AN ABSTRACT OF THE THESIS OF

Kenneth R. Yates for the degree of Doctor of Philosophy in
Zoology presented on June 5, 1989.

Title: The Feeding Ecology of the Gumboot Chiton,
Cryptochiton stelleri (Middendorff, 1846)

Abstract approved: _____ 𝐵𝓇𝓊𝒸𝑒 𝐴·𝑀𝑒𝓃𝑔𝑒 _____
                        Dr. Bruce A. Menge

        Investigations about the feeding ecology of a consumer
can facilitate prediction of its effects on prey populations
and the biological community. The aspects of feeding
ecology that are important to predicting consumer effects
include foraging movements, feeding preference and
selectivity, and the effects of physical factors on foraging
behavior and feeding rates. All of these aspects were
investigated for a large invertebrate marine herbivore,
Cryptochiton stelleri (Middendorff, 1846), the gumboot
chiton.

        The movements of 252 Cryptochiton were observed during
periods ranging from 1 to 512 days. Movements of subtidal
chitons were significantly greater than those of intertidal
chitons during the same time period. Movements of
intertidal chitons on emergent substrata were not
significantly different from those on submergent substrata.
The home ranges of subtidal chitons were, in general,

significantly larger that those of intertidal chitons. These patterns suggested that the impact of intertidal chitons on macroalgae will be more restricted in area than for subtidal chitons. Assuming that consumption rates are equal, the impact of an intertidal chiton would be more concentrated, thus causing a more patchy effect.

The feeding behavior of Cryptochiton was examined by comparing laboratory preferences to selectivity calculated from actual availability and feeding observations in the field. Laboratory experiments indicated that Cryptochiton chiefly prefers perennial red algae such as Iridaea cordata and Cryptopleura spp. The most available algae in the field were Hedophyllum sessile, Odonthalia floccosa and ulvoids. The actual field diet was a mixture of all these species, which suggests that preference behavior interacted with availability to yield a diet that was different than that expected due to either factor alone.

The effects of environmental harshness on the feeding behavior and consumption rates of the gumboot chiton, Cryptochiton stelleri were studied on the central coast of Oregon. Behavioral observations suggested that these chitons were much less active on substrata that were exposed at low tide than on submergent substrata. Intertidal chitons were much more active on low tides following heavy and medium wave action than following calm waves. Subtidal chitons were significantly more active during calm waves than during heavy wave action. Further, inclusion

experiments indicated that grazing rates on _Iridaea cordata_ were significantly higher at a wave-protected site than at an adjacent wave-exposed site.

The Feeding Ecology of the Gumboot Chiton,

Cryptochiton stelleri (Middendorff, 1846)

by

Kenneth R. Yates

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Doctor of Philosophy

Completed June 5, 1989

Commencement June 1990

APPROVED:

Bruce A. Menge

Professor of Zoology in charge of major

[signature]

Head of department of Zoology

John C. Ringle

Dean of Graduate School

Date thesis is presented   June 5, 1989

Acknowledgments

Many people have contributed directly and indirectly to the completion of this thesis: it is difficult to thank them all. Primary thanks go to my major professors, Dr. Bruce Menge and Dr. Jane Lubchenco for their expertise, financial and moral support, patience, enthusiasm, editorial suggestions and friendship. Field assistance was gratefully received from a succession of stoic friends, undergraduates and graduate students including, Keith Merkel, Jason Dunham, Richard Greene, Lisa Ellingson, Dr. Terry Farrell, David Booth, and Katie Boula. All of the Zoology graduate students from the fifth floor at Cordley Hall of Oregon State University over the last eight years have contributed to the concepts, field techniques and analyses used in this thesis. Annette Olson, Carol Blanchette and Peter Van Tamelen deserve special thanks for plotting figures and graphs. Brian Tissot receives my heartfelt thanks for being a fellow dude and donating an incredible amount of advice on computers, data analysis, and the intricacies of computer programs. Dr. Lavern Weber of the Hatfield Marine Science Center provided financial support, laboratory space, friendship and more than a few encouraging prods to finish. Dr. Brian T. Yates and Dr. Gary Kovenor both should receive thanks for encouraging me to attempt and finish my degree. Special thanks go to Elizabeth Taft for her patience, encouragement, and caring during the final phases of this thesis. I dedicate this thesis to my father, the late Dr.

