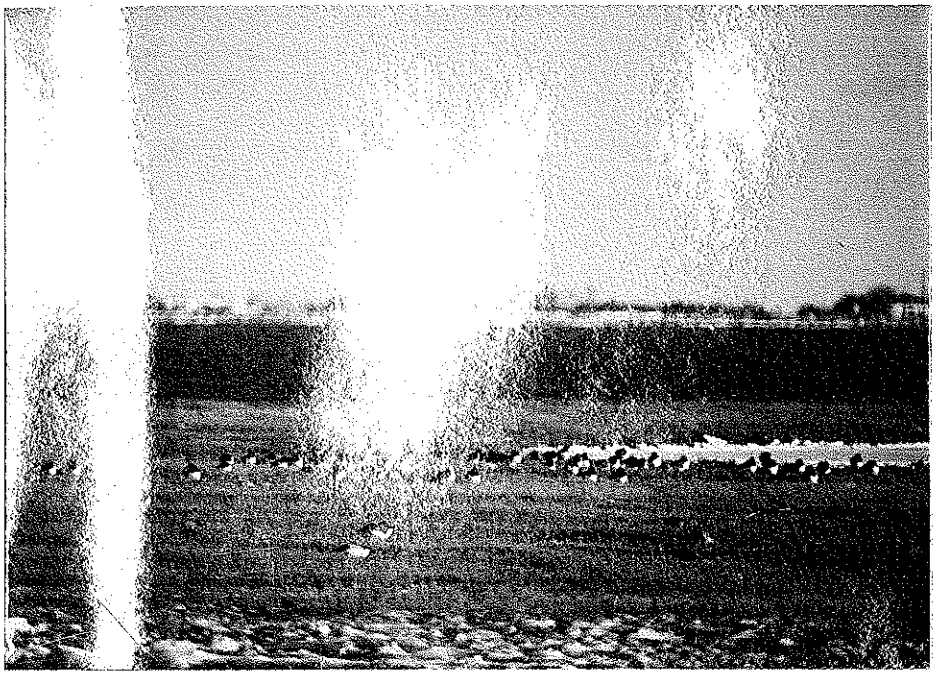
as they were obtained. No indications of starvation were observed, and inspection of the high water roost following the cold spell did not reveal any dead birds. However, they may have been stressed by the cold. During this period, the birds frequently stood on one foot in the cold water while feeding, a behaviour which was never observed in warmer weather. Many birds were seen flying with their legs under their belly instead of extended behind, under the tail. These behaviours probably minimize heat loss through the legs and thus conserve energy in very cold conditions.

4.1.3 Tidal pattern of use of oyster beds

During daylight hours when the beds were water-covered, and hence unavailable for feeding, the flock roosted on the high water roost indicated on Fig. 2 and Plate 1. There were other roosts located around Shelly Bay and Queen's Sound which were used by flocks feeding in different localities. Generally, the majority of birds using this roost fed on the study oyster bed. This roost appeared to be selected because it was dry and close to the oyster bed. When a spring tide flooded the high tide roost, the flock would fly south across Shelly Bay in search of other roost sites.

The birds tended to roost close to water. The flock concentrated either along the edge of the island or beside a pond in the middle of the island. They generally avoided tall vegetation and often stood on bare mud. The birds roosted close together, 100 birds covering a patch approximately 5m x 10 m. The flock roosted more tightly in cold weather. While on the roost, birds preened occasionally but spent most

Plate 1. The high water roost.



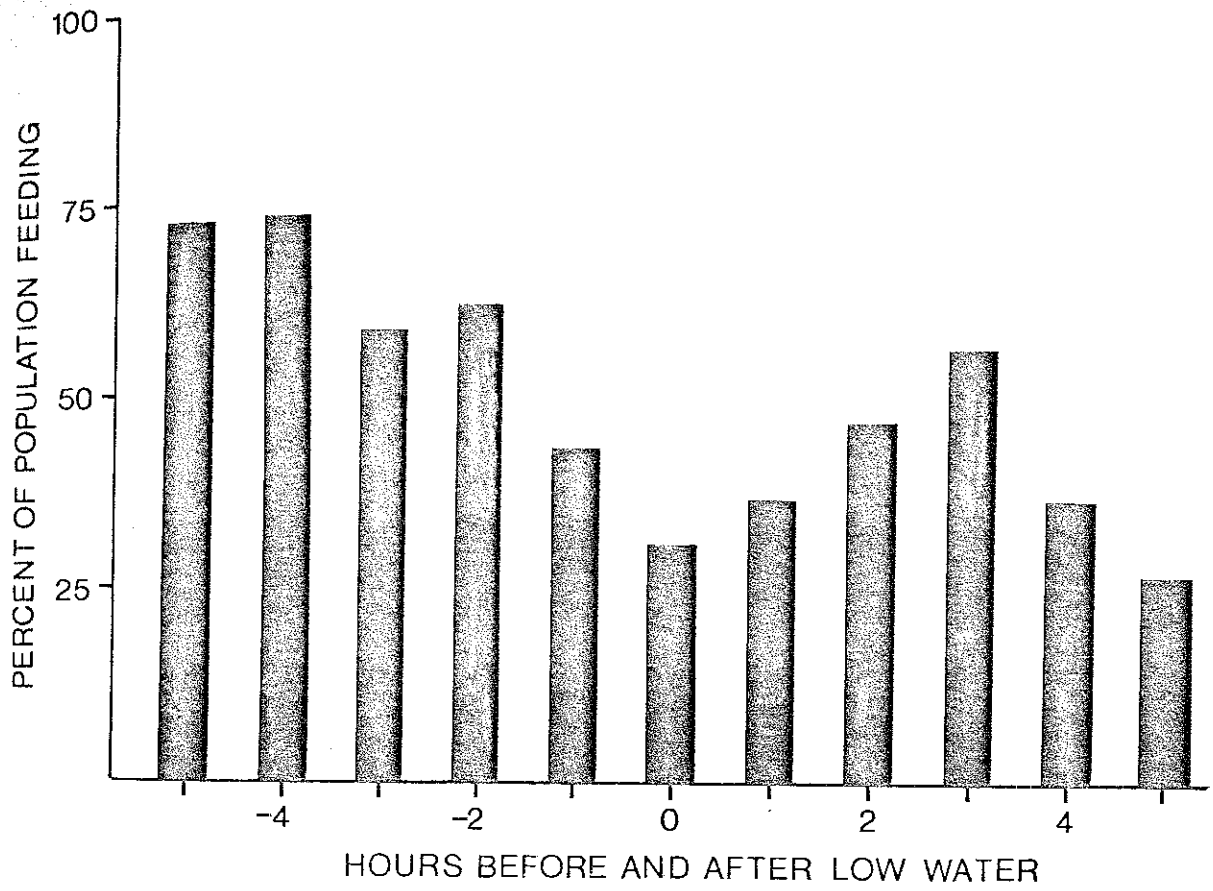
of their time standing on one leg with their bill tucked beneath their scapulars to conserve energy (Plate 1).

On the ebb tide, small groups of one to five birds left the roosting flock and circled over the covered oyster beds. No observations were made of birds landing in water which was too deep to allow them to stand. However, birds frequently landed briefly, but returned to the roost if the water was too deep for them to feed properly.

Attempts by birds to begin feeding before prey was available is indicative of a strong motivation to feed. If young birds feed less efficiently than adults, they might be expected to arrive on the oyster beds as soon as they are available and leave them last. A significant ($P = 0.019$, $n = 12$) Binomial one-tailed test (Siegel 1956) indicates that immature birds tend to use the beds sooner on a falling tide and later on a rising tide than do the adults. This might indicate that adults are not under the same energetic stress that is experienced by the younger birds.

The first few birds to arrive usually landed in water that was belly-deep, and began feeding immediately. The number leaving the roost increased rapidly as soon as the birds were able to feed so that most of the birds were feeding as the tops of the bars became visible above the falling tide. Figure 6 shows the pattern of use of the beds by the oystercatchers over the tidal cycle. The large peak early in the falling tide is probably caused by hunger and optimal prey availability. Oysters are most vulnerable to predation as they are being uncovered by the tide because they are gaping then after several hours of submersion.

Figure 6. Mean percentage of birds feeding at hourly intervals throughout the tidal cycle. Values represent the mean percentage of the maximum number of birds seen feeding each day.


100
75
50
25
PERCENT OF POPULATION FEEDING
-4
-2
0
2
4
HOURS BEFORE AND AFTER LOW WATER

The birds fed during the falling tide for various lengths of time before resting. Most flew to rest on the loafing area, a particularly high oyster bar located to the SE of the bars under observation (Figs. 2 and 3). They gathered there in a loose flock, using the bar as a windbreak on cold and windy days. Some birds, however, rested on the bars upon which they were feeding. They simply walked to the top of the dry, exposed bar, where they stood or slept until they were ready to begin feeding again. Observation of several birds for prolonged periods of time revealed that the birds alternated periods of resting and feeding.

Figure 6 shows the general pattern of use of the beds, with less feeding being attempted at low water than on a rising or falling tide. Similar patterns have been reported by Dewar (1915), Drinnan (1957), Davidson (1967), Baker (1969), Goss-Custard et al. (1977a). At low water, much of the oyster bed is exposed and dry, and the birds may be resting because of limited food availability at this time. The rising tide floods and covers large areas of oyster bed, creating another peak in feeding activity.

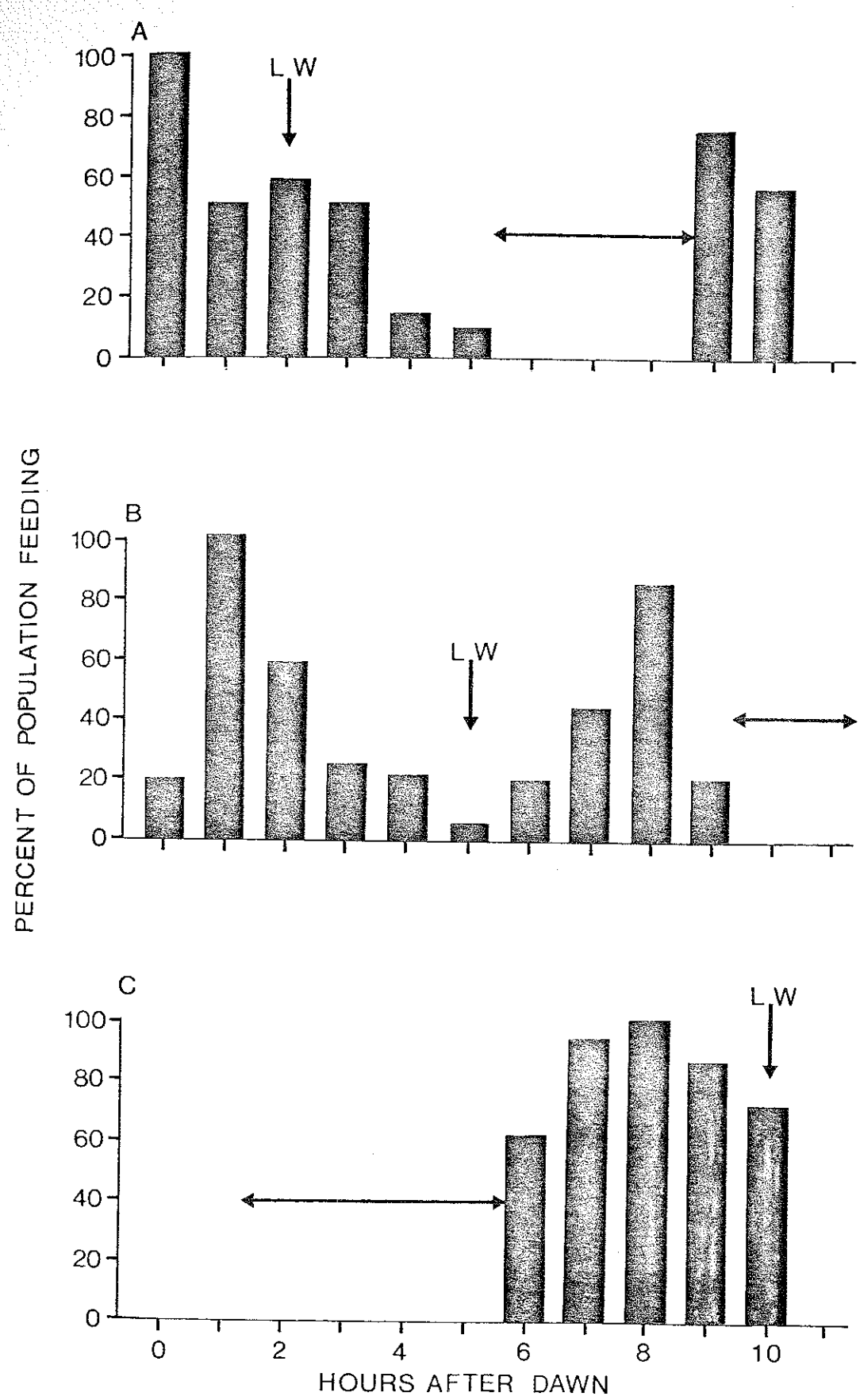
The pattern demonstrated in Figure 6 was derived from the average of all observations. The pattern of use of the beds on a daily basis is somewhat dependent upon the timing of the cycle of the tide. Figure 7 shows the pattern of use of the beds when low tide occurs in the morning, near noon, and in the late afternoon. The birds adjusted their daily routine to the time available to them and sometimes fed in large numbers at low tide in the early morning - presumably because they had not fed previously for at least 12 h.

Figure 7. Percentage of birds feeding at hourly intervals throughout the tidal cycle with low water (L W) occurring at different times of day.
Ihe double headed arrows indicate times when the oyster bars were covered by the tide and thus unavailable to foraging oystercatchers.

A. January 22, 1979.

B. February 8, 1979.

C. January 30, 1979. Note that no birds fed on the rising tide early in the day, despite the availability of the oyster beds.


A
B
C
L W
L W
L W
100
80
60
40
20
0
0
2
4
6
8
10
PERCENT OF POPULATION FEEDING
HOURS AFTER DAWN

The birds began to move to the high water roost when the rising tide covered most of the the oyster bars, making them unavailable for foraging. They used the loafing area described above as a temporary staging area before moving to the high water roost. Similar behaviour has been noted by Drinnan (1958a), who called these groups of birds "intermediate sand flocks", as did Davidson (1967) and Baker (1969). Birds usually moved from the resting area to the high tide roost as a flock. A few birds (notably immatures - see p. 39) fed until the beds were completely covered. These birds flew directly to the high tide roost, where the flock settled for the high tide period. However, there was less of a tendency to feed on a rising tide that had covered the beds, than on a falling tide (Fig. 6). Oysters gape less when first covered by the rising tide than after several hours of submersion by a high tide. Additionally, by the time the tide is rising, the birds had often been feeding for several hours and were less motivated to feed than they were on the ebb tide.

4.1.4 Available time spent feeding

Because of my inability to age birds on the roost, the estimate of the use of the beds by the different age classes is probably only a rough approximation of the true patterns. First-year birds appear to spend more time feeding than older birds, but there are no significant differences between the age classes (Table 1). The low value for second-year birds is probably the least reliable of the estimates because there were far fewer of them than any of the other age classes.

4.2 Comparison of foraging apparatus

Although the bills of young oystercatchers attain adult length within 4 months, they continue to grow in width and height for more than 2 yr (Baker 1975). It is therefore important to investigate attributes of both bill and skull morphology of the various ages of oystercatcher to determine what effect, if any, these differences might have on the functional capabilities of the birds.

Recent findings in biomechanics (Kummer 1972) reveal that bone is stronger at sites where the greatest stresses occur. Currey (1968) observed that the strength of bone is at least partially determined by the density of the bone in that region. Dense bone, which has high energy absorbing capacity (Buckland-Wright 1978), is important for resisting forces created by the activity of the animal. Because dense bone is less likely to fracture (Currey 1968), birds with denser bone in areas of stress are able to withstand greater stress than birds showing lower density of bone in that region. This will tend to modify the capabilities of the respective birds by setting different limits to their activities. These limits are of special interest to this study, because of their possible value in determining age-related foraging capabilities.

The rhamphotheca consists of keratinized epithelium overlying the bony core of the bill. It is the part of the bill which comes into contact with the hard shell of the oyster. The bill tips of the American Oystercatcher are laterally flattened to a great extent, and are almost blade-like distally. They are modified to stab between the gaping valves of a bivalve mollusc, to withstand lateral stress during

levering, to chisel flesh from the shell and to grasp the loose flesh for withdrawal and subsequent swallowing. Plate 2 shows the rhamphothecae and Table 3 the dimensions of the bill tips of the three age classes. Only one male and one female specimen of first-year and three specimens of second-year male birds were available for comparison. Therefore, while these results are suggestive, they must remain tentative until further specimens are examined. Norton-Griffiths (1967), however, also noted that young European Oystercatchers have narrower bill tips than adults. The entire rhamphotheca of the first-year American Oystercatcher appears to be narrower than that of older birds (Plate 1). This was also noted by Bent (1929) who described the bill of first-year American Oystercatcher as being noticeably more slender than that of the adult.

The tips of the bill are used to chisel flesh from the oyster shell. The bills of first-year birds are narrower dorso-ventrally, the broad spatulate lower mandible of the adult is well-suited for chiselling. Second-year birds appear to be intermediate in bill tip size between those of first-years and adults. There is a wide range of sizes of bill tips among second-year birds, even within a sample of only three birds (Table 3).

Figure 8 is a diagrammatic representation of an oystercatcher skull showing areas of the skull which are mentioned below. The terminology of Baumel et al. (1979) is used to label specific bones. The skull of an adult is more robust than that of an immature (Plate 3). The pre-orbital processes are larger and the frontal bone (Os frontalis) is heavier. The frontal bone of the American Oystercatcher allows light

Plate 2. Rhamphothecae of (A) adult, (B) second-year and (C) first-year American Oystercatchers.

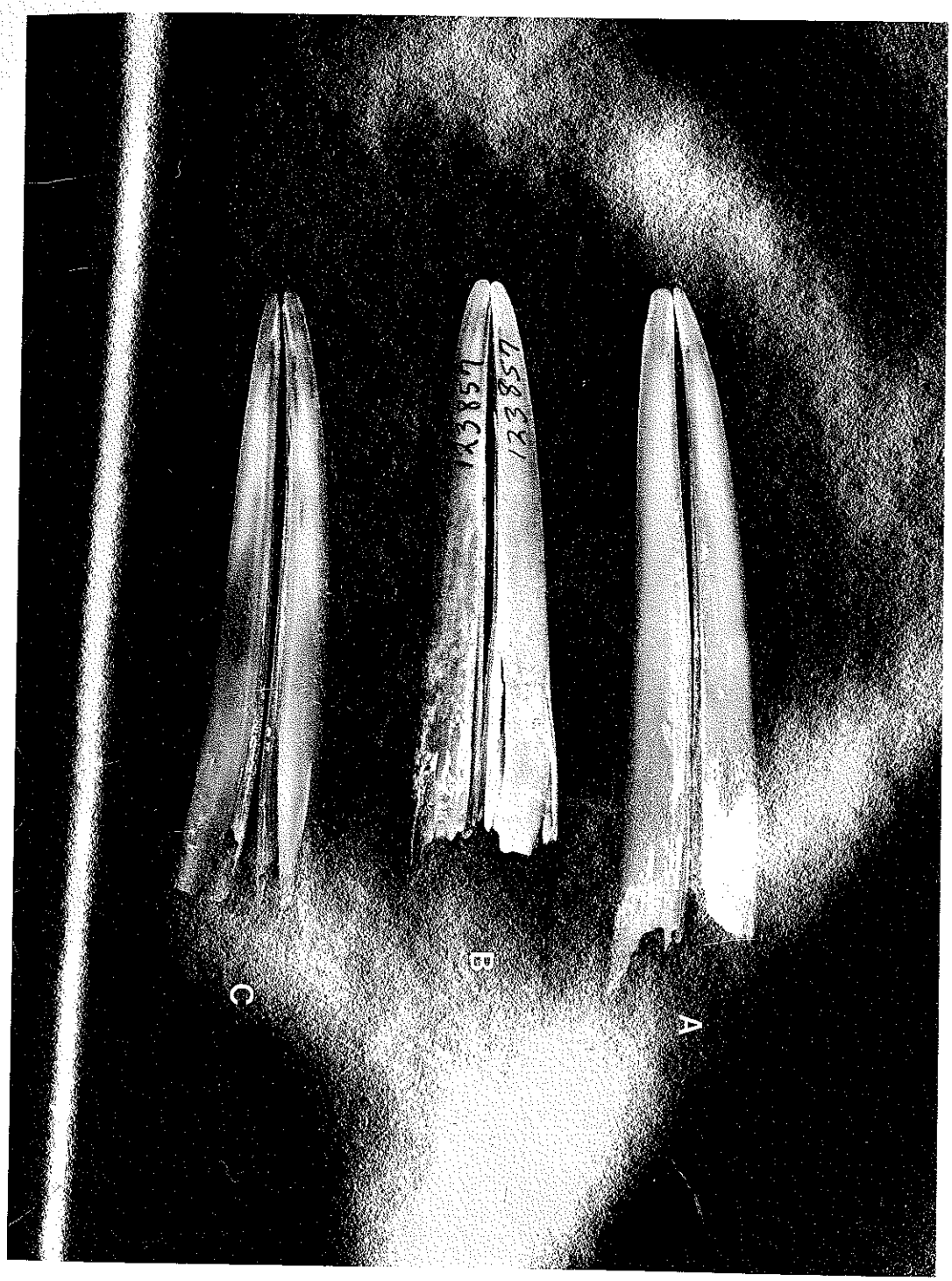

A
B
C

Table 3. Mean dorso-ventral height of the bill tips of first-year, second-year and adult American Oystercatchers.

Age	Height* (mm)	
	Mean ± S.D.	n
First-year	3.40 ± 0.10	2
Second-year	4.57 ± 1.00	3
Adult	4.38 ± 0.50	21

* The tips of both mandibles were measured separately and added together. Data for males and females are pooled.

to pass through it in the form of a translucent patch on either side of the medial ridge. These patches shrink with age, likely because of ossification.

On the X-rays (Plates 3 - 11), whiter areas on the skull and mandible indicate denser bone. The most noticeable difference in the skulls is the increasing ossification or density of bone with age. The Os frontalis is particularly notable in this regard. In families like the Haematopodidae, which show kinesis (Bock 1966), the Os frontalis is the region of the nasal frontal hinge (Plates 4 and 5). This is the weakest area on the upper jaw, and the point which limits the degree of stress put on the upper jaw (Bock 1966). Therefore, because denser bone is equated with greater strength (Kummer 1972), the adult skull should be able to withstand greater stress during foraging.

The Os nasale is more densely ossified in the adult bird. This bone is likely to be of importance in levering and chiselling, as it supports the Os premaxillare dorsally (Plates 6 and 7). The Os premaxillare is generally more densely ossified in older birds, with particularly dense areas occurring laterally (Plates 4 and 5). Again, there is increasing density of bone with age, and the dense bone appears to continue further both distally and proximally in the adult. When an oystercatcher levers laterally, the fulcrum is the posterior edge of the oyster valve. The lateral edge of the Os premaxillare is the part of the bill which underlies the portion of the rhamphotheca which will be in contact with the fulcrum, and hence will receive much of the strain of the leverage. The adult is thus equipped with a more robust lever which allows for more powerful levering.

Figure 8. Diagram of the skull and mandible of an American Oystercatcher showing the location of bones named in the text.

A. Os frontalis

B. Os nasale

C. Os premaxillare

D. Proc. mandibulae medialis

E. Os dentale

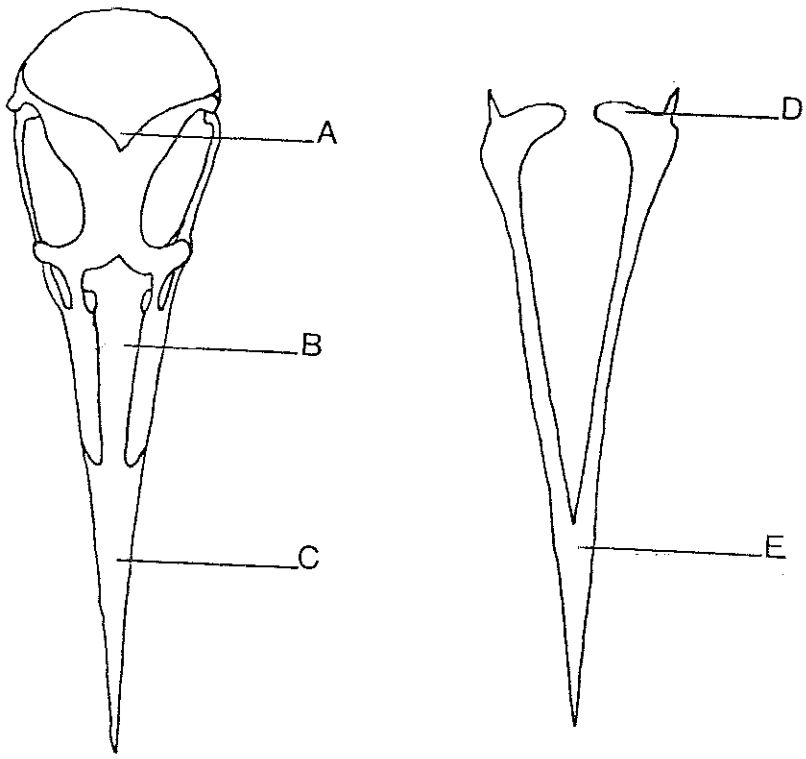

A
B
C
D
E

Plate 3. Dorsal view of the skulls of (A) first-year, (B) second-year and (C) adult American Oystercatchers.

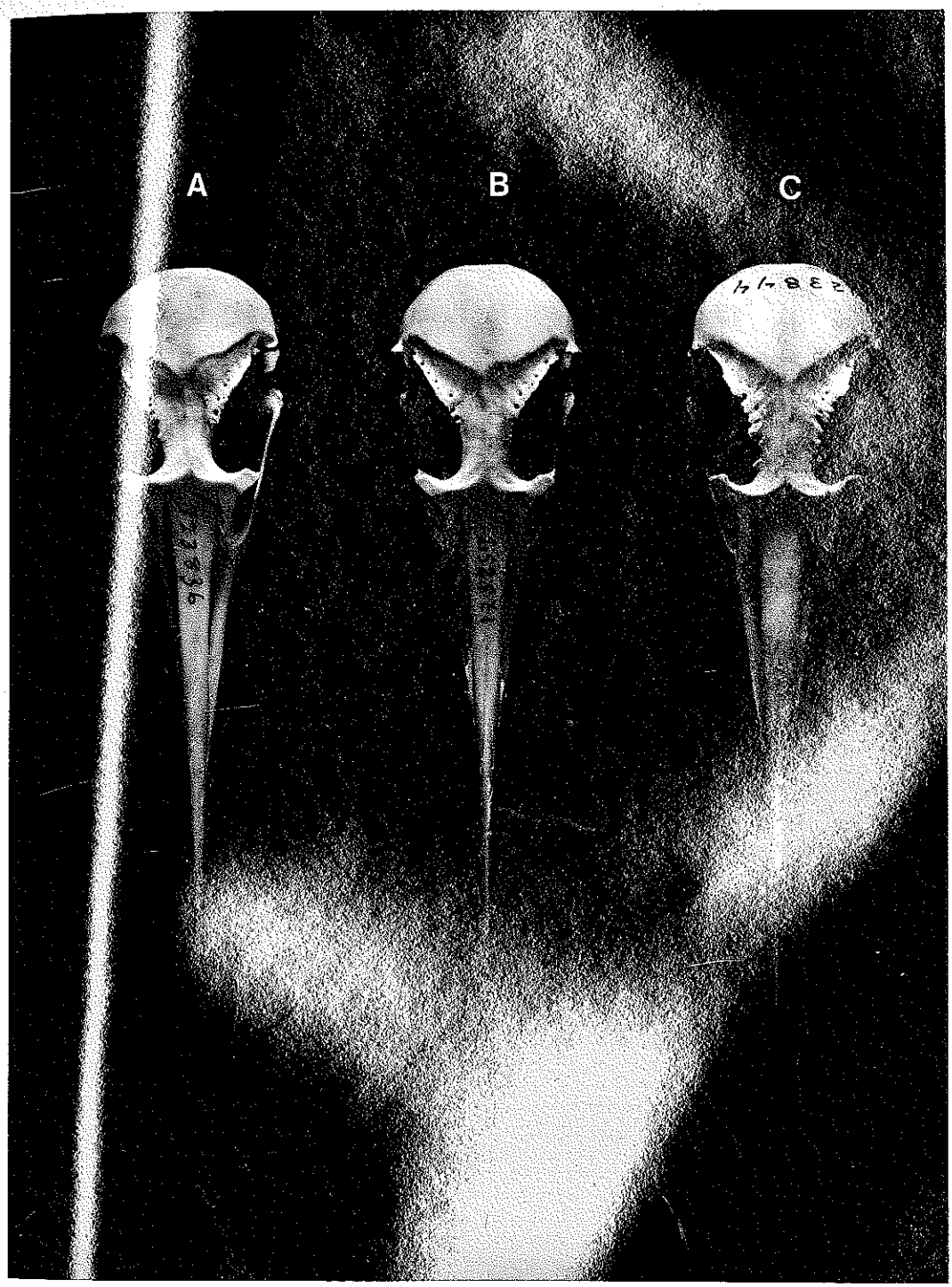

A
B
C

Plate 4. X-rays of the skulls of (A) adult and (B) first-year American Oystercatchers from the dorsal aspect.

A



B

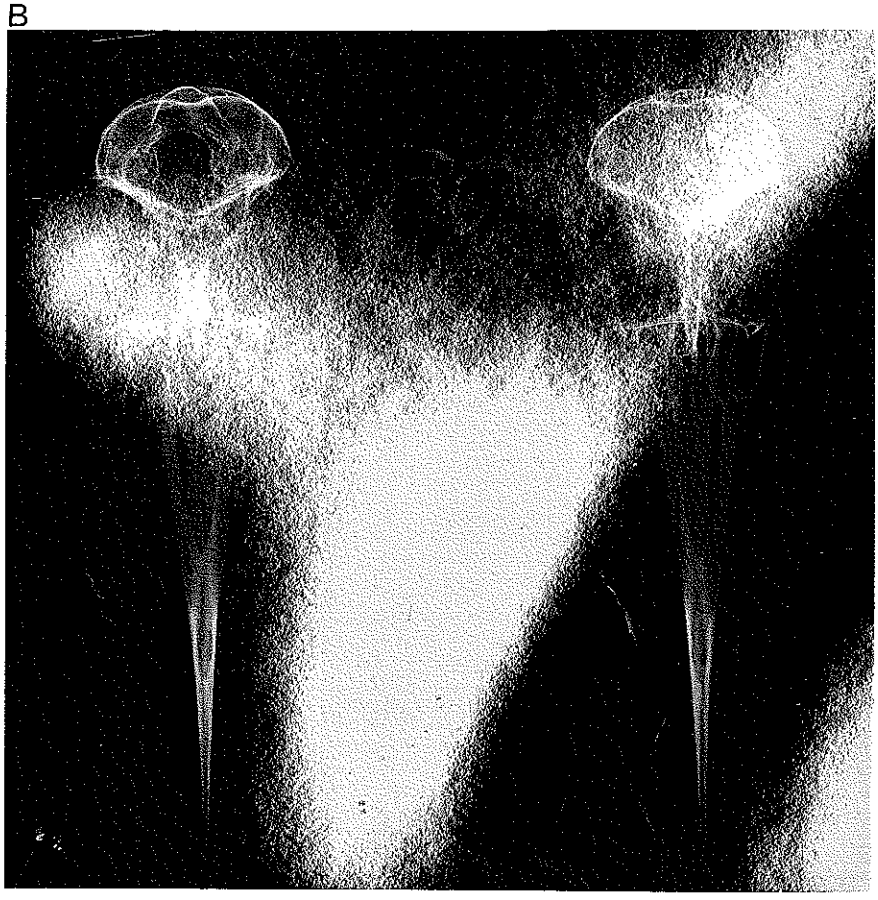


Plate 5. X-rays of the skull of a second-year American Oystercatcher from the dorsal aspect.



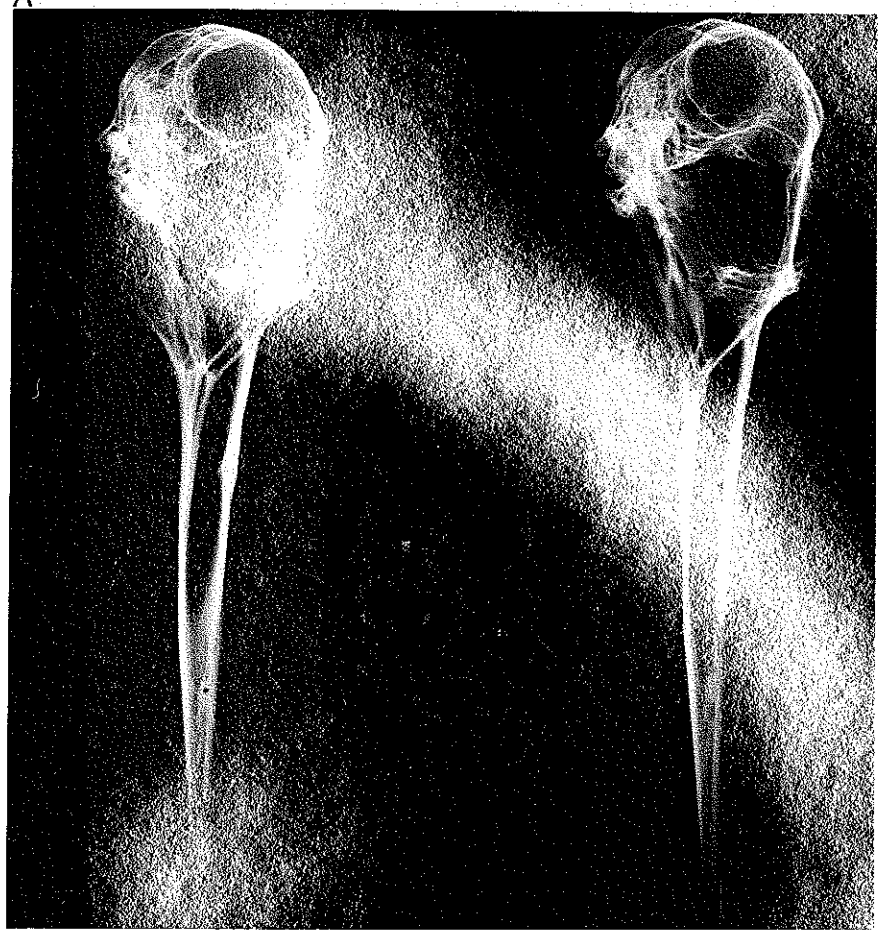
Another area of the adult skull which is more densely ossified is the area of jaw articulation. Greater ossification in this region is probably important in the dissipation of stress created by levering and rotation in both mandibles (Burton 1974). Like the Os premaxillare, the Os dentale (Plates 8 and 9) is more ossified, particularly laterally. As with the upper jaw, these areas of dense bone continue further proximally and distally.

The Haematopodidae have two regions of jaw articulation (Bock 1960). The entire proximal region of the lower mandible, which is the area of jaw articulation, is more heavily ossified in the adult bird (Plates 8, 9, 10 and 11). The fact that the Haematopodidae possess a Proc. mandibulae medialis, which acts as a secondary jaw articulation, is evidence that exceptional stress is put on the primary jaw articulation (Bock 1960). Greater development of the lower jaw articulation will presumably provide greater strength to this region, which would be important in resisting the stresses of leverage and twisting (Burton 1974).

This comparison of the skulls of oystercatchers, even though based on very few specimens, is highly suggestive. Adult birds appear to be generally more robust and are likely to have different capabilities than young birds because of this. Additionally, because adults are heavier, it is likely that they possess greater muscle mass and are stronger than immature birds, which will further improve their foraging proficiency. Thus adults probably can not only lever open oysters more quickly, but also can lever open larger oysters. Both the stage of morphological development and the stage of learning should be considered in the deter-

Plate 6. X-rays of the skulls of (A) adult and (B) first-year American Oystercatchers from the lateral aspect.

A



B

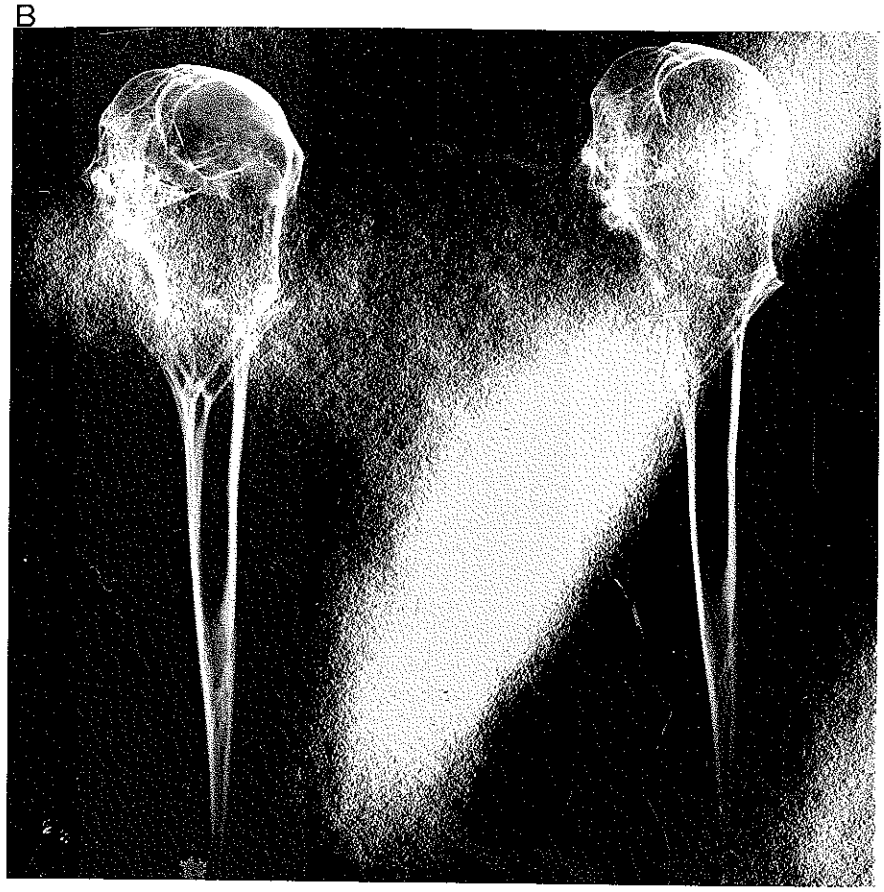


Plate 7. X-rays of the skull of a second-year American Oystercatcher from the lateral aspect.

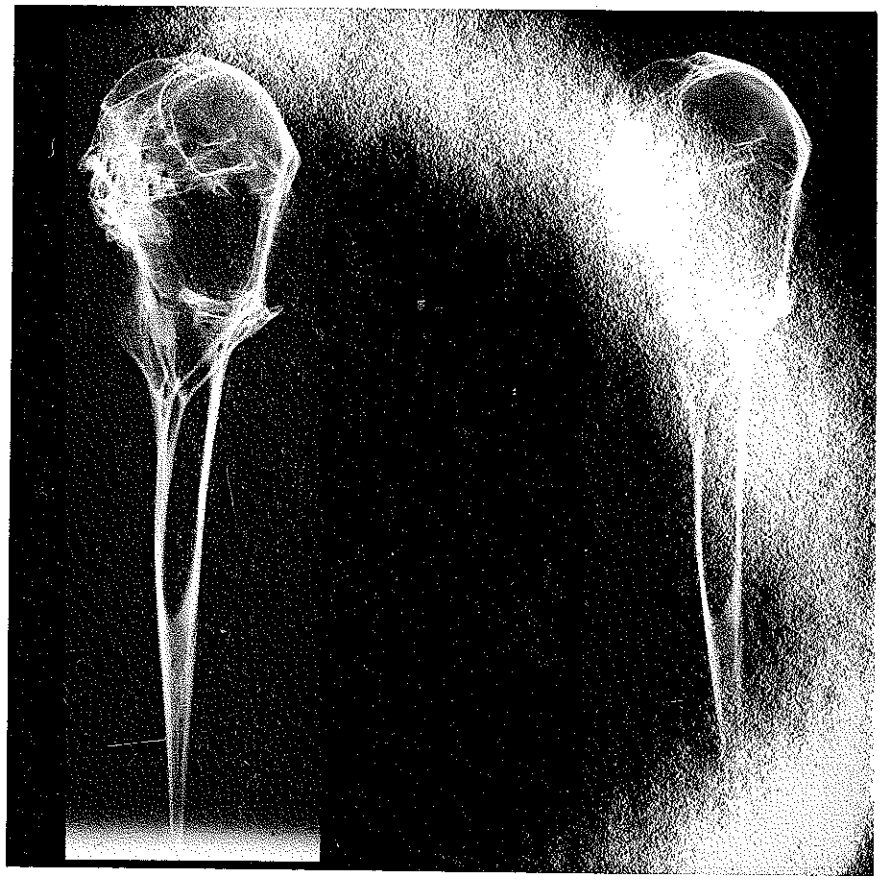


Plate 8. X-rays of the lower mandible of (A) adult and (B) first-year American Oystercatchers from the dorsal aspect.