Kenneth P. Yates and my mother, Evelyn T. Yates, for giving

me the impetus and tenacity to finish this degree.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

THE FEEDING ECOLOGY OF THE GUMBOOT CHITON, CRYPTOCHITON

STELLERI (MIDDENDORFF, 1846)

CHAPTER 1: INTRODUCTION

The interactions between marine plants and herbivores have recently received increasing attention by ecologists. Although marine herbivores can affect the distribution, abundance and species diversity of marine plants, many aspects of plant- herbivore interactions and many specific interactions have received little attention (Black 1976; Castenholtz 1961; Dayton 1975; Duggins 1980; Hay 1981, 1985; Lawrence 1975; Lubchenco 1978, 1980; Lubchenco and Gaines 1981; Nicotri 1977; Ogden et al. 1973; Paine and Vadas 1969; Underwood 1980; Underwood and Jernakoff 1981). For example, knowledge of how environmental characteristics affect the foraging of an herbivore could be used to predict the variation in herbivore effectiveness along environmental gradients. Changes in herbivore effectiveness under different environmental regimes will determine the probability of partial or complete escapes for algae from herbivores in these regimes. Decreased foraging movement or consumption rates will decrease the chance that an alga will be encountered or, when encountered, how much will be consumed (Lubchenco and Gaines 1981).

In addition, the food preferences of very few herbivores are known. Preferences of an herbivore will determine which among an array of available algae are most likely to be damaged when they are encountered and which will be damaged the most (Lubchenco and Gaines 1981). This

information, when combined with the competitive
relationships of the plants and measures of consumption
intensity, can facilitate prediction of the dynamics of the
effects of an herbivore on plant species diversity
(Lubchenco 1978, Huston 1979).

The marine herbivores that have been studied
extensively are those that are accessible, abundant or both.
These include limpets, some herbivorous snails, several
species of urchins, several fish and a few chitons.
Although studies of these species have yielded much
information about plant-herbivore interactions, robust
ecological generalizations require information on some of
the less abundant, less accessible species. Logistic
difficulties involved with studies of herbivores that
inhabit the low intertidal and shallow subtidal zones
require that much effort and time be expended to gather
data. Although these difficulties affect the amount and
type of research that can be done, information on less
accessible species can make valuable contributions to
ecological theory. Indeed, since these zones are in general
relatively benign in terms of physical factors, research in
these areas can provide valuable insights into interactions
that are controlled more by biological than physical
factors. Specifically, the effects of <u>Cryptochiton</u>
<u>stelleri</u>, the largest extant chiton, have been ignored
although it is a large herbivore which may be locally
abundant in both low intertidal and shallow subtidal areas

along the northern Pacific coast (Morris et al. 1980; this dissertation, Chapter 2). One of the primary reasons for the lack of ecological work on this chiton may be the difficulty of conducting research in the low intertidal and subtidal zones.

The dynamics of plant herbivore interactions have been organized into a useful, predictive model by Lubchenco and Gaines (1981). They define expected herbivore damage as the product of three elements: (1) the probability that an individual plant will be encountered by an herbivore; (2) the probability that an herbivore will eat at least a portion of an encountered plant; and (3) the fitness cost of being eaten. The first element depends on the encounter rate of plants by the herbivore, i.e. does the herbivore move enough to encounter a plant and is the plant actually available to the herbivore? The second element depends on the preferences of the herbivore for different plant species. The final element depends on how much and what parts of the plant are eaten or damaged. The purpose of this thesis was to investigate aspects of these key elements for the interactions between _Cryptochiton_ _stelleri_ and its prey species.

Since so little was known about _Cryptochiton_ my first task was to gather natural history information such as its distribution and abundance, prey items, predators, and behavior. This is the subject of Chapter 2.

The next three chapters present results relating to the Lubchenco-Gaines model. Specifically, Chapter 3 deals with Cryptochiton movement, a critical determinant of the probability of an individual being encountered. The range of movements of individual Cryptochiton provides information about its possible impact on its prey. A restricted range would suggest patchy but concentrated effects whereas a wide range of movements suggest more diffuse effects. Moreover, Cryptochiton's movements indicate its foraging range and the kinds of algae that are actually available to it. A comparison of amount of movement under different physical conditions provides information about the effects of these conditions on this behavior.