A



B

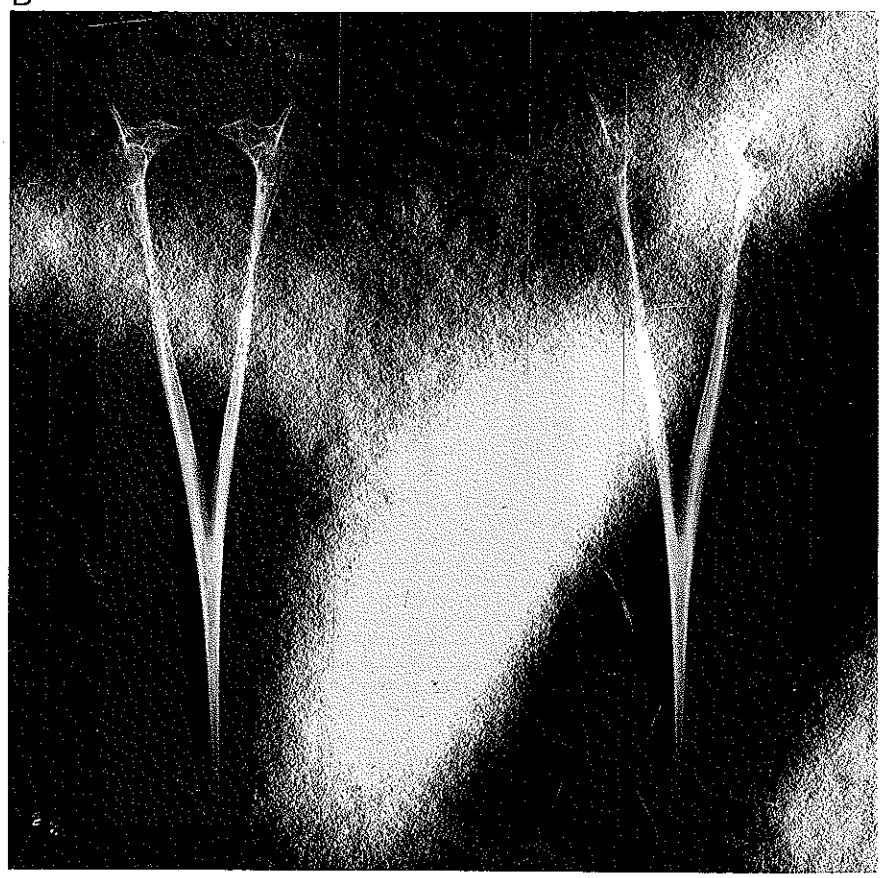


Plate 9. X-rays of the lower mandible of a second-year American Oystercatcher from the lateral aspect.

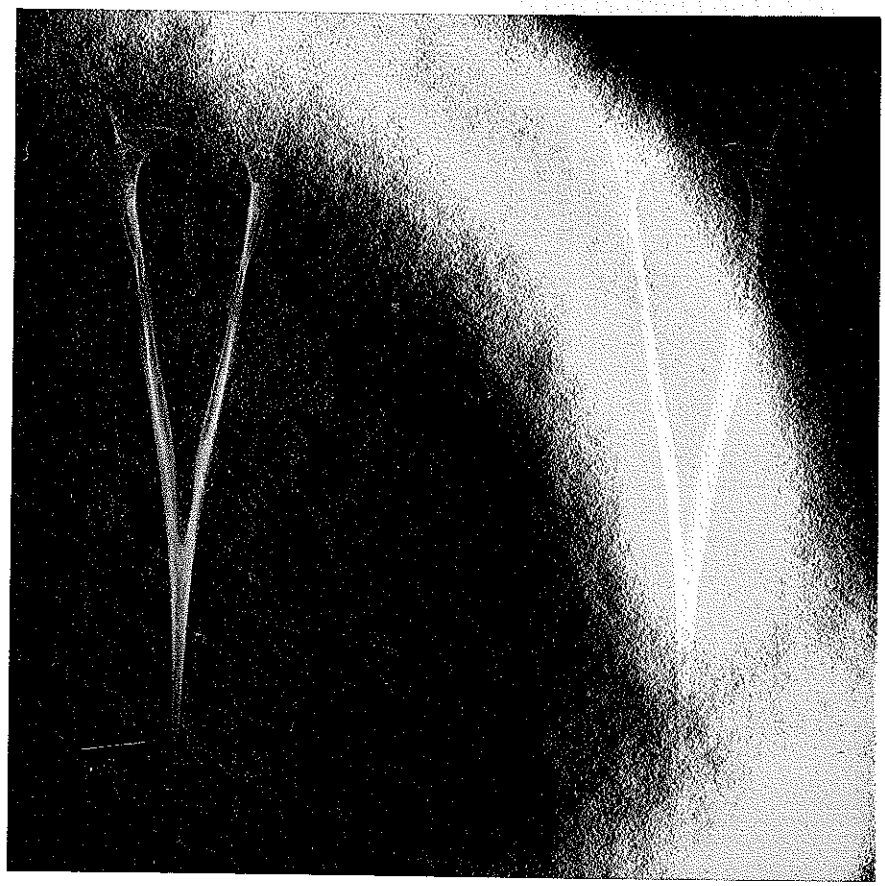
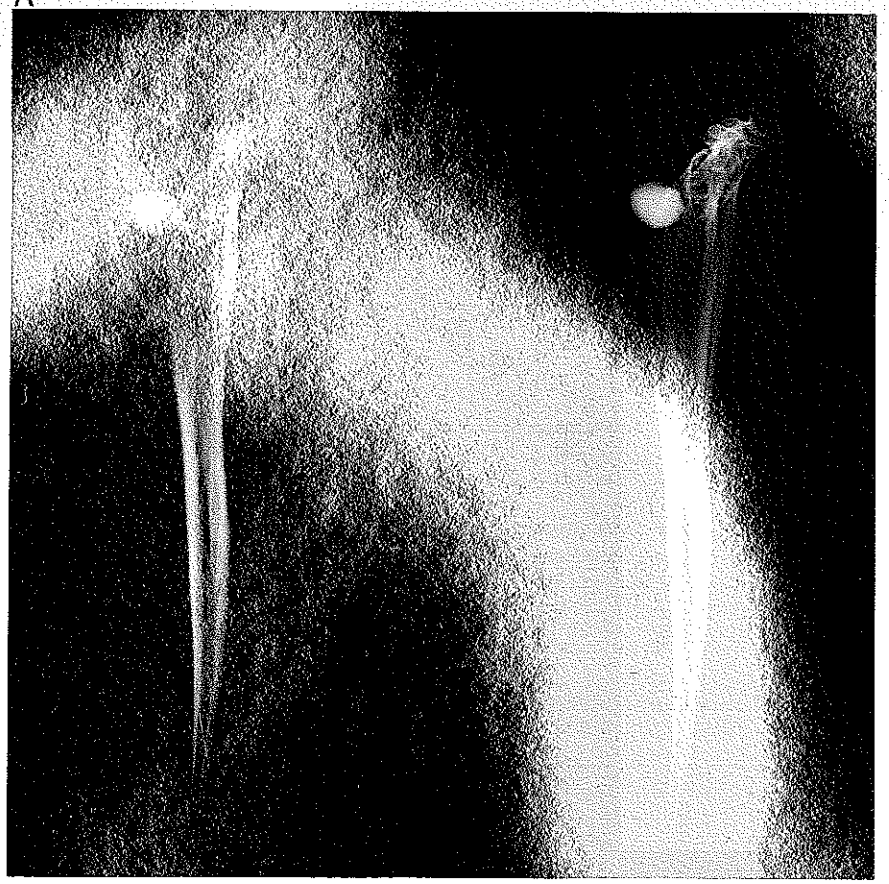


Plate 10. X-rays of the lower mandible of (A) adult and (B) first-year American Oystercatchers from the lateral aspect.

A



B

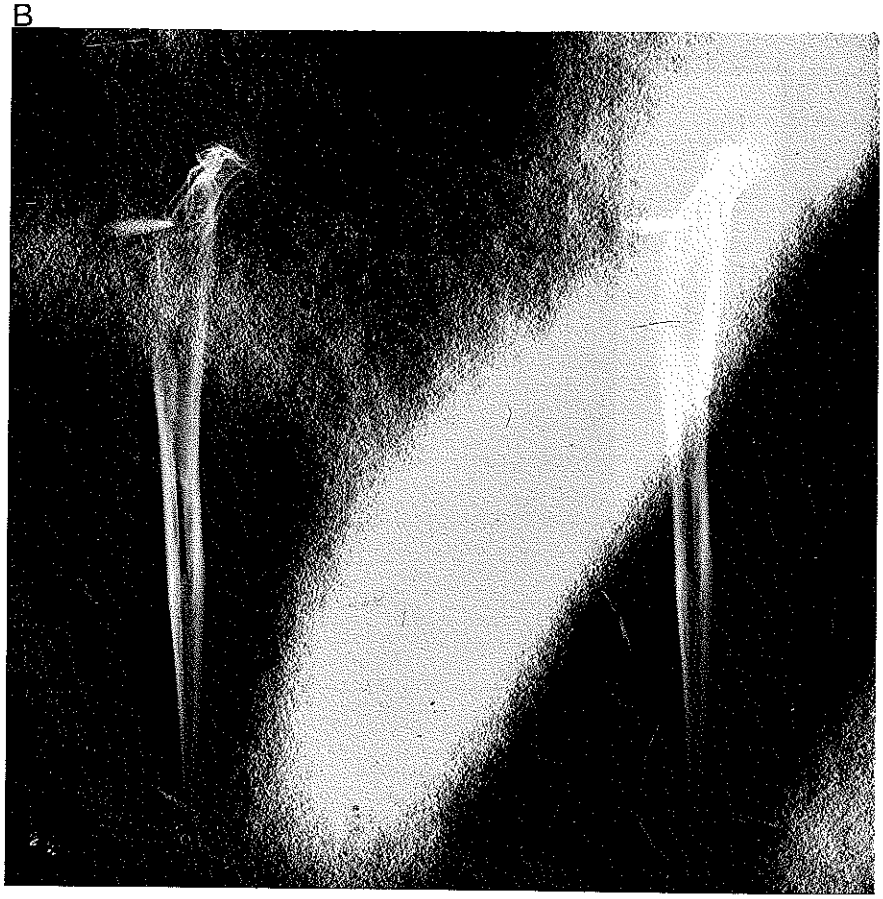
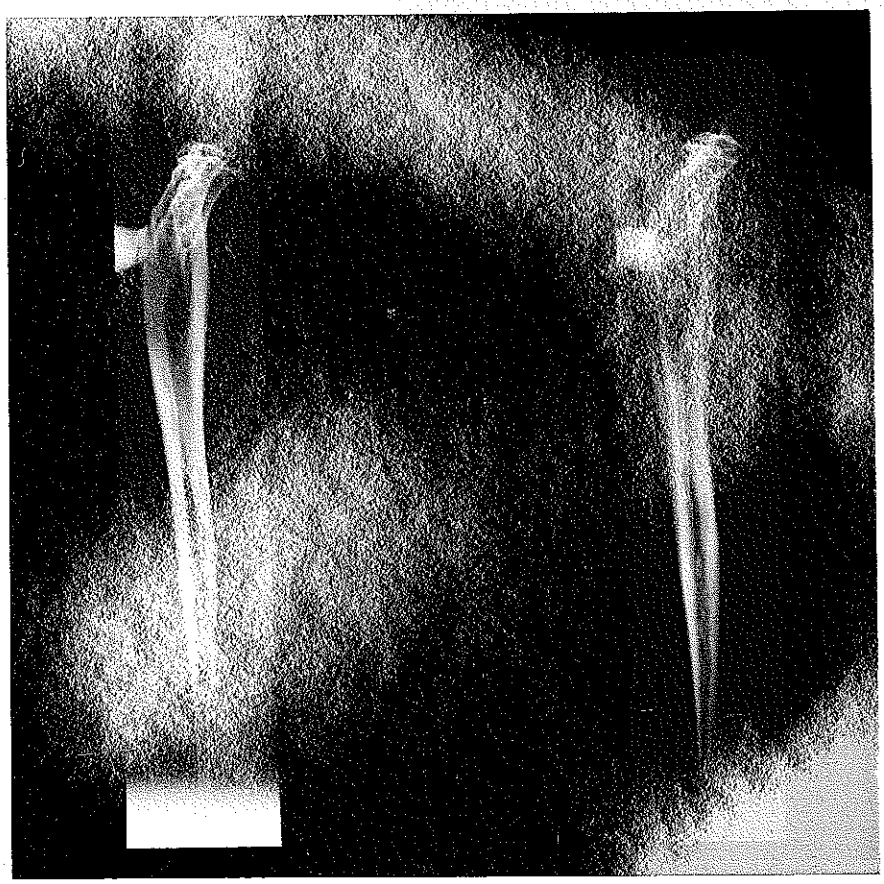


Plate 11. X-rays of the lower mandible of a second-year American Oystercatcher from the lateral aspect.



mination of appropriate prey sizes for oystercatchers of different ages.

4.3 Density and size of oysters on the oyster beds

Each microhabitat (the top and edge of the main bars, and the islands) has significantly different oyster density (Table 4). The islands exhibit the highest oyster density of 73.6 oysters per 0.0625 m^2 compared to densities of 46.5 and 31.2 oysters per 0.0625 m^2 for the top and edge respectively. The higher density found on the islands is probably a result of their longer submersion time.

The sizes of oysters on the edge of the main bars and the islands are not significantly different, but both of these microhabitats exhibit larger average oyster size than the tops of the main bars. Again, exposure time is probably of some importance here, as the tops of the main bars are exposed for longer periods each day than are the other microhabitats. Hence the oysters there will have less opportunity to feed each day.

Table 4. Density and size of oysters in each microhabitat. Densities represent the number of oysters in a 0.0625 m^2 quadrat. Sizes represent the grand mean of the size of oysters in each quadrat.

Microhabitat	Oyster Density	Oyster Size (ml)	
	Mean ± S.E.	Mean ± S.E.	n
Main bars - Top	46.5 ± 5.2*	1.86 ± 0.1	24
Main bars - Edge	31.2 ± 3.3*	3.57 ± 0.3+	24
Islands	73.6 ± 6.4*	4.04 ± 0.3+	16

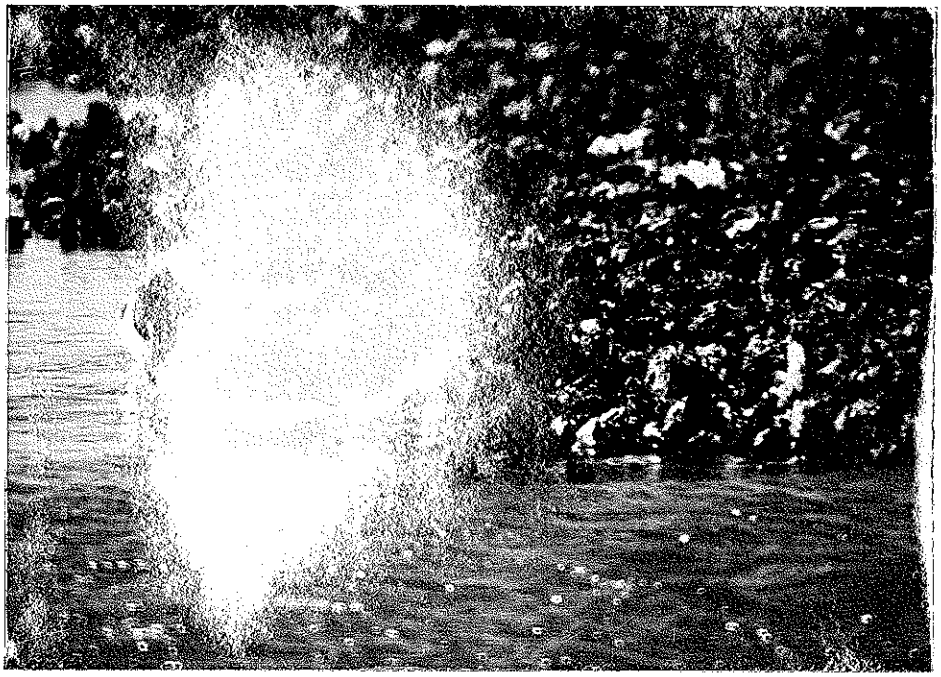
* Means differ significantly ($P < 0.05$, Student-Newman-Keuls Test).

+ Means do not differ significantly ($P > 0.05$, Duncans Multiple Range Test).

4.4 Searching behaviour

When searching for oysters, an oystercatcher walks forward with its bill pointing downward, so that the tip is approximately 2-5 cm above the substrate (Plate 12). The bird locates prey visually and occasionally pecks rapidly at a vulnerable oyster. Visual location of prey is indicated by the foraging behaviour of the bird. As the bird walks, it frequently moves its head from side to side and up and down, to allow itself a clear view of the oyster bed. Many oysters are partially hidden and difficult to see from directly above. Tomkins (1947) has suggested that the birds find oysters by touch rather than by sight. Neither my own observations or the available literature supports Tomkin's postulate. When feeding on prey beneath mud or sand, where touch rather than vision is important in prey location, various species of oystercatcher tend to use multiple pecks (Baker 1974b, Hulscher 1976, pers. obs.) By keeping the bill in the mud, the bird is able to contact a larger area with its sensitive bill tips (Heppleston 1970), thus increasing the likelihood of finding randomly distributed prey. On the oyster bars, the oysters are found in a three-dimensional conglomeration of shells, each oriented in a slightly different direction. This means that the detection of vulnerable prey by touch would be extremely difficult. Because single pecks are made and the orientation of the peck must be extremely precise to open an oyster, it is much more likely that the birds locate oysters visually. Moreover, night hunting would be possible if vulnerable oysters could be found and extracted by touch alone; no night feeding, however, was observed during this study.

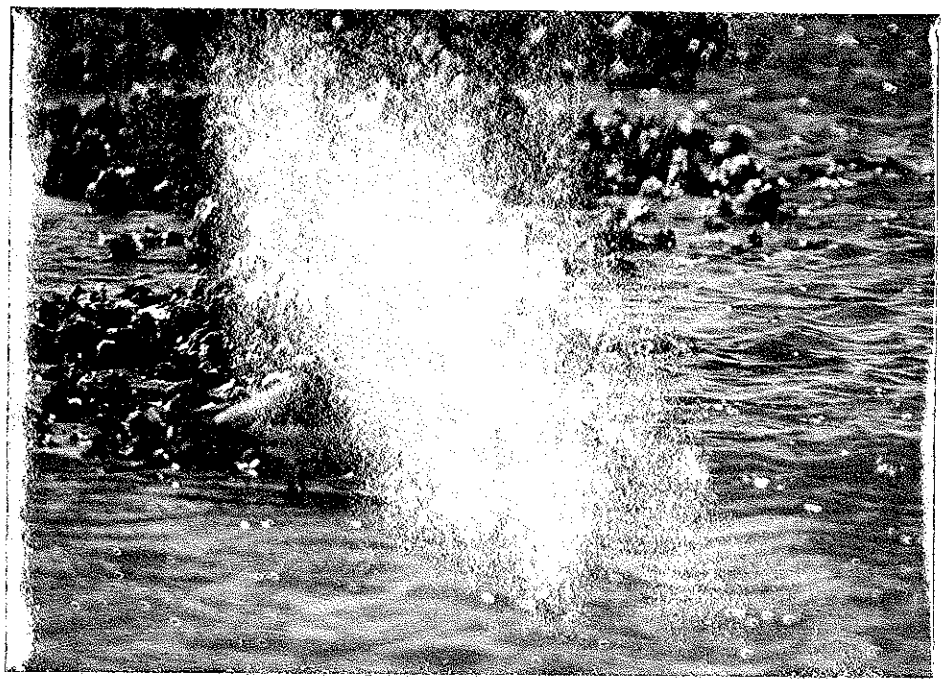
Plate 12. Foraging pose of an American Oystercatcher. The bird on the left is actively hunting.



Because the surface of the oyster bed is uneven, the bird must adjust its step length to the surface of the substrate to maintain balance while hunting. As the tide falls, the bird is able to walk on mud along the fringes of the oyster bars (Plates 12 and 13). The bird appears to prefer to walk on the flat, mud surface, presumably because it can move more quickly there and cover a larger area of the oyster bed. However, during the winter the birds do not take prey items which are submerged beneath the mud; they peck only at oysters on the oyster bars or occasional small clumps of oysters between bars. In the breeding season, birds were frequently seen taking Stout Razor Clams (Tagelus plebius) from mud between the bars.

Hunting birds tend to search in a path that is generally parallel to the length of the oyster bar. The short-term pattern of movement is extremely tortuous as the birds move from side to side to investigate various oyster clumps and to adjust to the contours of the local substrate. By moving parallel to the edge of the bar, the birds can remain in flooded or moist areas, avoiding the drier parts of the bed which contain less vulnerable prey. This is also a useful mechanism to avoid retracing their own path and losing valuable time on unproductive areas.

Plate 13. Oystercatcher disabling an oyster. Note that the bird on the right has adjusted its head and bill orientation to suit that of the oyster.



4.4.1 Step rate

Step rate varies greatly within each microhabitat, due to the complex structure of the surface of the oyster bed. There is no significant difference in the overall step rates of the first- and second-year birds ($P > 0.5$) so these data have been lumped into a single age class - the immatures. Table 5 shows that generally adults and immatures step at the same rate. There is a tendency for adults to step more slowly in most foraging situations, but none of these trends are significant (Table 5). Although the data are highly variable, birds of different ages show a tendency to walk more quickly on the dry than on the wet oyster bars. Fewer oysters are vulnerable in these areas, so that birds may be either moving quickly to a more productive foraging area, or are, particularly in the case of first-year birds (see Scavenging, Table 23), scouring the area for dead oysters and scraps of oyster flesh left in the shell.

4.4.2 Peck rate

When data from all foraging situations are combined, first- and second-year birds do not peck at significantly different rates ($F = 0.31$, $P = 0.5788$), so these data are lumped. Adults show a significantly lower peck rate of 1.52 pecks/10 s than do immatures which peck at an average of 1.67 pecks/10 s (Table 6). When each of the foraging situations is considered separately, adults peck at a significantly slower rate than immatures only on the edge of the main bars (low density) and the islands (high density) (Table 6), but not on the wet or dry oyster bars. Both adult and immature oystercatchers peck at signi-

Table 5. Step rates for adult and immature American Oystercatchers in each foraging situation. Step rates represent the number of steps in 10 s.