The goals of Chapter 3 were to (1) compare the movements of individual Cryptochiton in the intertidal zone to those in the subtidal zone; and (2) determine the foraging range of Cryptochiton in the intertidal zone.

Chapter 4 focuses on the second term of the herbivore effects model, the dietary preferences of Cryptochiton. Consumers usually discriminate among the potential prey in their environment, avoiding some species and seeking others. Knowledge of this behavior and the conditions under which it changes can help ecologists predict the impact of a consumer on the potential prey species within a community (Lubchenco and Gaines, 1981). In addition, study of the characteristics of the preferred and avoided prey can

contribute toward the understanding of how prey can escape consumption.

The purposes of Chapter 4 were to (1) use laboratory experiments to determine the preference of Cryptochiton stelleri for selected species of algae; (2) estimate the field selectivity of chitons for all species of algae that are observed to be eaten; (3) compare laboratory preference to field selectivity; and (4) compare seasonal patterns of availability and algal utilization to preferences to determine the relative importance of availability and preference behavior in the field diet of Cryptochiton.

The research reported in Chapter 5 investigates terms 1 and 3 of the herbivore effects model. The effects of physical factors on the foraging and feeding behavior of an herbivore determine whether a plant is actually encountered (available) and how much damage is done to the plant (i.e. feeding rates).

The goal of this chapter was to determine the effects of environmental stress on the foraging of Cryptochiton stelleri. Specifically, I examine (1) the effect of wave shock on the activity of subtidal chitons, (2) the influence of emergence and previous wave shock on the behavior of intertidal chitons, and (3) the effect of wave exposure on the feeding rates of intertidal chitons.

Literature Cited

Black, R. 1976. The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. Ecology 57:265-77.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42:783-94.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137-59.

Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology 61:447-53.

Hay, M. E. 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat. Bot. 11:97-109.

Hay, M. E. 1985. Spatial patterns of herbivore impact and their importance in maintaining algal species richness. Proc. 5th Int. Coral Reef Congr. 4:29-34.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101.

Lawrence, J. M. 1975. On the relationship between marine plants and sea urchins. Oceanogr. Mar. Biol. Annu. Rev. 13:213-86.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.

Lubchenco, J. 1980. Algal zonation in a New England rocky intertidal community: an experimental analysis. Ecology 61:333-44.

Lubchenco, J. and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. 12:405-37.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal Invertebrates of California. Stanford University Press, Stanford, Cal. 690 pp.

Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58:1020-32.

Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by the echinoid Diadema antillarum Philippi: formation of halos around West Indian patch reefs. Science 182:715-17.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr. 14:710-719.

Underwood, A. J. 1980. The effects of grazing by gastropods

and physical factors on the upper limits of
distribution of intertidal macroalgae. Oecologia
46:201-13.

Underwood, A. J., and P. Jernakoff. 1981. Effects of
interactions between algae and grazing gastropods on
the structure of a low-shore intertidal algal
community. Oecologia 48:221-33.

CHAPTER 2: The Natural History of <u>Cryptochiton</u> <u>stelleri</u>

(Middendorff, 1846)

Introduction

Although <u>Cryptochiton</u> <u>stelleri</u> is a large, locally
abundant marine herbivore along the Pacific Northwest Coast
of North America, very little is known about its natural
history or ecology. The following natural history
information sets the stage for an examination of
<u>Cryptochiton</u>'s ecological role.

Description of Organism

<u>Cryptochiton</u> <u>stelleri</u> (Mollusca: Polyplacophora:
Acanthochitonidae; Morris et al. 1980) is the largest chiton
in the world, reaching lengths of 33 cm. It is the only
chiton that has a mantle completely covering the 8 valves or
plates. The thick, leathery mantle is brick red to reddish
brown with occasional mottling of lighter colored blotches.
Although tough, the mantle is often damaged, especially
during times of heavy wave action. The broad, ventral foot
functions in both locomotion and adhesion. When disturbed
by wave action or hand, <u>Cryptochiton</u> can clamp firmly enough
to the substratum that it is nearly impossible to dislodge
by hand. It can clamp so firmly that soft rock such as
sandstone and mudstone actually fails and remains attached
to the foot when the chiton is removed (K. Yates, personal
observations). These observations are contrary to the
description of Morris et al.(1980), which state that "These
animals do not attach firmly to rocks, as other chitons do
when disturbed...." (p. 424) but is based on hundreds of

observations of <u>Cryptochiton</u>'s often frustrating tenacity. This chiton also can be found loosely attached to the substratum when it is moving, foraging, feeding or undisturbed.