Foraging Situation	Step rate				2-Iailed Wilcoxon test
	Adult		Immature		
	Mean ± S.E.	n	Mean ± S.E	n	
Oyster Density					
High	11.33 ± 0.8	41	11.29 ± 0.7	27	n.s.
Low	9.95 ± 0.6	54	10.33 ± 0.5	55	n.s.
High vs. Low	n.s.		n.s.		
Dry oyster bar	12.76 ± 1.5	12	14.47 ± 1.5	9	n.s.
Wet oyster bar	9.64 ± 0.5	38	11.15 ± 0.9	23	n.s.
Wet vs. Dry	*		n.s.		
All data pooled	10.49 ± 0.4	145	11.05 ± 0.4	114	n.s.

ficantly higher rates in the high oyster densities of the islands than in the lower densities of the edge (Table 6).

There are several possible explanations for the elevated peck rate of young birds. Firstly, young birds may persist in pecking at inedible objects, as has been described in pre-fledging European Oystercatchers (Dewar 1920, Lind 1965, Norton-Griffiths 1967), in young Spotted Flycatchers (Muscicapa striatus) (Davies 1977a) and the Domestic Chicken (Dawkins 1971). Dewar, Norton-Griffiths and Dawkins, however, each noted a waning of stimulus-specific responsiveness to inappropriate items, while Lind described oystercatchers still pecking at and mandibulating inedible objects after fledging. As this is probably a method of assessing the palatability of various items, it seems unlikely that such behaviour would persist until 18 months (second winter), or even 6 months (first winter). Alternatively, immatures may maintain a higher peck rate because they tend to take smaller more abundant prey than do adults (see Table 22 and Fig. 10), and so have more available prey at which to peck. A third possibility is that young birds learn to perfect their foraging techniques gradually. Pecking (the "dart-probe" see p) is likely improved considerably with experience through trial-and-error learning. While the young bird is perfecting its dart-probe, it may well miss more prey than adults, in a manner similar to that described in several species of birds in which the birds learn their foraging techniques by experience (Recher and Recher 1969, Orians 1969, Dunn 1972, Buckley and Buckley 1974, Groves 1978, Morrison et al. 1978, Quinney and Smith 1980). The precise orientation, direction, location and force of the dart-probe will vary necessarily with oyster size, and must be learned. It is probable that while this learning process is

Table 6. Peck rates for adult and immature American Oystercatchers in each foraging situation. Peck rate is defined as the number of pecks made in 10 seconds of foraging.

Foraging Situation	Peck rate: Adult Mean ± S.E.	n	Peck rate: Immature Mean ± S.E.	n	F-values Adults v. Immatures
Oyster density					
High	1.60 ± 0.33	49	1.83 ± 0.55	37	7.48**
Low	1.49 ± 0.36	89	1.67 ± 0.36	73	12.45***
High vs. Low	7.74**		4.39*		
Dry oyster bar	1.66 ± 0.41	17	1.43 ± 0.33	10	2.25 n.s.
Wet oyster bar	1.48 ± 0.05	66	1.61 ± 0.06	40	2.65 n.s.
Wet vs. Dry	2.51 n.s.		6.82 *		
All data pooled	1.52 ± 0.40	221	1.67 ± 0.41	160	6.80 ***

taking place, young oystercatchers make more unsuccessful attempts than do adults. Consequently, young birds will make more attempts at prey per unit time to compensate for lower foraging success. Buckley and Buckley (1974) and Groves (1978) have found higher food intake rates in birds which make more attempts at prey.

Adults that peck at a slow rate take more oysters per unit time feeding than adults pecking at a fast rate ($F = 12.91^{***}$, $r = -0.24$, Fig. 9). This negative relationship does not hold for younger birds, which show no significant relationship between peck rate and number of oysters eaten ($F = 2.76$ n.s., $r = -0.13$). Adults thus seem capable of assessing patch quality, and when in a good "patch" will be very selective in their pecking attempts. Young birds apparently cannot determine patch quality, and hence maintain their elevated peck rate in all areas of the bed.

4.4.3 Search time

Search time consists of the time taken from finishing one oyster to the dart-probe into the next. There is no significant difference between the search times of first- and second-year birds (Wilcoxon test, $P = 0.9098$), so these data are pooled. On average, adults find an oyster every 44.35 s while immatures have a successful predation every 42.2 s. These values are not significantly different (Table 7).

Adults find prey significantly more quickly ($P < 0.01$) on wet oyster bars than on dry bars (Table 7) whereas immatures do not. In the field, it was difficult to determine whether birds were cleaning scraps from previously opened shells or taking live oysters. I seldom made the

Figure 9. Correlation of peck rate and the number of oysters eaten in 5 min for (A) adult and (B) immature American Oystercatchers.

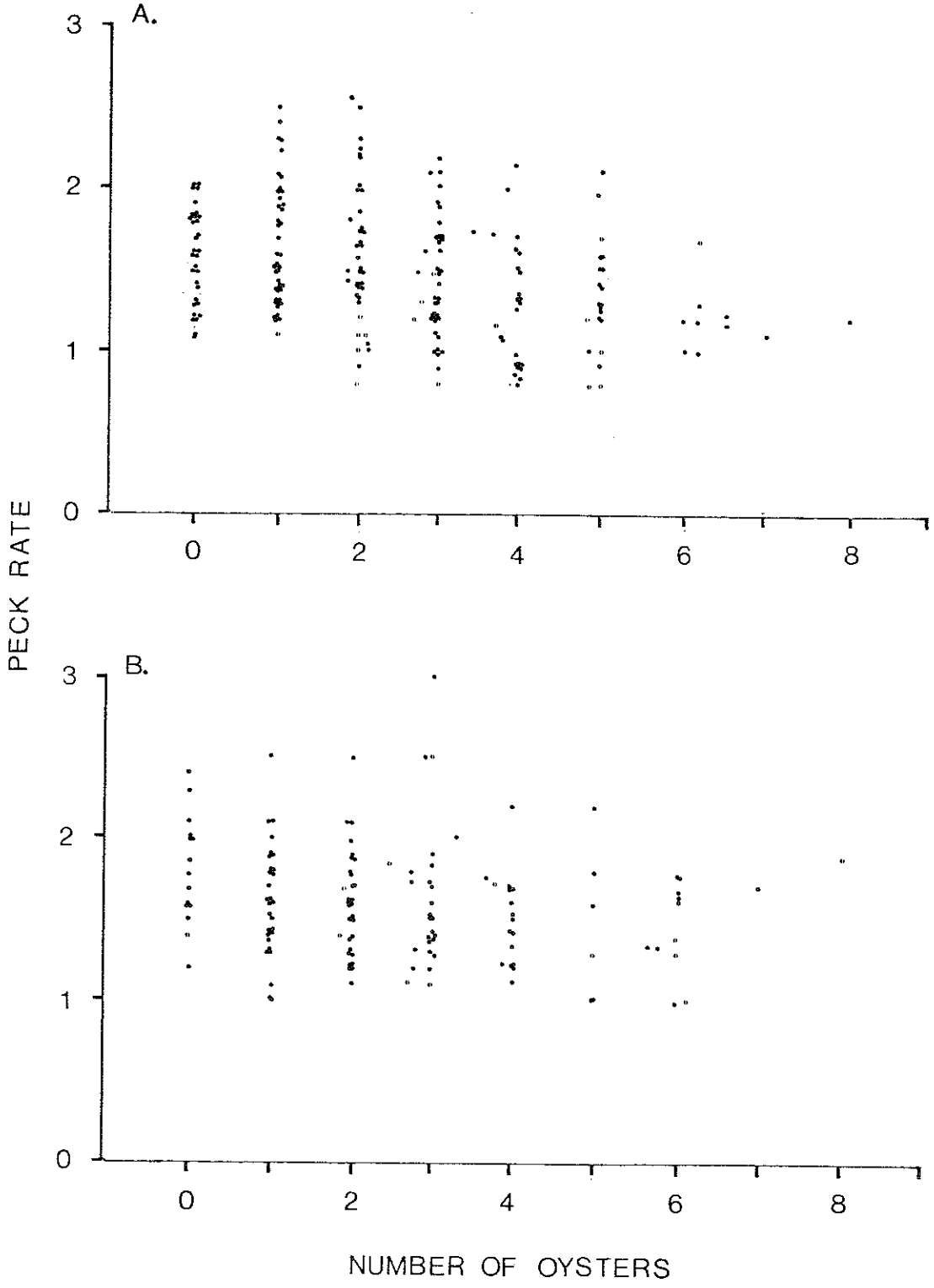

A.
B.
3
2
1
0
0
2
4
6
8
PECK RATE
NUMBER OF OYSTERS

Table 7. Search time for adult and immature American Oystercatchers in each foraging situation.

Foraging Situation	Search time: Adult Mean ± S.E.	n	Search time: Immature Mean ± S.E.	n	2-Tailed Wilcoxon test
Oyster density					
High	50.66 ± 6.3	68	51.75 ± 5.1	80	n.s.
Low	51.20 ± 4.1	183	46.47 ± 3.7	180	n.s.
High v. Low	n.s.		n.s.		
Exposure					
Dry oyster bar	50.65 ± 7.0	46	32.44 ± 4.6	39	*
Wet oyster bar	35.14 ± 2.6	214	34.57 ± 2.6	150	n.s.
Wet v. Dry	**		n.s.		
All data pooled	44.35 ± 2.1	511	42.22 ± 2.1	449	n.s.

distinction during data collection. Much of the data on young birds on dry oyster beds probably consist of observations of the cleaning out of scraps from previously opened shells. Adults (generally) did not forage for these scraps. Therefore, immature birds had significantly shorter search times between succesive food items than adults on the dry oyster bars (Table 7) because more food items were available to them. Somewhat surprisingly, there was no difference in search time in either adults ($P > 0.8$) or immatures ($P = 0.0717$) when feeding in the two microhabitats with different oyster densities (Table 7).

4.5 Oyster-opening technique

The methods used by the American Oystercatcher to open oysters have been described briefly by Tomkins (1947). Lunais (unpub.) has described predation by the European Oystercatcher on the Japanese Oyster (Crassostrea gigas) in France. Although the techniques used on oysters are similar to those used on mussels (Mytilus edulis) as described by Dewar (1908, 1910), Drinnan (1958a), Norton-Griffiths (1967) and Baker (1974b), there are several important differences. These differences apparently result from the oyster being cemented to its substrate, rendering only the right valve moveable (Yonge 1960, Galtsoff 1964). However, the techniques used by H. palliatus differ considerably from those used by H. bachmani to open the Japanese Oyster (Butler and Kirby-son 1979), and in several respects from the methods used by H. ostralegus (Lunais unpub.).

Norton-Griffiths (1967) developed a terminology for the techniques used by H. ostralegus to open and eat mussels, and this is used below in describing oyster opening techniques employed by H. palliatus.

4.5.1 Disabling the Oyster

Oysters are most vulnerable to opening attempts by American Oystercatchers when they are gaping. When the adductor muscle of an oyster is relaxed, its ligament (located at the hinge, Fig. 5) forces apart the valve margins, creating a slight gape through which the oyster feeds when it is submerged (Yonge 1960). Dewar (1908) noted that mussels gape when water-covered and in "moist situations" which occur locally within the bed above the tide line for some time after first exposure to the air. Also, Hartwick (1976) described a "splash-zone" in which wet but not submerged mussels gape. This likely applies also to oysters, and explains how an oystercatcher is able to take oysters above the tide line. Tomkins (1947) thought that oysters could only be taken when covered by the tide, though Maynard (1881) and Forbush (1925) had previously noted otherwise.

The American Oystercatcher gains entry to an oyster with a dart-probe. After visually locating a gaping oyster, the bird rapidly stabs into the gape with its bill aligned along the longitudinal axis of the gape. The bill is laterally flattened at the tip, so that the bird is able to place at least the tips of the mandibles inside the oyster. The irregular arrangement of the oysters and the narrowness of their gape requires that the dart-probe be perfectly aligned to strike between the gaping valves. If the first dart-probe does not penetrate between the

valves, the bird will look for another prey item, as the oyster reacts quickly to disturbance and closes the gape.

Only the extreme tip of the bill will penetrate when the gape is very small, and the bird must apply as much force as possible to the bill tips to rapidly push the bill deep into the oyster to allow for effective levering (defined below). As oysters tend to gape only when water-covered or moist, the size of the gape decreases as the water level drops and the oyster becomes drier. For this reason, the "forcing" technique (Lunais unpubl.), otherwise known as "power thrusts" (Baker 1974b), is used mostly on oysters above the water line.

When the bird has at least its bill tips between the valves of the oyster, it quickly adjusts its body postion so that the bill is usually (but not always) vertical. It then moves its head rapidly from side to side using the bill as a lever. Each valve margin is used as the fulcrum as the bird moves its head to that side. The birds usually lever through 20^{o} - 40^{o}, though they occasionally lower their head through almost 90^{o} to one side. Lunais (unpubl.) was able to visit oysters which had been recently opened by European Oystercatchers, and found that the valve margins of each oyster were broken by the levering efforts of the bird. I was unable to check this on my study area.

Levering must begin very soon after a succesful dart-probe, as the oyster responds by closing its valves. Oyster adductor muscle has a short reaction time, and the tension it generates increases at an average rate of 0.67 $kg/cm^2/s$ (Millman 1964). Therefore, if the muscle is not quickly disabled, the oystercatcher has little opportunity for successful predation. Adductor muscles are greatly weakened if forced to

stretch (Dewar 1908). If an oystercatcher can surprise the oyster with a dart-probe and rapidly lever the right valve away from the left by stretching the adductor slightly, it should then be able to complete the predation. The bird usually disables an oyster in 5-7 s (Table 9). It is probable that the dart-probe and first attempt at levering determines the success or failure of the predation. The remainder of the time required to disable the oyster is occupied in levering and twisting (see below) until the adductor is either broken or stretched to the point at which it cannot effectively close the valves. While levering, the bird works its bill deeper between the valves, thus allowing more effective levering which puts more pressure on the right valve and further weakens the adductor muscle.

Twisting serves the same purpose as levering, and was often used directly following a dart-probe. It appeared that twisting was often used on prey that were difficult to lever. For example, if the bird was unable to position itself correctly above the oyster, levering would be difficult, and provide less force than the bird could create with the proper body position. However, twisting was also used alternately with bouts of levering and not only when levering was impossible. In "twisting", the bird rotates its bill using the longitudinal axis of the bill as the axis of rotation. It does this by twisting the head and upper body alone (Plate 13), or, when using the bill vertically, by holding its neck stiff and walking 90^{o} to the right or left. The laterally flattened bill of the oystercatcher means that the width of the bill is much less than the height. Because of this, as the bird twists the valves are forced apart to the height of the bill which is sufficient to extend the adductor muscle of the oyster and substantially weaken it.

Dewar (1908), Webster (1941) and Baker (1974b) found that oystercatchers twisted to the left when opening mussels. Although I did not record the direction of twisting often enough to test for differences, I noticed no trends to twist preferentially to one side.

4.5.2 Extracting the flesh

Following levering or twisting, the valves are separated by a large gape at the posterior of the oyster through which the bird can work to extract the flesh. The bird places its bill tips 3 - 4 mm apart (Norton-Griffiths 1967) with the flat lateral surface of the bill against the flat inner surface of the shell. The bill is then moved rapidly in and out, up to six strokes per second in 3 - 4 mm strokes (Norton-Griffiths 1967) and makes scissor-like movements with the bill tips. These serve to cut the flesh from its attachment to the shell. Oyster flesh is attached delicately to the shell along the mantle margins (see Fig. 5) by the periostracum (Yonge 1960), by the radial pallial muscles of the mantle, which insert near the base of the adductor, and by the adductor muscle itself (Yonge 1960). The adductor is the major area of attachment. I was unable to ascertain the order in which the muscles are detached from the shell. However, the mantle must be cleared before the bird is able to reach the base of the adductor. As the radial pallial muscles insert close to the adductor, they are probably sheared away from the shell at the same time the adductor is detached. Norton-Griffiths (1967) states that the first chiselling bout frees the mantle and adductor of the mussel, and subsequent chiselling cleans up any remaining bits of flesh. Oysters, however, are frequently much larger than the mussels taken by the European Oystercatcher and I

have recorded as many as 15 chiselling bouts on one oyster, many of which were followed by flesh extraction and swallowing. In these instances, the bird is cutting pieces from the oyster and eating them while most of the flesh is still in the shell. Again, the size of the oyster is of significance here, as it would be extremely difficult for an oystercatcher to swallow and extract whole a 10 ml sizedoyster. As large pieces of prey attract gulls and other oystercatchers, it is perhaps more advantageous to extract smaller pieces that can be swallowed easily.

After the flesh has been fully detached from the oyster shell, it is often gathered up in the bill by rapid grab-pecking (RGP). The motion involved resembles chiselling in that there is a rapid in and out movement. However, in rapid grab-pecking, the mandibles are placed on either side of a loose piece of flesh and each time the bill tips close the flesh is pulled slightly. It is thrown in short bursts towards the mouth of the oystercatcher, and is gathered between the mandibles until the bird can lift it out in one bite. Ihe bill is then withdrawn from the oyster, and the flesh is snapped back and swallowed.

Ihe bird does not always use rapid grab-pecking to remove loose flesh from the shell. Occasionally, the bird simply grasps the loose flesh between its mandible tips and slowly withdraws its bill from the shell. Withdrawal of flesh by this method is slow and the motions are performed slowly and carefully. When small pieces of oyster flesh are left deep within a shell, the bird may not be able to perform rapid grab-pecking because of the restrictive proximity of the valves. In such cases, grasping is used.

4.5.3 Sequencing of techniques

The general pattern of oyster-opening techniques is

dart-probe → lever/twist → chisel → (RGP or grasp) → swallow

However, there are many variations on this pattern. Levering and twisting are commonly used at the same time, probably because rotation of the bill provides greater leverage than the use of the flat, lateral surface alone. Levering and twisting are also used alternately to disable the oyster. After several bites have been extracted, levering is occasionally used to widen the gape and allow access to other parts of the interior of the shell.

For small prey items with a volume of less than 1 ml, levering and twisting are often omitted because the initial dart-probe has pushed the bill far enough into the oyster to render the adductor functionless. In this case, the bird proceeds directly to chiselling and removal of the flesh. Norton-Griffiths (1967) concludes that levering and twisting are stimulated by the contraction of the valves, which places pressure on the mandible tips following the dart-probe. Heppleston (1970) has shown that the European Oystercatcher has concentrations of Herbst corpuscles in the bill tips, which are tactile receptors that aid the bird in finding prey and in sequencing its prey-opening techniques (Norton-Griffiths 1967). American Oystercatchers foraging on the oyster beds frequently struggled to free their bill tips which were trapped between the valves of an oyster. Presumably, these oysters had felt the presence of the

bird's bill, and had been able to contract before the bird had weakened the adductor. There appears to be a threshold level of pressure on the bill tips above which an escape or withdrawal mechanism is stimulated. Several violent jerks of the whole body with the weight of the bird pivoting on its pelvis are sometimes necessary to remove the bill tips. Baldwin (1946) discovered the skeleton of an American Oystercatcher, its bill still firmly wedged between the valves of a large clam (Venus sp.) which it had obviously attempted to open and, failing that, to escape from.

4.6 Oyster-opening efficiency

4.6.1 Giving Up

Oystercatchers frequently make unsuccessful attempts to open oysters. In such cases, they must "give up" and search for another oyster. During the course of feeding, the birds often give up in less than 3 s. These brief attempts were classified as pecks and included in the analysis of peck rate (p. 66). The data analysed here are composed of those unsuccessful attempts which lasted for more than 3 s. These attempts represent a considerable waste of energy, so the capacity to judge the availability of a prey item is important to efficient foraging.

Adults and immatures "give up" at the same frequency (Chi-square = 0.63, $P > 0.5$) and after approximately the same handling time (Table 8). It appears, then, that immature birds are as able as adults to determine whether an oyster is vulnerable enough for successful predation.

Table 8. Giving up time for each age class. Giving up time is the time from a dart-probe until the bird finishes an unsuccessful attempt at an oyster.

Age	Giving-up time		Maximum[+]
	Mean ± S.E.	n	
First-year[++]	14.35 ± 0.99	80	50
Second-year[++]	12.93 ± 1.09	29	25
Adult[++]	15.04 ± 0.91	137	74

[+] The longest unsuccessful predation attempt. [++] Means do not differ significantly (P = 0.8591, Kruskal-Wallis test).

Presumably, the birds can usually ascertain within the first 3 s if they will be able to open a particular oyster. Such an ability is highly advantageous and seems to be learned before the first winter of a bird's life.

4.6.2 Disabling time

The time taken from a dart-probe to the first pause during the opening of the oyster is termed the "disabling time". First-year and second-year birds do not differ significantly in disabling time so these data have been pooled. Adults disable oysters more quickly than immatures in most of the oyster size classes, and when data from all size classes are combined ($P < 0.001$, see Table 9). Samples of size classes above 8 ml are too small to show significant differences.