The organs of <u>Cryptochiton</u> which interact with the external environment include the subradular organ, the radula and the ctenidia. The primary sense organ is the chemosensory subradular organ, which is located in the buccal cavity. It is applied to surfaces prior to using the radula and is thought to function in food choice. The radula, which is used in feeding, is a large structure with two tricuspid, magnetite capped, teeth ("dominant teeth"; Fretter and Graham, 1962) and fifteen other median and marginal teeth per row (Lowenstam 1962). Gas exchange occurs in up to 80 ctenidia in each pallial groove. Each of these ctenidia each has a stiffening rod to facilitate exposure to the air during aerial respiration, which can occur when the animals are exposed during low tide (Peterson and Johansen 1973).

The physiology of <u>Cryptochiton</u> is fairly well known for an invertebrate, probably because the animal has large organs and is therefore easier to study than smaller invertebrates. Isolated portions of the intestine have been shown to transport selectively certain amino acids and to transport actively carbohydrates against a concentration gradient (Greer and Lawrence, 1967; Lawrence and Lawrence, 1967; Robbins, 1975). The circulatory system also has been

studied in some detail, including blood volume, flow, glucose concentration and the response of blood-sugar levels to injections of hormones such as insulin, norepinephrine and serotonin (Michael 1975). Muscle response has also been studied in this chiton (Harrison 1975).

Cryptochiton is dioecious and reproduction is by free spawning of gametes when the animal is submerged. Eggs are released as a greenish, gelatinous mass that clings together until dispersed by wave action. Sperm release by the males is triggered by female egg release (Tucker and Geise 1962). During observations of eight animals that were spawning in the laboratory, both males and females were observed to hold their posterior ends(where the gonopores are located) up and away from the substratum. Cryptochiton spawning was observed at the Hatfield Marine Science Center Aquarium during May of 1982 (3 males and two females) and 1983 (3 females and 4 males). Tucker and Geise (1962) observed that spawning occurs between March and May in northern California, but the observations of Palmer and Frank (1974) indicate that spawning occurs between June and early July on the southern Oregon coast (Cape Arago). My observations, which include both laboratory and 2 field observations of actual spawning, indicate that Cryptochiton may spawn earlier than June on the central Oregon coast. The discrepancy between the spawning times observed by different workers could also be due to natural variation between years and location.

Larval development is relatively quick: larvae hatch
from the eggs 5 days after fertilization and are free-
swimming for up to 20 hours, after which they settle and
metamorphose. This ontogeny suggests that the larvae are
lecithotrophic because their short stay in the plankton
probably requires little or no feeding.

Very little is known about the recruitment of
Cryptochiton. Small individuals are rare (MacGinitie and
MacGinitie 1968, Tucker and Geise 1962, Palmer and Frank
1974). As part of a study on growth in Cryptochiton, Palmer
and Frank (1974) conducted a special search for small
chitons which they defined as weighing 50 grams or less. 20
small chitons were found and marked during this search but
none were relocated at the end of a year. Most of the other
Cryptochiton encountered in the field during their study
weighed (in air) between 500 and 800 grams and ranged
between 20 - 30 cm when relaxed. During field observations
from 1982 to 1986, I found only 3 that were less than 3cm in
length. One was in the low intertidal zone at Boiler Bay,
Ore. and two were from a subtidal bench at Whale Cove, Ore.
None of these chitons were weighed. Recruitment may be high
and the cryptic nature of small C. stelleri may conceal
their true numbers. An alternative explanation is that
recruitment is patchy in time and place and therefore
difficult to detect.

Palmer and Frank (1974) found that the size of
Cryptochiton is difficult to measure because of the flexible

body and variable morphology. When a <u>Cryptochiton</u> is disturbed it will roll up into a ball and is more tense compact when clamped to the substratum (Ken Yates, personal observations). However, rough estimates of length can be obtained from undisturbed and relaxed animals. Also, weight may be measured but variable gut contents and water content produce natural variation. In spite of these complications when weighing <u>Cryptochiton</u>, Palmer and Frank (1974) decided on estimating growth by measuring weights in air.