Disabling time does not change with increasing oyster density or with the state of exposure of the oysters (Table 10). Although there is a tendency for adults to take longer to disable oysters on the dry oyster bars than on wet ones, the difference is not significant.

Table 9. Time taken by adult and immature American Oystercatchers to disable oysters of each size class.

Prey size (ml)	Disabling time: Adult Mean ± S.E.	n	Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
0.5	5.31 ± 0.30	67	7.91 ± 0.68	58	**
2	5.71 ± 0.18	237	7.15 ± 0.36	155	***
4	5.71 ± 0.23	119	7.69 ± 0.63	65	***
6	4.90 ± 0.31	52	8.37 ± 0.84	27	*
8	7.00 ± 0.66	11	8.94 ± 1.08	16	n.s.
10	5.30 ± 0.79	10	12.00 ± 7.00	2	n.s.
12	9.00 ± 1.15	3	5.00	1	*
14	4.25 ± 0.95	4	8.33 ± 1.33	3	n.s.
16	2.00	1	5.00	1	n.s.
All data pooled	5.66 ± 0.14	541	7.64 ± 0.26	337	***

Table 10. Time taken by adult and immature American Oystercatchers to disable oysters in each foraging situation.

Foraging Situation	Disabling time: Adult Mean ± S.E.	n	Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
Oyster density					
High	5.35 ± 0.27	160	7.22 ± 0.55	46	***
Low	5.59 ± 0.20	188	8.15 ± 0.41	136	*
High vs. Low	n.s.		n.s.		
Dry oyster bar	6.26 ± 0.49	46	7.43 ± 0.79	23	n.s.
Wet oyster bar	5.77 ± 0.26	111	7.67 ± 0.67	57	*
Wet vs. Dry	n.s.		n.s.		

4.6.3 Handling time and prey size

American Oystercatchers in their first-year handled oysters of each size class as quickly as second-year birds, so these data are pooled (Table 11). Immatures open oysters with a volume of less than 1 ml as quickly as older birds (Table 12). Beyond this small size, however, the older birds are able to open almost all oysters in significantly shorter handling time than immatures. The ability of young birds to open only small prey as efficiently as adults is evidence that younger birds are still learning the essential opening and flesh extraction techniques.

Small oysters require a shorter handling time, and are probably opened more easily than are larger prey. There are several reasons why the young birds might be as efficient as adults in the predation of small oysters, but not as efficient on all larger prey. The adductor muscle of small prey is weaker, making them easier to disable, and less chiselling of the flesh is necessary because the attachments to the shell are smaller. The flesh of oysters of less than 1 ml is always removed in one bite, requiring less coordination of chiselling and rapid grab-pecking. Less precise orientation of techniques will be necessary with a smaller, and consequently weaker, oyster. Levering will be extremely damaging to a small oyster whether or not the correct angle of leverage is utilized. Also, chiselling need not be as perfectly oriented as in larger oysters owing to the close proximity of the attachments in a small oyster. The bird may well be able to shear the adductor attachments as it chisels at the mantle margins. On small prey, an initial dart-probe is more likely to reach and damage the

Table 11. Handling times of first- and second-year American Oystercatchers for each size class of oyster.

Oyster size class (ml)	Handling time: First-year Mean ± S.E.	n	Handling time: Second-year Mean ± S.E.	n	2-Iailed Wilcoxon test
0.5	16.31 ± 1.38	122	19.28 ± 3.16	46	n.s.
2	29.99 ± 1.07	201	28.82 ± 1.65	85	n.s.
4	41.60 ± 2.17	88	45.14 ± 4.19	22	n.s.
6	51.55 ± 4.61	29	51.55 ± 9.91	8	n.s.
8	89.31 ± 5.70	16	146.50 ± 19.50	2	*
10	-		130.33 - 32.52	2	-
12	205.00	1	55.00	1	-
14	239.00	1	149.00	1	n.s.
16	-	-	225.00	1	-

Table 12. Handling time of each size class of oyster by adult and immature American Oystercatchers. Data from all foraging situations pooled.

Oyster size class (ml)	Handling time: Adult Mean ± S.E.	n	Handling time: Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
0.5	15.29 ± 0.76	133	17.12 ± 1.32	168	n.s.
2	24.89 ± 0.85	345	29.64 ± 0.90	286	***
4	34.63 ± 1.35	164	42.36 ± 1.92	102	***
6	57.36 ± 4.54	61	52.38 ± 4.14	37	n.s.
8	66.57 ± 10.59	14	95.67 ± 6.85	18	**
10	61.00 ± 6.62	12	130.33 ± 32.53	3	*
12	130.75 ± 31.63	4	130.00 ± 75.00	2	n.s.
14	126.50 ± 10.51	4	209.00 ± 43.26	3	*
16	100.00	1	225.00	1	-

adductor muscle. Ihis diminishes the need for levering and twisting, and simplifies the opening procedure. Additionally, small prey are abundant on the oyster bed, and are frequently taken by immature birds (Fig. 10), so they have more experience with the characteristics of small prey in particular, and may have greater facility in opening them because of this. Small oysters are less likely to damage the foraging apparatus of an oystercatcher. The morphology of the bill and skull of the American Oystercatcher develops for more than two years. Therefore it seems possible that young birds are as efficient at opening small prey because, like adults, their bill is strong enough to permit the application of sufficient pressure to force open these smaller oysters. Ihe adductor muscle of small oysters will be more likely to be overpowered by a given force and so is potentially less dangerous to the bill of the young bird. Further, the bill tips of the first-year bird are sharper than older birds (Plate 2, Iable 3) which may be of use in opening small prey, but somewhat of a hindrance in the predation of larger oysters.

Adults are able to handle most prey sizes significantly more quickly than immatures at low oyster density (Iable 13). Oysters of 6 ml are opened equally well by both age classes. At high oyster densities, adults are able to open most prey sizes in a shorter handling time, but due to small sample sizes, only the difference in size class 4 is significant ($P < 0.05$).

Adults handle prey of all sizes more quickly than immatures on the wet oyster bars, but are significantly faster only with oysters of 2 and 4 ml (Iable 14). Oysters larger than 4 ml are rarely taken in this

Figure 10. Percentage composition of the diet of (A) first- and second-year , and (B) adult and immature American Oystercatchers feeding on the study oyster bed from January to March 1979.

A. The diet of first-year birds is shown in black and second-years' in white.

B. The diet of adults is shown in white and immatures in black.

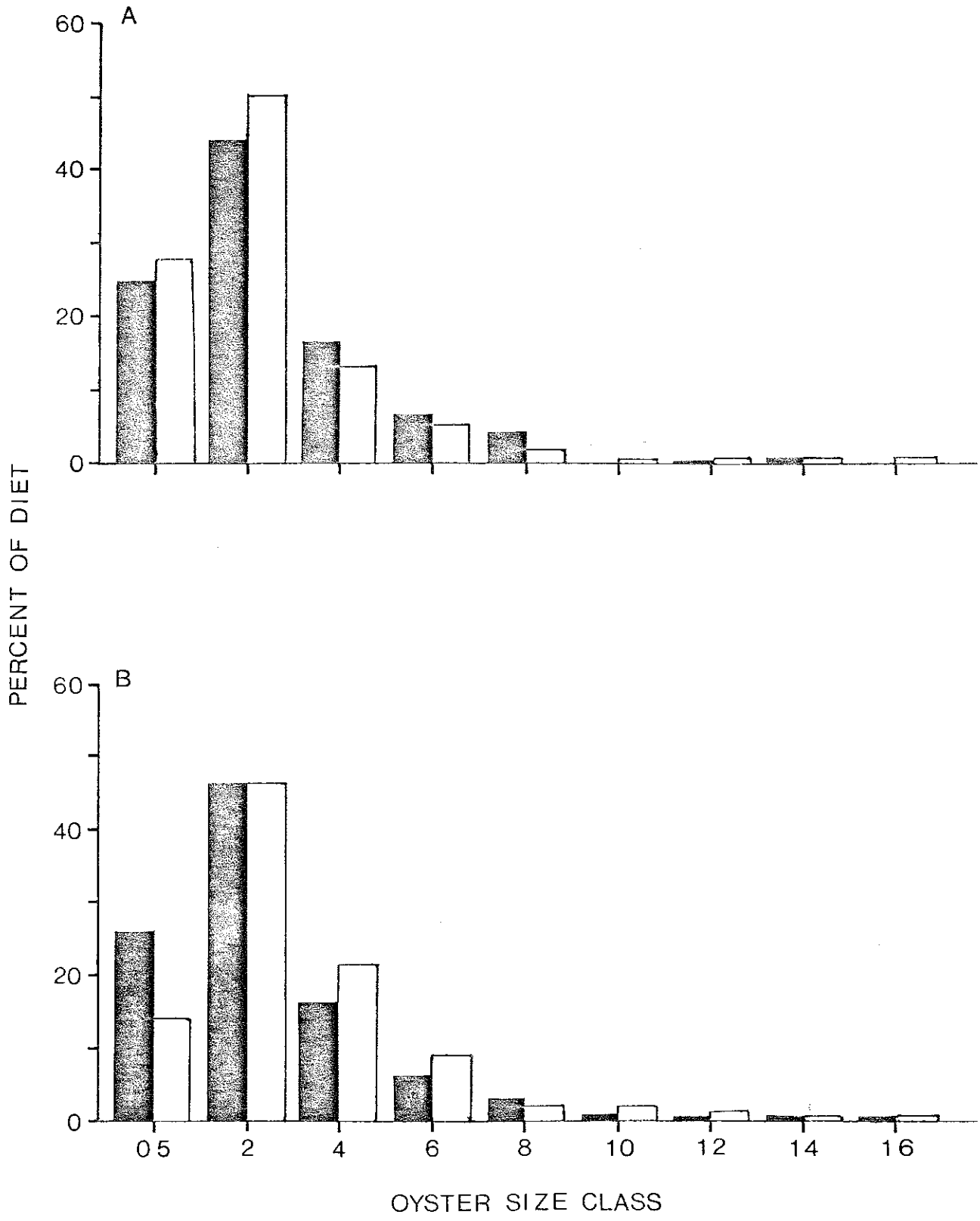

A
B
60
40
20
0
PERCENT OF DIET
0 5
2
4
6
8
10
12
14
16
OYSTER SIZE CLASS

Table 13. Effect of oyster density on handling time of adult and immature American Oystercatchers. Handling times are computed for each oyster size separately.

Oyster density	Oyster size class (ml)	Handling time: Adult Mean ± S.E.	n	Handling time: Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
Low	0.5	14.57 ± 1.11	46	19.16 ± 2.91	68	n.s.
	2	27.00 ± 1.60	108	29.35 ± 1.50	100	*
	4	35.97 ± 2.15	66	44.51 ± 3.14	51	*
	6	55.78 ± 6.54	27	53.57 ± 5.35	23	n.s.
	8	64.33 ± 14.71	9	95.56 ± 7.42	9	**
	10	69.71 ± 9.28	7	156.50 ± 33.50	2	*
	12	154.67 ± 29.28	3	55.00	1	n.s.
	14	124.00 ± 5.00	2	239.00 ± 54.00	2	n.s.
	16	100.00	1	225.00	1	-
High	0.5	16.44 ± 2.97	18	15.98 ± 1.82	40	n.s.
	2	28.87 ± 3.13	31	34.78 ± 2.99	37	n.s.
	4	37.21 ± 3.41	34	45.69 ± 4.88	13	*
	6	66.53 ± 10.81	15	57.38 ± 9.33	8	n.s.
	8	77.50 ± 17.68	4	93.17 ± 17.48	6	n.s.
	10	48.80 ± 6.64	5	78.80	1	n.s.
	12	59.00	1	-		-
	14	104.00	1	149.00	1	-
High vs. Low	0.5	n.s.		n.s.		
	2	n.s.		n.s.		
	4	n.s.		n.s.		
	6	n.s.		n.s.		
	8	n.s.		n.s.		
	10	n.s.		n.s.		
	12	n.s.		n.s.		

habitat.

Few prey were taken on the dry oyster bars. The birds seldom foraged there, most oysters above the tide line being firmly closed to avoid desiccation. Usually, by the time the tops of the bars are dry, other parts of the oyster bed which offer more profitable foraging possibilities, such as the edge of some bars and the islands, have become available. However, birds of all ages - but young birds in particular - occasionally fed on the dry oyster bars, where they scavenged for scraps of flesh left in opened shells, and looked for dead oysters or pockets of water in which an oyster might be gaping. Adults rarely fed on the dry oyster bars, though they frequently walked across the top of the dry bar in moving from one edge to another. The oysters taken from dry oyster bars by adults were taken mostly during several days in February, when ice covered the edges of all oyster bars, allowing access to only the tops of the bars for most of the available feeding time. Immature birds, however, appeared to spend more time on the dry oyster bars.

Adults are unable to open prey more quickly than immatures on the dry oyster bars (Table 14). Indeed, the tendency is for the younger birds to open each class at a slightly faster rate than the adults. As suggested above, this is probably due to the greater amount of time expended by immatures on dry oyster beds, resulting in their taking more oysters which are in some way disabled than do adults.

Adults, but not immatures, were generally able to handle oysters larger than 1 ml on the wet oyster bars more quickly than on the dry bars (Table 14). Immature birds achieve significantly shorter handling time on oysters of less than 1 ml on the dry oyster bar than they attain

Table 14. Effect of state of exposure on handling time of adult and immature American Oystercatchers. Handling times are computed for each oyster size class separately.

State of Exposure	Oyster size class (ml)	Handling Time: Adult Mean ± S.E.	n	Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
Wet	0.5	15.22 ± 1.19	51	16.83 ± 1.35	48	n.s.
	2	21.81 ± 0.78	173	28.41 ± 1.24	125	***
	4	30.38 ± 1.90	55	39.47 ± 2.59	34	**
	6	51.00 ± 9.31	16	58.50 ± 21.50	2	n.s.
	8	-		105.00		-
Dry	0.5	16.22 ± 1.90	18	10.58 ± 1.28	12	n.s.
	2	30.36 ± 4.91	33	29.38 ± 3.40	24	n.s.
	4	41.00 ± 6.31	9	28.75 ± 4.42	4	n.s.
	6	59.67 ± 11.10	3	32.50 ± 7.51	4	n.s.
	8	43.00	1	99.00 ± 19.00	2	n.s.
	10	-		-		-
	12	-		205.00	1	-
	14	154.00	1	-		-
Wet vs Dry	0.5	n.s.		*		
	2	*		n.s.		
	4			n.s.		
	6	n.s.		n.s.		

on the same size class when water-covered (Table 14). This results because young birds on the dry oyster bars are taking scraps from previously opened oysters.

The scraps left in the oyster shells are usually the stumps of the adductor muscles, but occasionally larger, softer pieces of flesh were seen to be extracted. Small pieces of oyster were probably left in the shell after most predations. Adults foraging on a water-covered oyster bar appeared to be less careful to extract all of the flesh from the oysters on which they were feeding, moving on quickly to the next oyster. They appear to choose to omit the removal of remaining scraps in favour of finding another oyster. Table 15 shows that significantly fewer bites ($P < 0.05$) are taken by adults from oysters in size class 2 when they are water-covered, than from the same size class on dry oyster bars. Immature oystercatchers show the same trend but the differences are not significant. Either the young birds have not learned this strategy, or, as seems more likely, their less efficient prey handling ability makes it more efficient for them to extract all of the flesh from each oyster they open. A recent study by Sih (1980) presents a model with which the "optimal" behaviour of a predator which eats its prey in more than one bite can be determined. One of the predictions of the model is that an increase in prey availability should decrease the optimum time spent on a prey item. Adults observed in this study were essentially conforming with the prediction by taking fewer bites (and hence presumably leaving more flesh behind) in oysters in areas where they were more available.

Table 15. The number of bites taken to eat small oysters on wet and dry oyster bars.

Age class	Oyster size class (ml)	Number of bites: Dry oyster bar Mean ± S.E.	n	Wet oyster bar Mean ± S.E.	n	1-Tailed Wilcoxon
Adult	2	1.84 ± 0.20	33	1.45 ± 0.06	173	*
	4	3.00 ± 0.71	9	1.93 ± 0.19	55	n.s.
Immature	2	2.04 ± 0.19	24	1.88 ± 0.10	125	n.s.
	4	4.50 ± 0.87	4	3.24 ± 0.39	34	n.s.

4.6.4 Number of bites taken by adults and immatures

Adults extract the flesh from oysters of most size classes in fewer bites than younger birds (Table 16). Beyond size class 8, the sample sizes are small and are of little use in this analysis. When feeding on oysters smaller than 10 ml, adults take fewer bites than younger birds on all but the 6 ml size class. This is the largest oyster size which an oystercatcher can swallow in one bite. As described previously, the bird has great difficulty in swallowing a bite of this size. It is likely that adults have difficulty deciding whether to eat an oyster of 6 ml in one bite, or to extract it in several smaller bites. To follow the latter procedure is relatively time-consuming; the extraction of a piece of flesh too large to swallow however, will attract scavenging gulls and other oystercatchers, and may result in considerable loss to the bird's energy budget.

4.6.5 Handling time and number of bites

In this analysis, I have employed the original prey size classes as they were collected in the field. The oysters have not been placed into 2 ml categories because I want to compare handling times to the number of bites taken from an oyster. According to my method of data collection, an oyster of 2.0 ml can be taken in either one bite of 2.0 ml, or in four bites of 0.5 ml. Table 17 shows the handling time resulting from taking prey sizes 2.0-3.5 ml in various numbers of bites. Sizes larger than 3.5 ml can be taken in increasingly numerous permutations of numbers of bites, and are not included in the analysis. The important trends are evident in the smaller sizes of oysters.

Table 16. Number of bites used to eat each oyster size class by adult and immature American Oystercatchers.

Oyster size class (ml)	Number of bites: Adult Mean ± S.E.	n	Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
2	1.72 ± 0.07	359	2.11 ± 0.06	292	***
4	2.46 ± 0.15	173	3.17 ± 0.23	104	**
6	3.78 ± 0.36	68	4.18 ± 0.51	38	n.s.
8	5.41 ± 1.00	17	7.92 ± 1.00	20	*
10	4.85 ± 0.41	13	13.31 ± 5.00	3	n.s.
12	13.00 ± 2.74	6	10.50 ± 4.50	2	n.s.
14	12.00 ± 2.00	4	20.33 ± 3.80	3	n.s.
16	11.50 ± 0.50	2	10.00	1	n.s.

In three of the four size classes, adults handle prey significantly faster when they take fewer bites. Immatures demonstrate the same trend, but significant differences occur only in oysters of sizes 2.0 and 2.5 ml. Clearly, feeding is most efficient when an oystercatcher removes the flesh from an oyster shell in the least number of bites possible. Adults remove prey in fewer bites than immatures in most prey size classes (Table 16), and this is instrumental in significantly lowering the handling time of adults in most prey size categories (Table 12). However, when taking oysters of 2.0 and 3.5 ml, adults have significantly lower handling times than younger birds when both remove flesh in as few bites as possible. Therefore, adults are able to handle prey more quickly as a result of generally superior technique, and the ability to take prey in fewer bites.

There is no difference between adult and immature oystercatchers in the handling time of oysters from 2.0-3.5 ml when the maximum number of bites are used on each prey size (Table 17). There are two possible explanations for this. Either the adults taking prey of this size in the maximum number of bites are highly inefficient individuals, and/or the prey which were extracted in the maximum number of bites were extremely difficult to open or gain access to. This may be caused by the extreme irregularity and complexity of the oyster bed, and because oysters grow on top of each other, making some shells difficult to open wide enough for efficient extraction of flesh.

If the latter explanation is correct, then it seems that adults normally avoid such difficult prey, while immatures take them using a large number of bites. However, it seems more likely that adults were

Table 17. Handling times for adult and immature American Oystercatchers when eating oysters in various numbers of bites.

Prey size (ml)	Number of bites	Handling time: Adult Mean ± S.E.	n	Handling time: Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
2.0	1	19.53 ± 0.54	203	23.70 ± 0.93	103	***
	4	46.31 ± 4.74	13	46.65 ± 3.24	26	n.s.
1 vs. 4 bites+		***		***		
2.5	2	29.70 ± 2.12	50	29.68 ± 1.52	37	n.s.
	5	62.47 ± 8.72	15	57.09 ± 5.75	11	n.s.
2 vs. 5 bites+		***		***		
3.0	3	36.94 ± 3.27	17	45.00 ± 4.75	14	n.s.
	6	38.50 ± 5.74	4	51.80 ± 7.74	5	n.s.
3 vs. 6 bites+		n.s.		n.s.		
3.5	4	43.80 ± 3.75	15	56.23 ± 4.21	5	*
	7	71.50 ± 14.50	2	57.00 ± 3.56	7	n.s.
4 vs. 7 bites+		*		n.s.		

+ 1-Tailed Wilcoxon test

better able to use, orient and sequence the motor patterns involved in the opening techniques than younger birds. Only when the flesh was extremely difficult to gain access to, were adults forced to remove the prey in many small pieces.

4.6.6 Rate of gain of calories (RGC)

By subtracting the rate of energy expenditure from the rate of energy intake while handling prey, I have calculated the RGC for each prey size for adult and immature oystercatchers. Adult American Oystercatchers are heavier than young birds and consequently have different metabolic rates. Therefore, as each age class handles prey, they will expend energy at different rates. This will modify the rate of gain of calories (RGC) from an oyster. The RGC is fundamental in assessing whether the oystercatchers are selecting the prey which maximizes their energy intake. However, the difference in the metabolic rate of adults and immatures is of minor importance compared to the handling time and calorific content of the prey in all oyster size classes.

A comparison of the RGC of adults and immatures for each prey size within each foraging situation (Tables 18 and 19) reveals that for most oysters larger than the smallest size classes, adults gain energy at a higher rate than immatures. On the dry oyster bed, the young birds tend to have a higher RGC than adults for most prey sizes (Table 18). These results have been explained above. The extremely high RGC of immatures feeding on oysters of 6 ml on the dry oyster bar suggests the presence in the sample of oysters incapacitated by cold.

Table 18. Effect of state of exposure on rate of gain of calories (RGC) for adult and immature American Oystercatchers for each oyster size class.

State of oyster exposure	Oyster size class (ml)	RGC Adult Mean ± S.E.	n	RGC Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
Wet	0.5	35.32 ± 2.65	51	32.04 ± 2.76	48	n.s.
	2	96.22 ± 3.32	173	74.61 ± 3.18	125	***
	4	139.84 ± 8.53	55	108.86 ± 11.59	34	u*d
	6	141.26 ± 19.60	16	103.58 ± 39.21	2	n.s.
Dry	0.5	32.88 ± 4.71	18	46.77 ± 5.91	12	*
	2	77.75 ± 6.15	33	78.15 ± 9.92	24	n.s.
	4	107.55 ± 21.51	9	132.26 ± 23.28	4	n.s.
	6	93.12 ± 16.28	3	192.59 ± 43.32	4	*
	8	164.08		72.37 ± 14.49	2	n.s.
	10	-		-		-
	12	-		49.55	1	-
	14	78.48	1	-		-

Table 19. Effect of oyster density on rate of gain of calories (RGC) for adult and immature American Oystercatchers for each size class.

Oyster density	Oyster size class (ml)	RGC Adult Mean ± S.E.	n	RGC Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
High	0.5	37.85 ± 5.74	18	36.64 ± 3.43	40	n.s.
	2	86.24 ± 10.90	31	64.68 ± 6.39	37	*
	4	117.32 ± 8.73	34	84.72 ± 7.63	13	
	6	105.75 ± 15.50	15	104.46 ± 12.08	12	n.s.
	8	107.17 ± 26.76	4	86.91 ± 13.90	6	n.s.
	10	193.62 ± 23.57	5	112.24	1	n.s.
	12	179.69	1	-		-
	14	117.80	1	-		-
Low	0.5	35.52 ± 2.70	46	35.97 ± 2.60	68	n.s.
	2	87.38 ± 5.00	108	74.24 ± 3.75	100	*
	4	120.07 ± 7.65	66	102.45 ± 8.48	51	
	6	132.05 ± 16.04	27	117.52 ± 10.19	23	n.s.
	8	133.97 ± 15.28	9	75.73 ± 5.75	9	**
	10	141.58 ± 20.63	7	57.14 ± 12.90	2	*
	12	71.00 ± 11.95	3	193.20	1	n.s.
	14	98.43 ± 4.10	2	52.42 ± 12.55	2	n.s.
	16	140.64	1	60.87	1	-

Several important facts concerning the RGC of adults and immatures are revealed when data from all microhabitats are combined (Table 20). Adults and immatures have the same RGC for oysters of less than 1 ml, but adults have significantly higher RGC on most larger oysters. Adults have a higher mean maximum RGC than younger birds (163 and 122 cal/s respectively). The peak RGC occurs on oyster size 10 for adults, and size 6 for immatures, with a general decrease for larger oysters in either case.

4.6.7 Choice among prey sizes

First- and second-year birds choose oysters of approximately the same size (Fig. 10, Wilcoxon test $P = 0.3349$), so these data are pooled. The mean size of oysters eaten by an adult American Oystercatcher was 2.97 ml while immatures took oysters which averaged 2.50 ml. These values differ significantly ($P < 0.001$, Table 21 and Fig. 10). The principal difference between the age classes is that immatures take more prey in the smallest size class and fewer oysters larger than the 2 ml size class, than do adults (Fig. 10). Oysters of the 2 ml size class represent 46.1% of the diet of both adults and immatures (Fig. 10).

The same tendency for adults to select larger prey is evident in each foraging situation, with the exception of the dry oyster bed (Table 21). As discussed earlier, it is likely that immature birds are taking more naturally disabled or dead oysters on the dry oyster bed, some of which are larger than the live oysters which they normally take.

Table 20. Rate of gain of calories (RGC) for adult and immature American Oystercatchers for each oyster size. Data from all foraging situations pooled.

Oyster size class (ml)	RGC: Adult Mean ± S.E.	n	RGC: Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
0.5	35.40 ± 1.69	133	35.78 ± 1.62	168	n.s.
2	90.79 ± 2.57	345	73.49 ± 2.34	286	***
4	125.44 ± 4.76	164	103.50 ± 5.90	102	***
6	126.08 ± 99.62	61	122.06 ± 9.80	37	n.s.
8	128.46 ± 12.57	14	78.51 ± 5.52	18	**
10	163.26 ± 16.70	12	75.51 ± 19.82	3	*
12	98.18 ± 28.46	4	121.78 ± 71.83	2	n.s.
14	98.29 ± 8.20	4	62.09 ± 12.08	3	*
16	140.64	1	60.87	1	-

Table 21. Mean oyster size taken by adult and immature American Oystercatchers in each foraging situation.

Foraging situation	Oyster size: Adult Mean ± S.E.	n	Immature Mean ± S.E.	n	1-Tailed Wilcoxon test
Oyster density					
High	3.72 ± 0.26	109	2.51 ± 0.24	106	***
Low	3.30 ± 0.16	269	2.82 ± 0.16	257	**
High vs. Low	n.s.		n.s.		
Exposure					
Wet	2.33 ± 0.08	295	2.05 ± 0.08	210	*
Dry	2.33 ± 0.27	64	2.60 ± 0.35	47	n.s.
Wet vs. Dry	n.s.		n.s.		
All data pooled	2.97 ± 0.08	778	2.50 ± 0.09	633	***

Io understand more fully the choice of prey items by oystercatchers, it is important to examine the frequency distribution of prey sizes on the three microhabitats of the oyster bed. Overall oyster density and that of each microhabitat have been described in Iable 4. By comparing the prey taken with the prey available (Figs. 11 and 12), I have determined Electivity Indices (Ivlev 1961) for each oyster size class for both adults and immatures in each foraging situation.

Iable 22 gives the Electivity Indices of both adults and immatures in each foraging situation. Recall that a value of E of less than 1.0 indicates that the predator is avoiding the prey item; a value greater than 1.0 means the predator is preferentially selecting this prey size class within a specific microhabitat. A value of 1.0 indicates no choice, as the item has the same percentage occurrence in the diet as it has in the environment. Each of the high E values in the larger prey sizes (12 and 14 ml) on the dry oyster bar is the result of predation on a single oyster. Ihese results can, therefore, be ignored as unrepresentative of the trends shown in the rest of the data.

Ihree important features are demonstrated in Iable 22. Firstly, both adults and immatures avoid the smallest prey sizes in all foraging situations, and adults always have a lower electivity index for this size class than do immatures. Secondly, the electivity indices of adults increase from the smallest size class to oysters of 6 ml while the pattern is not nearly so clear for the immatures. Ihirdly, both age classes have low values of E for prey sizes above 6 ml, indicating that they generally avoid the larger prey.

Figure 11. Comparison of the percentage composition of various size classes of oysters in the diets of adult (white) and immature (black) American Oystercatchers with that in microhabitats (grey) with (A) low, and (B) high oyster density.

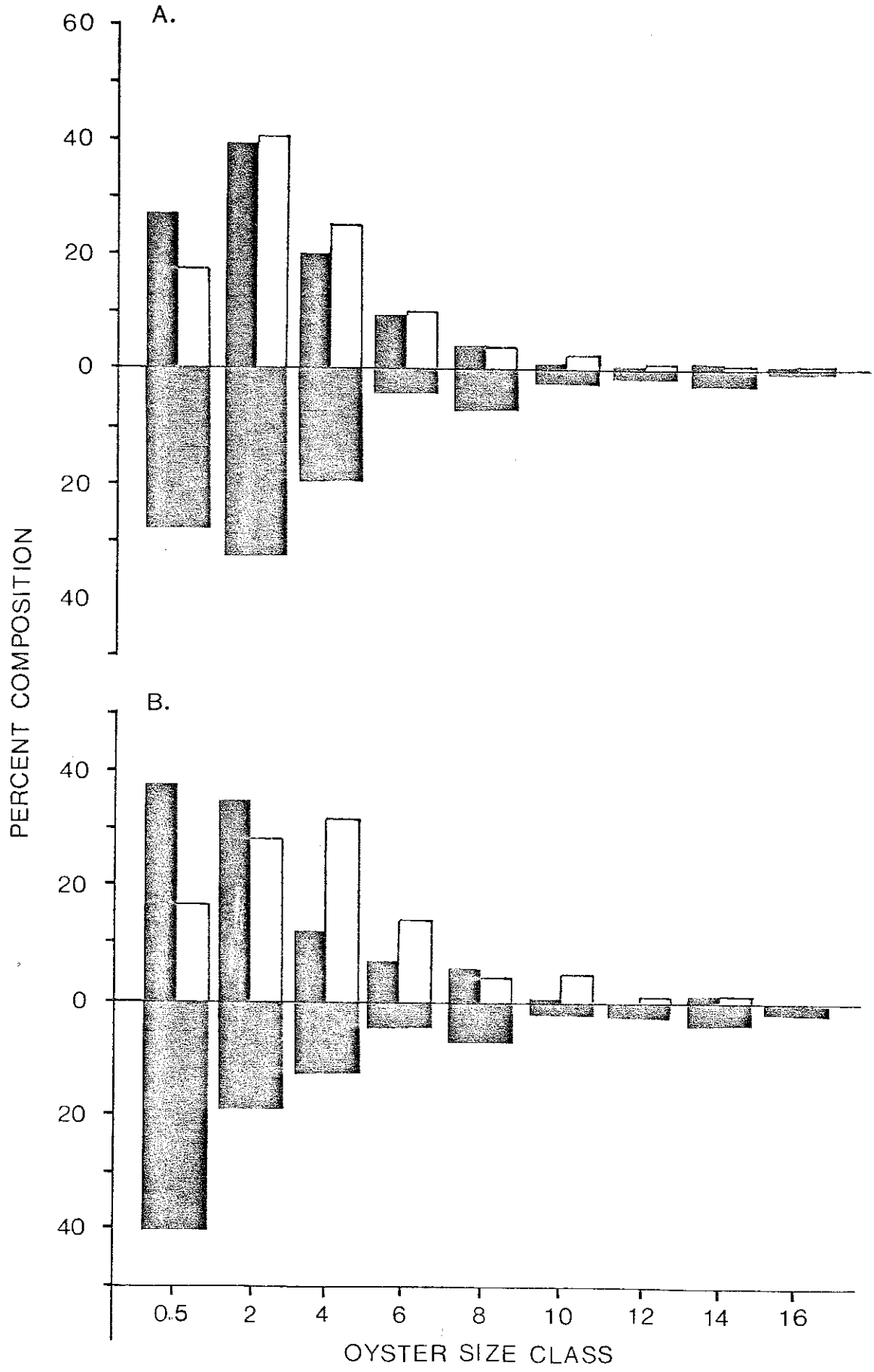

A.
B.
60
40
20
0
20
40
PERCENT COMPOSITION
0.5
2
4
6
8
10
12
14
16
OYSTER SIZE CLASS

Figure 12. Comparison of the percentage composition of various oyster size classes in the diets of adult (white) and immature (black) American Oystercatchers with that in the oyster population (grey).

A. Wet oyster bar

B. Dry oyster bar

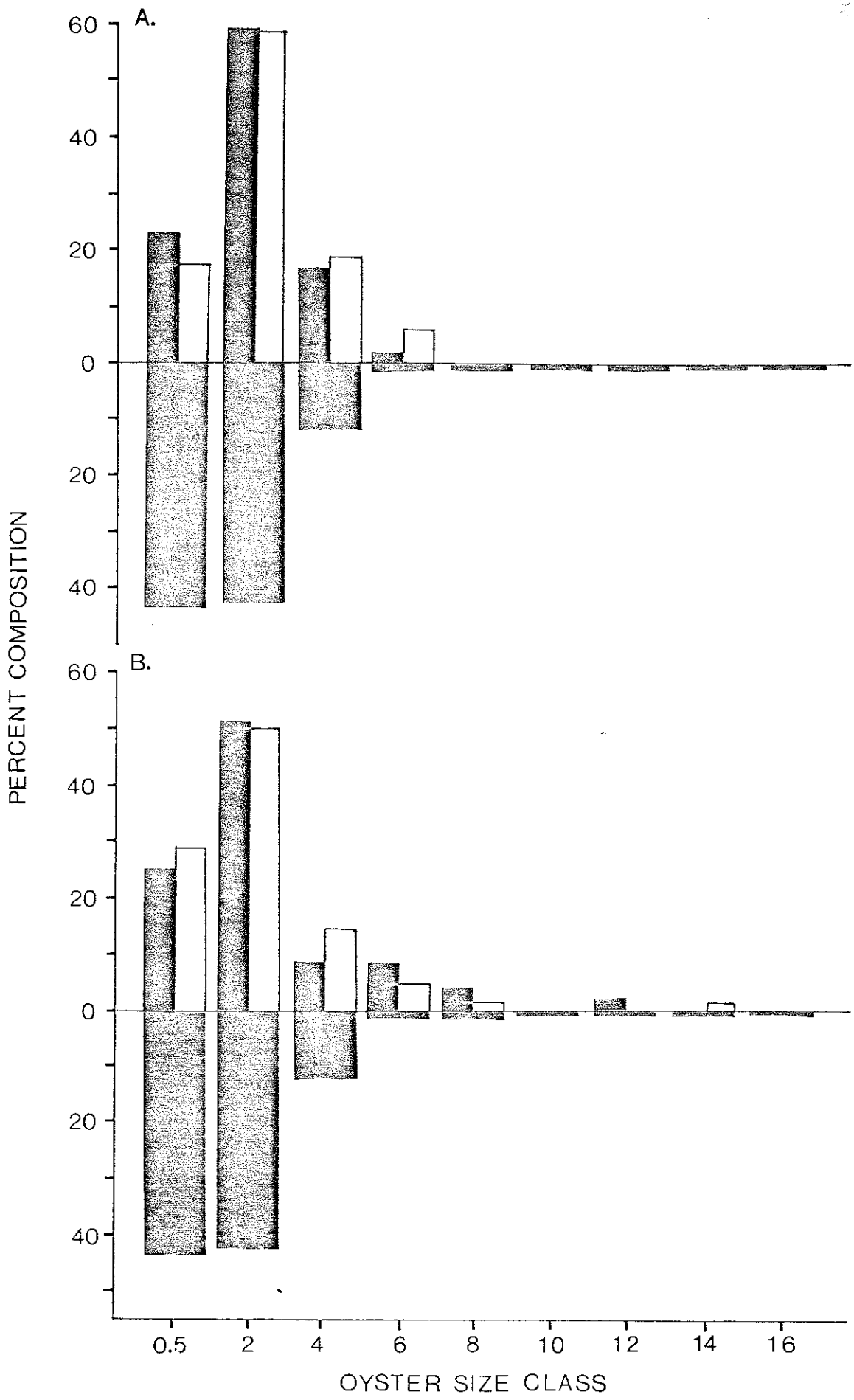
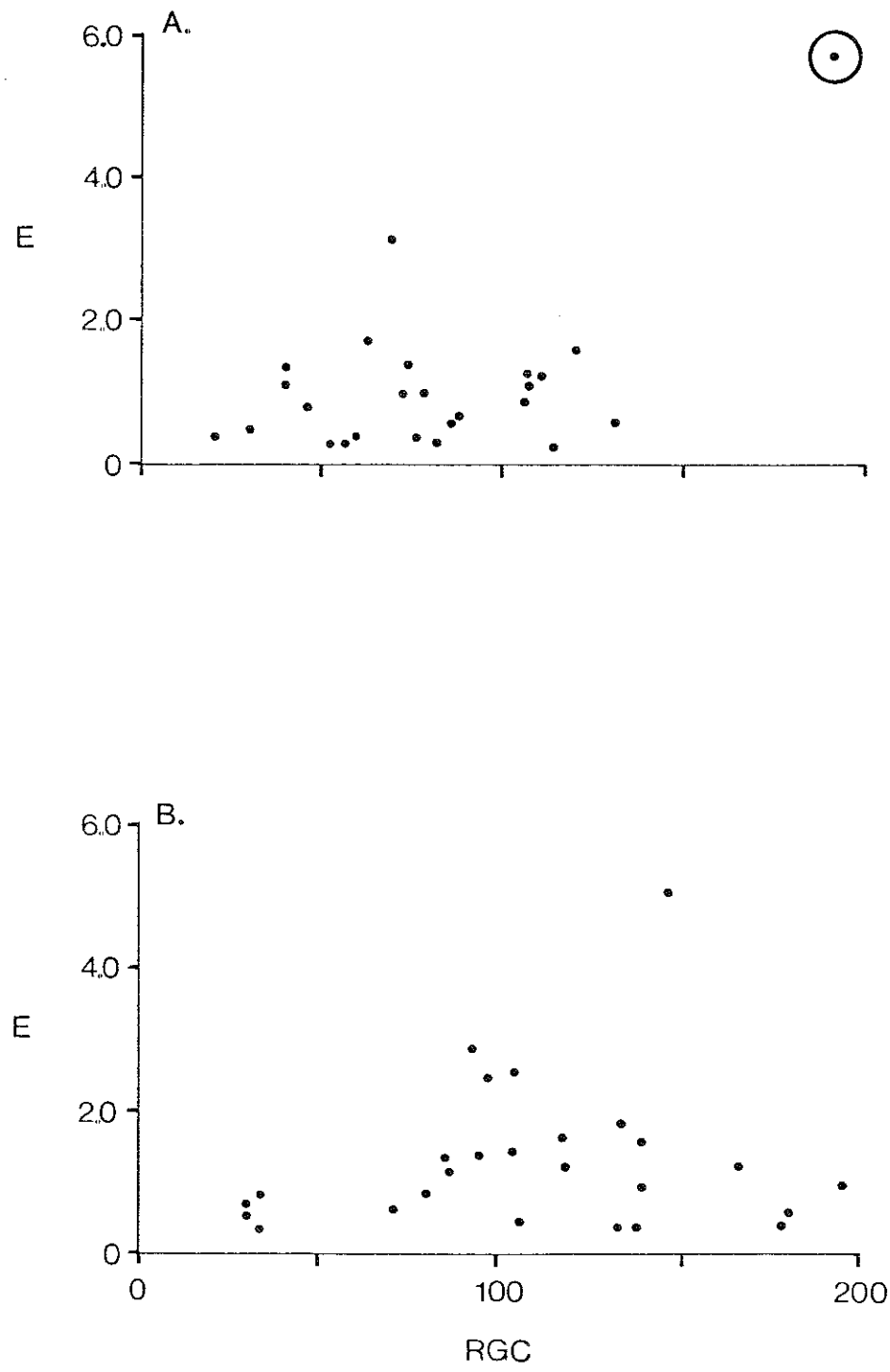

A.
B.
60
40
20
0
20
40
PERCENT COMPOSITION
0.5
2
4
6
8
10
12
14
16
OYSTER SIZE CLASS

Table 22. Electivity indices for adult and immature American Oystercatchers for each foraging situation.

Foraging Situation	Age	Oyster size class (ml)								
		0.5	2	4	6	8	10	12	14	16
Oyster density										
Low	Adult	0.61	1.21	1.26	2.43	0.46	1.10	0.73	0.29	0.49
	Immature	0.94	1.17	1.02	2.17	0.49	0.34	0.26	0.33	0.49
High	Adult	0.41	1.51	1.80	3.33	0.54	1.09	0.40	0.25	0
	Immature	0.94	1.86	0.71	1.81	0.83	0.21	0.40	0.25	0
Exposure										
Wet	Adult	0.40	1.37	1.64	4.82	0	0	0	0	0
	Immature	0.53	1.39	1.42	1.25	0	0	0	0	0
Dry	Adult	0.65	1.17	1.24	4.20	1.14	0	0	17.7	0
	Immature	0.59	1.20	0.75	7.59	3.80	0	21.1	0	0

Figure 13. Relationship between RGC and E for (A) immature and (B) adult American Oystercatchers, when data from all prey sizes and foraging situations are pooled.


A.
6.0
4.0
2.0
0
E
B.
6.0
4.0
2.0
0
E
0
100
200
RGC

4.6.8 Relationship between E and RGC

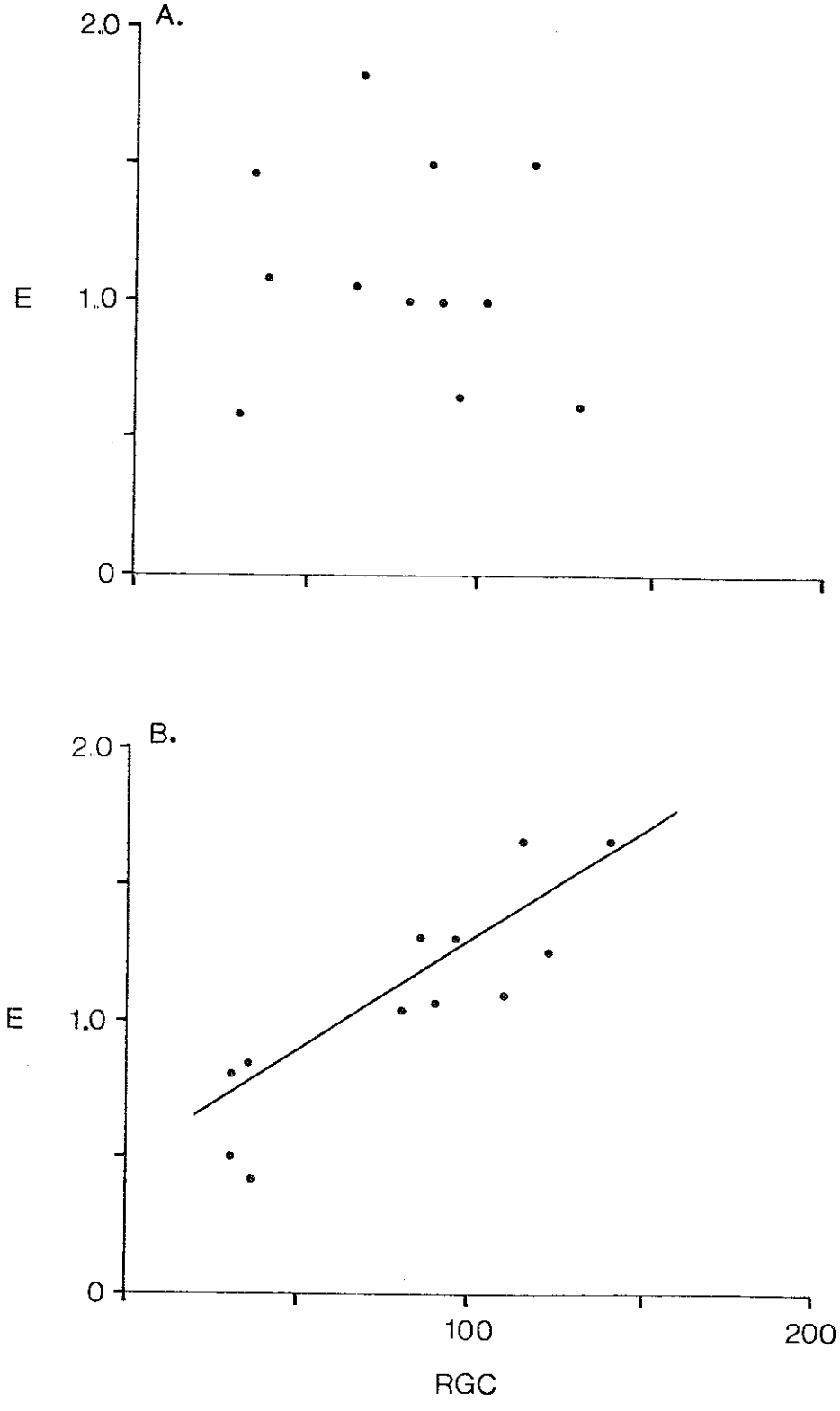
When the data from all foraging situations and prey sizes are combined (Fig. 13), E and RGC are correlated for immatures ($r = 0.588$, $P = 0.002$), but not for adults ($r = 0.008$, $P = 0.6953$). However, the significant correlation for the immatures is the result of a single outlying point and when this point is removed the correlation is not significant ($r = 0.175$, $P = 0.4136$). Although the birds generally have a reasonably high RGC when eating larger oysters (> 6 ml), they tend to avoid them in their diets. The avoidance of large oysters could be due to any or a combination of the following reasons. Large prey involve long handling times. The longer a bird is actively handling a prey item, the greater the risk that it will be noticed by a kleptoparasitic gull or another oystercatcher. The birds might avoid large prey sizes to prevent expending their effort on a prey item that is more likely to be stolen. Alternatively, because the large prey items are rare, the oystercatchers may not have sufficient contact with them to form an appropriate "search image" (Tinbergen 1960). I use the term "search image" here in the originally intended sense of "learning to see" a prey type through frequent encounter (Dawkins 1971). This must remain a highly speculative, however, because no observations of the formation of a search image for particular sizes of a prey species have yet been demonstrated. Thirdly, it seems unlikely that a bird the size of an oystercatcher would be able to disable a large healthy oyster with ease. Foraging oystercatchers are probably able to recognize and take weakened or dead large oysters when they are available. Because these are relatively easy to open, the bird obtains a high RGC. Most of the large oysters taken are probably weakened or dead. However, such oysters are likely to be rare, and so

large oysters will be taken less often than might be expected by looking at RGC alone.

Birds might avoid large, healthy oysters because they are more likely to damage their foraging apparatus on them. The powerful levering and twisting involved in disabling an oyster will place great strain on the bill of the foraging bird. Damage to the bill of an oystercatcher would be extremely serious and most likely fatal during the winter, when most feeding takes place on oyster beds, with oysters as practically the only available food. Slight damage to the bill, such as a chipped bill tip, is observed occasionally in breeding birds, but may be less dangerous because of the lower environmental stress and alternative feeding methods that are possible at this time of year. Further, because of the size and strength of large oysters, it is possible that foraging oystercatchers avoid them to avoid having their bill tips caught between the contracting valves of the alerted oyster. Baldwin (1946) has mentioned this lethal factor for American Oystercatchers feeding on large clams. Unlike most oystercatcher prey, the large oysters are firmly cemented to the oyster bed, preventing the bird from tearing the oyster free, as is the tactic employed when a mussel closes on the bill tips. Oystercatchers were occasionally observed tugging their bill tips free from the valves of an oyster, but I was unable to see the size of the oyster involved.

To avoid the problems involved with the inclusion of larger prey, I correlated RGC and Electivity for all prey in the 4 ml size class or smaller (Fig. 14). I have chosen to omit oysters in the 6 ml size class because birds seldom take them. Also the high electivity index and RGC

Figure 14. Relationship between RGC and E for (A) immature and (B) adult American Oystercatchers for oysters in the 0.5, 2, and 4 ml size classes.


A.
2.0
E
1.0
0
B.
2.0
E
1.0
0
100
200
RGC

for this size class shown on the dry oyster bar by immatures is probably caused by predation on naturally disabled or dead oysters and causes spurious results. This correlation involves approximately 90% of the data collected (Fig. 10). Adults show a highly significant correlation ($r = 0.894$, $P = 0.0001$), whereas younger birds show no such relationship ($r = 0.018$, $p = 0.9553$). Clearly, adults assess the RGC for oysters in each of these prey size classes, and select the prey according to the RGC, but immatures do not.

To explain why the immature birds do not show a clear correlation between E and RGC, I have examined the relationship in each foraging situation separately. Adults select their prey according to the RGC that is obtained from each size. This is demonstrated by the positive slope of the relationship of E and RGC in each foraging situation (Fig. 15). The young birds, in contrast, show a somewhat irregular array of responses in the various foraging situations. In three of the four, young birds show their highest electivity values on oysters in the 2 ml size class, despite the fact that they obtain more calories per second when taking oysters in the 4 ml class.

Immatures show a clear, positive relationship of E and RGC on the wet oyster bar. This is likely because the wet oyster bar may be considered the ideal foraging situation on the oyster beds. Many oysters are still gaping as the tide begins to uncover them, allowing foraging oystercatchers a good selection of prey. Furthermore, oysters are generally handled more quickly on the wet oyster bar than in any other situation (except on the dry oyster bed where many of the prey are probably scavenged) (Table 15). There are several reasons for this. The

Figure 15. Relationship between RGC and E for adult and immature American Oystercatchers in each foraging situation. Values of RGC and E restricted to oysters in the 0.5, 2 and 4 ml size classes are shown.

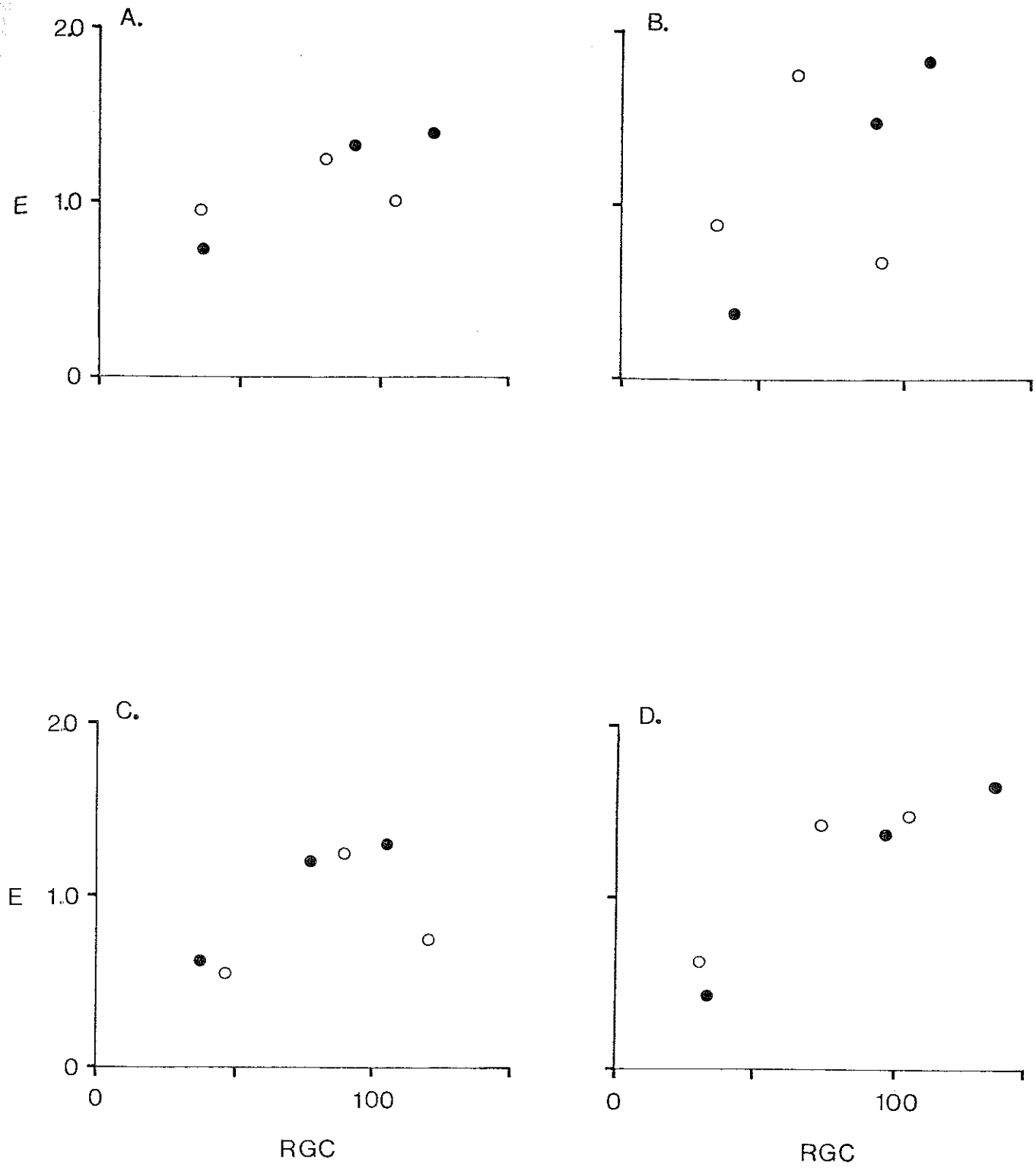
A. Low oyster density

B. High oyster density

C. Dry oyster bars

D. Wet oyster bars

● indicates adults
o indicates immatures


A.
B.
C.
D.
2.0
1.0
0
E
0
100
RGC

gape of the submerged or partially submerged oyster is likely to be at its maximum, resulting in maximum vulnerability, lower handling times and hence higher RGC. The preferential choice of 2 ml oysters by young birds on all but the wet oyster bar suggests that either they have not learned to forage for 4 ml prey, or that because of the weaker bill of the immatures, even oysters in the 4 ml class may be avoided because they are usually too difficult to open.

4.7 Scavenging

Foraging oystercatchers occasionally picked bits of oyster flesh and possibly other invertebrates from within the oyster bed. Usually, the bird simply picked scraps of flesh from previously opened oyster shells. Often the flesh was loose within the shell and the bird could extract it in less than 3 s, in which case I recorded it as scavenging. If the flesh extraction took more than 3 s the observation was classified as a normal predation. First-year oystercatchers scavenge more often than older birds (Table 23, Chi-square = 19.37, $P < 0.001$).

Table 23. The frequency of scavenging by first-year and older American Oystercatchers.

Age	Scavenging observed	Total observations	Percent of diet obtained by foraging[+]
First-year	65	144	3.9
Older	68	281	1.7

[+] Determined by comparing average intake from scavenging with overall food intake.

4.8 Kleptoparasitism

Norton-Griffiths (1967) noted stealing among European Oystercatchers in winter flocks; Brockmann and Barnard (1979) stated, however, that oystercatchers are not kleptoparasites. Nevertheless, kleptoparsitism was a common occurrence on the study oyster bed. Adults had approximately every fifth prey item stolen by other oystercatchers, whereas immatures lost one prey item in fourteen (Table 24).

Brockmann and Barnard (1979) have listed six characteristics which increase the likelihood of kleptoparasitism: (1) a large concentration of hosts; (2) large quantities of food; (3) large, high-quality food items; (4) predictable food supply; (5) visible food; and, (6) times of food shortage. Each of these characteristics applied to the situation on the study oyster beds at some time during observation, so that kleptoparasitism among oystercatchers there is predictable.

A foraging oystercatcher was often chased from an oyster during some stage of predation. Usually the "thief" chased the "host" when it had fully disabled the oyster and had only to remove the flesh from the shell. However, birds were chased from oysters at all stages of oyster preparation, from immediately following the dart-probe until after most of the flesh had already been eaten. There was very little overt aggressive behaviour in the stealing of prey. Feeding birds very rarely attempted to fight off a thief, but endeavoured to avoid kleptoparasitism by subtle aggressive postures. If a potential host became aware of a likely thief nearby, its posture became noticeably stiffer and the host would orient itself to obtain a clear view of the thief. This apparently functioned as a signal to the potential thief that the host

Table 24. The frequency of stealing from each age class by adult and immature American Oystercatchers.

Host	Thief[+]		Percent of prey items stolen
	Adult	Immature	
Adult	55	95	19.3
Immature	17	29	7.3

[+] Chi-square = 0.004, P > 0.9

was willing to defend the oyster. Kleptoparasitism was rarely attempted once the host was aware of the thief.

Kleptoparasitism was successful when the thief approached undetected from the rear. The thief walked or flew in behind the host, which, when startled, simply walked or flew away and began to search for another oyster. The ease with which a host usually gave up its prey is somewhat surprising. However, if the thief is highly motivated and willing to fight or at least disturb the host for some time, the host might be better off energetically by giving up its prey and searching for another. In support of this hypothesis, I observed several aggressive encounters over prey items which resulted in piping displays lasting several seconds, with neither bird eventually getting the oyster.

The surprise approach from the rear by thieves in intraspecific kleptoparasitic bouts has been reported in Herring Gulls by Drury and Smith (1959), and appears to be, as in oystercatchers, a method by which young birds are able to chase adults from their prey.

Immature oystercatchers steal more prey than adults (Table 24), and both adults and immatures tend to steal from adults (Table 25). Drury and Smith (1959) reported that immature Herring Gulls stole from adults, and that adults were less inclined to steal. This observation may be partially explained by Brockmann and Barnard (1979), who mention that kleptoparasitism occurs more often in times of food shortage. As young birds have more difficulty in obtaining food than adults, they are effectively in a state of "food shortage", and so are more likely to steal. Young birds may steal more often because they can obtain an energetic return approximately as great as that they can gain by feeding

Table 25. Frequency of intraspecific kleptoparasitism by adult and immature American Oystercatchers.

Age	Feeding observations	Observations of stealing[+]
Adult	300	72
Immature	231	124

[+] Chi-square = 48.1, $P < 0.001$

themselves. Adults steal infrequently, their superior prey handling capabilities apparently allowing them to obtain energy at a higher rate by finding other food for themselves (see Verbeek 1977a).

4.9 Ingestion rate

Ingestion rate is defined as the volume of oyster flesh eaten by a bird during a 5 min observation period. Rates are highly variable within each age class, due in part to the sampling procedure and to the great variance in food intake over a 5 min period. Variance due to sampling is the result of my decision to follow only birds which were actively hunting, giving me no indication of the time since their last prey item. Also, because I did not use birds which were actually eating an oyster at the beginning of a 5 min period, the results underestimate the true food intake.

Although first-year birds consume on average less oyster flesh per 5 min observation than do older ones, the differences in ingestion rate are not significant (Table 26). Second-year birds tend to take more oysters during a 5 min period than other ages (Table 27), but again the differences are not significant.

Table 26. Ingestion rate of first-year, second-year and adult American Oystercatchers. Ingestion rate is computed as the volume of oyster flesh eaten in a 5 min observation.

Age	Ingestion rate	
	Mean ± S.E.	n
First-year+	5.78 ± 0.36	169
Second-year+	6.75 ± 0.65	62
Adult+	6.83 ± 0.32	300

+ Means are not significantly different (Duncan's multiple range test $P > 0.05$).

Table 27. Number of oysters eaten in 5 min by first-year, second-year and adult American Oystercatchers.

Age	Number of oysters eaten[+]	
	Mean ± S.E.	n
First-year[+]	2.41 ± 1.69	169
Second-year[+]	2.76 ± 1.77	62
Adult[+]	2.40 ± 1.80	300

[+] Means do not differ significantly (Duncan's multiple range test, $P > 0.05$).

4.10 Daily food intake and daily energy requirements

The comparison of daily food intake and daily energy requirements shows that all age classes of oystercatchers were able to obtain their daily energy requirement on the oyster bed in the time available to them during daylight (Table 28). These values are calculated using the percentage of time spent feeding (Table 1), which, as explained above (p. 43) is only approximate, especially for second-year birds. My estimate of food intake is an underestimate of the actual overall intake rate, but even this value is enough to permit the avoidance of starvation. This is in marked contrast to the situation in some populations of wintering European Oystercatchers, which move inland to feed in fields at high tide to supplement their natural intertidal feeding regime, and also feed at night (Heppleston 1971). Heppleston found that the average daily intake of oystercatchers in northern Scotland was 317 kcal per day in October and 222 kcal per day in December and January. Heppleston estimated that both of these values were below daily requirements, but he calculated daily requirements by a rather imprecise method using food intake in captivity. Goss-Custard et al. (1977a) estimated daily energy intake of European Oystercatchers in southern England in winter to be 296 kcal per day. Like the American Oystercatchers in the Chincoteague area these birds were thought to acquire their energetic needs without feeding at night. The high density and availability of oysters and the ability of American Oystercatchers to open them efficiently allow the birds to obtain their daily energy requirements, even at the northern extreme of their winter range.

Table 28. Daily energy requirements and daily food intake of American Oystercatchers at 0°C.

Age	Feeding time/day (min)	Intake/min (cal)	Intake/day (kcal)	Energy requirement (kcal)
First-year	265.54	1040.2	276.2	269.8
Second-year	221.40	1214.8	269.0	269.8
Adult	249.37	1229.2	306.5	287.6

5 DISCUSSION

5.1 Age-related foraging efficiency

American Oystercatchers in their third year or older exhibit development of tactical and possibly also strategical aspects of foraging superior to that of immature birds. Adults open oysters relatively quickly and, unlike immatures, select oyster sizes which provide them with the maximum energy intake during prey-handling.

The traditional reason given for the superior tactical ability of adults has been that young birds have not yet learned to forage as capably as adults. The literature available on oystercatcher development (Dewar 1920, Lind 1965, Norton-Griffiths 1967) certainly provides evidence that learning occurs in young birds, and leads to improvement in the tactical components of feeding. Young oystercatchers have an apparently innate repertoire of foraging techniques which they employ on edible and inedible objects. Through trial-and-error learning (perceptual sharpening, see Hailman 1967) and food reinforcement, they learn to concentrate on edible items and gradually improve their efficiency in each of the techniques (Norton-Griffiths 1967).

Morphological maturity of the bill and skull is also likely to be of importance in the acquisition of adult foraging proficiency. Heppleston (1970) describes the bill of the chick at hatching as being about 16 mm in length, and extremely flexible due to lack of ossification of the bony core. The bill gradually lengthens and strengthens as the chick develops, and in the European Oystercatcher it attains adult length at nine weeks (Heppleston 1970). Variation in the strength of

the bill with age has not been considered previously, but the X-rays (Plates 4-11) suggest that the bills of adults are stronger than those of birds up to two years of age.

The strengthening of the skull and rostrum through bone deposition makes the foraging apparatus of adults better suited for levering and twisting open oysters. Adults will also be able to deliver the dart-probe more powerfully, thus aiding in the opening process by allowing the bill tips to penetrate further between valves of the oysters.

The more pointed bill tips of young birds are generally less well suited for chiselling bivalve flesh from the shell. Norton-Griffiths (1967) surgically blunted the bill of an immature bird to approximate the shape of the adult bill tip. He discovered that this young bird could then chisel with the proficiency of an adult. However, he did not consider the size of the prey involved. This single example should not be over-interpreted, but it certainly suggests that the young birds are limited by their morphological development. Norton-Griffiths (1967) has proposed that the bill of young European Oystercatchers remains sharp to help the bird maintain the capacity to probe for invertebrates. As no description of the summer diet of immature American Oystercatchers exists, it is possible that they forage by probing for other invertebrates such as worms when not on the wintering grounds. It is unlikely that they would feed on oyster beds throughout the year because the beds are preferred feeding areas during the breeding season for breeding birds, which defend the oyster beds as part of their exclusive feeding territory. In fact, breeding birds frequently chased several immature birds from the study oyster beds during April 1978. If other

invertebrates are important prey of young birds during the summer and fall, then the shape of the bill tips of the young birds may represent a compromise between its various year round needs, and hence, may not be perfectly suited to handling oysters. Alternatively, as discussed above, the bill of the immature oystercatcher may simply be a poorly developed foraging tool.

The development of prey handling ability in American Oystercatchers is probably dependent upon both learning and morphological maturation. As the young bird's foraging apparatus matures its capabilities are modified and it must learn how to use its abilities to maximum advantage. Adults are able to open all but oysters of the smallest size class in less time than immature birds. Handling time is a measure of the ability to open and disable the oyster and extract the flesh. Adults disable prey more quickly than do younger birds. To disable an oyster, oystercatchers use the dart-probe followed by rapid, powerful, precisely oriented levering and twisting. The strength of the bill and skull are instrumental in determining the limits of the force used by the birds in levering and twisting and the delivery of the dart-probe, and hence, the duration of disabling time. Adults are considerably less tentative and use noticeably more powerful movements during prey handling, which will serve to reduce handling time. Learning is important in the determination of levering ability, through the modification of the precise orientations used in levering and twisting (Norton-Griffiths 1967).

After disabling the oyster the bird continues to lever and twist until the valves are wide enough apart to allow for efficient removal of the flesh. Because of their superior chiselling ability, adults remove the flesh in fewer bites than younger birds (Table 16). Technique rather than strength of the foraging apparatus determines chiselling proficiency. Consequently, learning will be of paramount importance in the acquisition of efficient chiselling. Both this study and that of Norton-Griffiths (1967) suggest that chiselling ability improves beyond the age of two years. The intricate co-ordination of movement and precise orientations necessary for efficient chiselling are apparently extremely difficult for oystercatchers to learn. Additionally, the narrow bill tips of the young bird may be less well suited to chiselling, especially for oysters larger than 1 ml. Several other species of birds improve their prey-handling ability as they age. For example, Reed warblers (Davies and Green 1976) handle prey more quickly as they grow and gain experience, and Royal Terns in their first year drop their fish more often than do adults.

The lower peck rate exhibited by adults is more efficient and results in less energy expenditure in finding prey. The elevated peck rate of the young birds, which presumably is the result of inferior dart-probing technique, reflects more missed prey. Similarly Little Blue Herons miss their prey less often as they age (Recher and Recher 1969). However, when handling an oyster, immature birds can gauge as efficiently as adults whether they will be succesful in predation, and spend no more time than adults on such prey (Table 8).

Adults show a negative correlation between peck rate and the number of oysters taken in 5 min. This suggests that they make very selective dart-probes when foraging in a good "patch". Younger birds do not follow this trend, indicating that they are unable to judge patch quality. There is some evidence to suggest that American Oystercatchers improve in their ability to locate prey with experience. Second-year birds consume an average of more oysters per time foraging than first-year birds (but the difference is not significant, probably due to the small sample size of second-year birds (Table 27)).

Immatures exhibit higher electivity indices for oysters in the 2 ml size class than for those in the 4 ml class, despite the higher energetic return (RGC) from these larger oysters. They are apparently choosing a less efficient strategy than that used by adults, which have a higher electivity index for 4 ml than for 2 ml oysters. Because the skull is less robust and foraging techniques are still being learned, the young bird is unable to open prey as quickly as an adult. Also, adults are probably able to handle succesfully larger, more powerful oysters than young birds. However, even adults take few prey above the 4 ml size class despite the high RGC obtained from them. It seems probable that when healthy, these oysters are too difficult for oystercatchers to open, and that the high RGC values result from the birds finding a few large oysters which are particularly vulnerable or are disabled, perhaps due to cold or disease. These would be easy to open and would consequently provide a high RGC.

The strain put on the bill when levering larger, healthy prey will be excessive, and the young birds, with their less robust bills, will be forced to choose smaller prey than adults, which they are capable of handling. The fact that young birds elect to take more oysters of 6 and 8 ml on the dry oyster bed than do adults, indicates that they are, indeed, taking some weakened or dead oysters. Adults need not look for dead or injured oysters in the 4 ml size class, their bill and skull being better suited morphologically to handle this size of oyster. But immature birds are more likely to experience difficulty with 4 ml oysters, so they take fewer than adults because they are probably restricted to more vulnerable individuals.

Pyke et al. (1977), in a review of optimal foraging theory, have stated that optimal foraging is dependent upon heritable variation in foraging behaviour. Optimal foragers survive periods of food shortage, have more young, and must allocate less time to feeding (Charnov and Orians 1973). However, as pointed out by Goss-Custard (1979) it is only necessary for the predator to forage in a manner which is superior to its conspecifics and not necessarily to forage optimally. Efficient foraging becomes prevalent because the most capable foragers are most likely to pass on their foraging behaviour. This "heritable variation" in oystercatcher foraging behaviour probably entails the ability to learn and to gauge RGC. Birds which are able to gauge RGC most efficiently can utilize the techniques available to them to maximum potential, and select the most appropriate prey. Learning must be highly developed in these birds so that they acquire the most efficient techniques and learn relative prey value, as rapidly as possible. Therefore, birds of all ages will likely choose prey according to their

present tactical capabilities. Adults, with their powerful, robust skulls and bills, and their blunt bill tips will generally choose larger prey than young birds. Immature birds, which are still developing and perfecting their oyster opening techniques, have a less robust foraging apparatus and pointed bill tips. All of these factors combine to make the immatures better suited for the predation of small oysters.

Different aspects of foraging appear to be inherited in other species of birds. Loggerhead Shrikes (Lanius ludovicianus) (Smith 1973) and American Kestrels (Falco sparverius) (Meuller 1974) are able to recognize, capture and perform the complex techniques necessary to kill mice on their first exposure to them. Such efficiency may be essential early in life, as members of species which take large, occasional prey are in grave danger of starvation if they are unsuccessful in several consecutive attempts at predation (Ashmole and Iovar 1968).

Oystercatchers require the ability to learn because of their morphological specialization. Iheir bill grows in length for several months, and in width, height (Baker 1975) and strength for over two years. Flexibility of foraging technique and prey choice are essential to ensure the maximization of foraging potential of all ages.

The generally high rate of mortality among immature European Oystercatchers as compared to adults is evidence that young, independent oystercatchers are less well suited to meet the requirements for survival in their environment than adults. While mortality rates of H. palliatus have not been investigated to date, it seems likely that immature birds would suffer higher mortality in times of food shortage because of their inferior tactical and strategical proficiency. Young

European Oystercatchers are not as prepared as adults for the predation of shellfish, and suffer high mortality because of it, particularly first-year birds. They are constrained by the necessarily prolonged development of their foraging apparatus; as a result, they are less likely to survive the rigorous demands placed on them by the environment.

The prolonged development of oystercatchers is made clearer when their foraging ecology is related to breeding biology. Oystercatchers lay fewer eggs than most shorebirds, the modal clutch size being two or three eggs, depending on the species (Baker and Cadman, in press). They lay fewer eggs because, unlike most species of shorebirds, oystercatchers feed their young. Upon hatching, the chicks have small, plover-like bills which rapidly lengthen to reach adult length within several months (Baker 1975). The foraging techniques necessary to open and eat their shellfish prey must be learned and their bills must be of specific dimensions before they are useful in shellfish predation (Norton-Griffiths 1967). For these reasons, the young are unable to feed themselves and are under parental care for several months. Gradually, they improve their foraging technique through learning and morphological development.

It seems probable that the development of the bill and skull occur as rapidly as possible, given the constraints of the feeding capabilities of the young bird. When first independent, the young bird is probably able to take in barely enough food to survive, but as it learns and perfects foraging skills it will be able to increase food intake and thus deposit bone and strengthen its bill and skull.

The extreme ecological specialization of oystercatchers necessarily means that they are prone to a high rate of mortality in the first two years as they learn complex prey-specific feeding techniques. Harris (1967) has calculated that the average annual mortality of immature European Oystercatchers is 40%. Mortality beyond the second year is only eleven per cent (Harris 1967) so that birds which survive their second year are frequently long-lived.

There are three other possible explanations for the tendency of young birds to avoid prey which provide high calorific return: (1) Young birds select smaller prey to avoid competition with adults. This implies that immatures choose a less efficient strategy, which would not be selected for, unless perhaps prey was scarce. However, oysters are abundant on the beds. In addition, both adults and immatures take mostly oysters in the 2 ml size category, which would suggest that avoidance of competition is not of great importance in the selection of prey for either age class. It is more likely that young oystercatchers are limited by their lower foraging capacity as a result of the as yet imperfect learning of foraging technique, and morphological immaturity.

(2) Oystercatchers must learn the relative value of all sizes of oyster in their environment. Young birds may not choose 4 ml oysters as often as would be expected from RGC because they have not yet had sufficient experience with all prey sizes to rank them accurately. Small oysters provide them with sufficient energetic return, so they maintain a diet of these small prey despite the greater energetic return obtainable from larger oysters.

A capacity to quickly ascertain energetic return from various prey sizes and then to rank and choose prey accordingly would be a great selective advantage. The ability of predators to rapidly gauge prey value and to select prey accordingly has been shown in Great Tits (Parus major) by Krebs et al. (1977). It seems likely that oystercatchers of 6 to 18 months of age would have learned the relative values of the various size classes of oysters and would consequently select the most profitable prey. Davies (1977b) has demonstrated that young birds are able to rank opposing strategies. Young Spotted Flycatchers became independent of their parents when they were able to obtain energy more efficiently by feeding themselves than by begging from their parents.

(3) Young birds select small oysters because they differ somewhat in nutrient content. I am not aware of any literature on the chemical constituents of oysters of various sizes. It is possible that small oysters are richer in some essential nutrient (e.g. protein or Ca - Fisher 1972) which is of great importance to young birds. Immature birds may not be ranking oysters by energetic return alone and hence should not be expected to choose them on this criterion (Clark 1980). Without data to test this hypothesis it must remain a viable alternative to those listed above.

The superior capabilities of adults demonstrate that learning and probably also morphological development are of great importance in the acquisition of adult standards of proficiency. The observation that first- and second-year American Oystercatchers have very similar tactical and strategical capabilities is probably largely due to the small sample size of second-year birds and the large variability inherent in the collection of the foraging data.

5.2 Implications of superior adult foraging proficiency

Young American Oystercatchers gain energy at a lower rate than adults when handling oysters. Consequently, they steal more often (Table 25) and scavenge more often than adults, and do not breed.

Young birds tend to steal from adults (Table 24). Similarly, immature Herring Gulls steal prey from conspecifics more often than do adults (Verbeek 1977a). Verbeek reasoned that stealing becomes less important as a means of obtaining food as the bird ages, and suggested that adults steal infrequently because they can acquire energy more efficiently by finding food by themselves. Because immature H. palliatus handle prey less quickly and take smaller prey than adults, stealing could well be as profitable to them as seeking new prey to open. When stealing oysters, they usually chase a bird when it has either completed disabling the prey or during removal of the flesh. The resultant handling time will be shorter than if they had opened the prey by themselves, and consequently the rate of gain of calories during handling will be higher.

The stealing of prey by immatures from adults resembles the system of parental care exhibited during the time in which the birds are dependent on the adult for food. Dewar (1920), Lind (1965) and Norton-Griffiths (1969) have described how adults, during the time of chick dependence, partially disable the prey and then leave it for the young bird waiting close by. Adult and chick may even alternate bouts of levering on the same shellfish (Lind 1965, Norton-Griffiths 1967). Additionally, when presenting food to a dependent chick, the adult stands with its bill pointing vertically down at the prey item until the chick

approaches (Dewar 1920, Lind 1965, 1978, Norton- Griffiths 1967). Although there is erosion of this behaviour as the chicks age and become more self-reliant, it is clear that the young bird could associate food with an adult standing in the same posture described above, which is typical in the opening of oysters.

As there were very few marked birds in the population, it was impossible to determine how much of the stealing consisted of first-year birds taking prey from their parents. However, the parents of four marked birds seen over the winter were not observed on the study area. I occasionally saw these chicks steal from adults which were obviously not their parents. There were no overt indications of family ties within the wintering flock during the period of observation. Furthermore, all age classes of birds were involved in stealing to varying degrees, indicating that more than the taking of prey from parents is involved in intraspecific kleptoparasitism among American Oystercatchers. It is probable that it is more efficient energetically for adults to give up the oyster without a fight than it would be to defend it, especially when food is readily available.

First-year oystercatchers scavenged more than older birds. They looked for scraps of flesh left in shells by other oystercatchers, and spent more time on the dry oyster bed where dead or disabled oysters were more likely to be found. Because adults clean scraps from emptied shells and forage on the dry oyster bed less frequently, it might appear that immature birds are using inefficient foraging techniques. As there were few marked birds on my study area, it is possible that only very inefficient immature birds used these techniques to obtain food. These

inefficient birds would probably suffer high mortality rates before reaching adulthood, so that few adults would behave in this manner (Dunn 1972). However, scavenging, which represented at least 4% of total food intake of first-year birds, probably occurs because it is within the range of energetic efficiency of first year birds. The pieces of flesh which are scavenged are frequently as large as small oysters and are handled in a shorter handling time. Additionally, it seems probable that some of the small prey taken by immatures were, scavenged pieces of oyster flesh. Some pieces would probably be difficult to extract, and would require more than 3 s to handle. These were classified as normal predations on small oysters.

The fact that oystercatchers feed in flocks during the winter presents a distinct advantage to young oystercatchers. American Oystercatchers feed on a variety of food types during the breeding season, most of their feeding taking place on feeding territories in and around the salt marsh (Cadman 1979). When oystercatcher chicks are old enough to travel, they are taken to the feeding territory, where they are fed by the parents, and where they learn to feed themselves (Lind 1965, Norton-Griffiths 1967). The young birds may not be fed, or learn to feed on oysters, as they are often scarce on the feeding territory. Therefore, when the birds flock in winter and concentrate solely upon oyster beds, many young birds will be inexperienced with oysters. Flock feeding will aid the young birds in the recognition of oysters as prey through the example of the adults (Drury and Smith 1968, Turner 1965, Weigl and Hanson 1980), through removing scraps from previously opened shells, and through kleptoparasitism (Norton-Griffiths 1967). The removal of scraps and the stealing of partially opened prey will assist the

young birds in learning to efficiently handle oysters. Immature birds are able to supplement their diet with stolen prey because of the large number of adults in the flock. Also, when more oysters are eaten, more scraps will be left in shells. These scraps are of particular value to first-year birds.

Ashmole (1963) has hypothesised that deferred breeding is at least partially the result of the inability of young birds to feed at the level of efficiency necessary to successfully withstand the demands of breeding. The deferral of first breeding to at least 3 years of age in oystercatchers is consistent with this hypothesis, because it is at this age that they acquire foraging efficiency equal to that of breeding birds.

If third-year American Oystercatchers were able to forage as efficiently as adults on the oyster beds in winter, it does not necessarily follow that they would be capable of withstanding the rigorous demands of breeding (see Mercer 1968). The American Oystercatcher breeds on beaches and high salt marsh (Cadman 1979) and often defends a separate feeding territory elsewhere. Oysters are the major prey type on few of these territories, so that breeding birds need to be fully efficient in obtaining the other prey types available in the salt marsh and adjacent mudflats. Principal prey species there are the Stout Razor Clam, the Hardshell Clam (Venus mercenaria) and the Ribbed Mussel, each of which is obtained by different foraging methods (pers. obs.). The oyster beds are ideal foraging areas for oystercatchers, and third-year birds are more likely to show foraging efficiency equal to that of adults in this habitat. In the salt marsh environment, however, prey is much less

densely dispersed, and requires a wide range of foraging techniques which the third-year bird may not yet have perfected. A similar argument can be used to explain why second-year birds, which attain the same ingestion rate as adults, do not breed. However, the additional observation that second-year birds cannot handle prey as efficiently or select large energy efficient prey as readily as older birds, must also be of significance in their inability to breed.

Several species of birds which show deferred breeding exhibit relatively poor success in their first breeding attempt (Blus and Keahey 1978, Coulson and White 1956, 1958, Richdale 1949, Lack 1954, Ryder 1975, Ainley and Schlatter 1972). It is possible that third-year American Oystercatchers have lower breeding success than older birds. Lack (1954) has suggested that deferred breeding may occur because young, inexperienced birds are more likely to suffer mortality through an early breeding attempt than are older birds. Mortality rates of young kittiwakes (Rissa tridactyla, Wooler and Coulson 1977) provide evidence in support of this hypothesis. Thus, it might be more efficient for third-year oystercatchers which are not fully proficient in their foraging ability to delay breeding until their fourth year or later.

Norton-Griffiths (1967) has shown that European Oystercatchers continue to improve their foraging ability until at least their third winter. European Oystercatchers, however, rarely breed at three years of age, the usual age of first breeding being four or five years (Harris 1967). The situation may be different in North America. I tentatively identified two birds, which were members of breeding pairs in the Chincoteague area, as third-year birds. It is possible that American Oys-

tercatchers would be able to begin breeding at three years because of reduced competition for breeding space (see Lack 1968). Populations of American Oystercatchers were severely reduced during the nineteenth century (Bailey 1876, Beyer 1908), and started to recover slowly in the twentieth century (Bowdish 1909). The rapid expansion of the range and population of the American Oystercatcher during this century has been well documented in American Birds. This rapid extension of range might permit younger birds, normally unable to breed through lack of space, to form pairs and attempt breeding. In Europe, the range of the oystercatcher is more stable, and populations are much larger than those of the American Oystercatcher (Dare 1966). This might enable only a few third-year birds to attempt to breed.

Additionally, no mortality was observed among first-year birds and all ages achieved their daily energy requirements at Chincoteague, the northern extreme of the winter range. This suggests that American Oystercatchers may also be subject to less feeding stress than their European congeners, and hence may attempt to breed at a younger age. Ashmole (1963) indirectly supports this idea in stating that in years of food abundance, birds which are usually too young to breed will attempt breeding.

Deferred breeding has been generally accepted in the literature regarding age-related foraging efficiency to be due to poorly developed foraging techniques in younger birds. In immature American Oystercatchers, foraging efficiency seems to be attributable to both the degree of learning and the morphological constraints in the growing bill. The latter aspect is deserving of study in other species to determine its

general relevance for foraging theory.

6 SUMMARY

1. X-rays of the skulls of American Oystercatchers reveal that ossification of bones of the skull continues beyond two years of age. It is proposed that the more robust skull of the adult is a more powerful foraging tool, and hence is better suited for opening large oysters, and opening smaller oysters more quickly.

2. American Oystercatchers wintering in Shelly Bay near Chincoteague, Virginia, foraged in intertidal oyster beds where they fed almost exclusively upon oysters. They did not feed at night or at high water when the oyster beds were unavailable.

3. Adults possess superior predatory ability. They handled oysters in less time than did immatures; they disabled them more quickly and removed the flesh in fewer pieces than did immatures.

4. Immatures, on average, took smaller oysters than did adults. However, both age classes were generally restricted to small oysters, such that only 10% of prey items were of 5 ml volume or larger.

5. When all oyster sizes were considered, neither adult nor immature American Oystercatchers preferentially selected the large oysters which provided them with maximum energy return. It is proposed that large healthy oysters were too powerful to be taken by American Oystercatchers, and that the apparent high energetic return from these oysters was a result of the occasional predation of disabled or dead individuals.

6. When only oysters of less than 5 ml were considered, adults preferentially selected oyster sizes which provided them with maximum energetic profit, while immatures did not. It is proposed that immature American Oystercatchers, because they are less well developed morphologically, were more restricted than adults in their choice of prey sizes. Therefore, even oysters of approximately 4 ml, which were most energetically profitable for immatures, were not selected as often as would be predicted from their high profitability because they were difficult for the young birds to open. When oysters of less than 3 ml are considered, both adult and immature American Oystercatchers preferentially selected more profitable sizes of prey.

7. First-year, second-year and adult American Oystercatchers had similar ingestion rates; each age class generally achieved its daily energy requirements. However, first-year birds supplemented oyster predation with scavenging for bits of oyster flesh left in oyster shells by other oystercatchers. Also, immature birds tended to spend more time on dry oyster bars, where they appeared to take more disabled oysters than adults. Immatures supplemented their diets further by stealing prey from adults, thus increasing their own ingestion rate while decreasing that of older birds.

8. American Oystercatchers do not breed until they are at least 3 years old, the age at which they acquire foraging proficiency equal to that of older birds. These findings are consistent with the hypothesis that deferred breeding is at least partially the result of inadequate foraging skills of immature birds, as postulated by Ashmole (1963).

7 LIIERAIURE CIIED

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