Lengths were obtained in my study by measuring the animal in a straight line from the anterior to the posterior edge of the girdle. The majority of <u>Cryptochiton</u> observed during my research ranged from 15cm to 30cm in length. Chitons of less than 15cm in length were rare. Approximately 12 chitons in the 10cm to 15cm size class were observed during the course of my research. Measurements of 25 chitons from Chiton Cove at Boiler Bay ranged from 10.8cm to 27.0cm (mean = 21.0cm, standard error = .76).

Chiton weights were obtained by weighing them in water with a Pesola spring scale. This method was chosen to avoid the variability introduced by changing water content of the pallial cavity, foot and girdle surface. The animals were allowed to roll up into a ball, placed in a neutral buoyancy net and weighed in a bucket of seawater. Although I attempted to track the weights of individuals over time, estimates were obtained over a period of only two months, which is too short to give meaningful estimates of growth.

Potential seasonal fluctuations in gut content and gonad weight due to spawning suggest that growth estimates need to be obtained over a full year at the minimum. The animals that were tagged in this study could not be relocated a year later. Weights of individuals ranged from 25 to 96g (pooled over all sampling dates) and means ranged from 46 to 61g on different sampling dates. The weight data are summarized in Table 2.1. These weights are not compared easily to those obtained by Palmer and Frank (1974) because the methods they used were different. These researchers weighed Cryptochiton in the air, which yields higher weights than when weighing in water due to the absence of buoyancy. The weights of Cryptochiton obtained in their study ranged from <50g to 1200g, but most of the individuals weighed between 500 and 800g (Palmer and Frank 1974).

Natural History

Distribution and Abundance

One of the primary reasons why so little is known about the natural history and ecological role of Cryptochiton is that it is found predominantly in the low intertidal and subtidal zone of wave-swept rocky shores, areas which are relatively inaccessible to researchers. In addition, its distribution and abundance are patchy. The vertical range of this chiton extends from the low intertidal zone to subtidal depths of at least 10 m. These zones

Table 2.1. Weights in water of <u>Cryptochiton</u> at Manipulation
Cove, Boiler Bay, Ore.

Date	n	Mean Wt.(grms)	Std. Err.	Maximum	Minimum
6/30/84	8	53.5	3.45	73.0	40.0
7/13/84	14	50.57	2.13	72.0	37.0
7/14/84	17	61.71	3.36	96.0	40.0
8/25/84	8	46.63	5.18	70.0	25.0

have limited accessibility, especially toward the northern
parts of the range where wave action often makes working in
the low intertidal and shallow subtidal zones dangerous.
Shallow subtidal areas along these shores generally
experience substantial wave action, rendering direct
observation difficult. Cryptochiton ranges from the Aleutian
Islands in Alaska to San Miguel Island and San Nicholas
Island in the Channel Islands of southern California, and on
the east coast of Asia from northern Hokkaido Island to the
Kurile Islands, Kamchatka (Morris et al. 1980).

One of the first goals of my research was to obtain
quantitative and qualitative information on: (1) sites where
Cryptochiton was abundant on the coasts of Oregon and
California; (2) the relative distribution of these chitons
between intertidal and subtidal zones at sites where they
occur; and (3) factors responsible for the patterns of
distribution.

Intertidal Distribution and Abundance

In Oregon, relatively high densities of chitons can be
found in the low intertidal at several sites. During
extensive searches of many intertidal areas along the
central and southern Oregon coast, I found that chitons are
particularly abundant in the intertidal zone at two areas,
Boiler Bay and Cape Arago. Several of the small coves in
Boiler Bay have high densities of chitons. "Chiton Cove",
which is near the southern end of Boiler Bay, has the

highest density. Intertidal Cryptochiton are also common in
North Cove and South Cove of Cape Arago, approximately 180
km south of Boiler Bay. These chitons occur, but are rare,
at Whale Cove and Pirates Cove, close to Depoe Bay, Ore.; at
Yaquina Head, approximately 8 km north of Newport, Ore.; and
at Otter Rock, 16 km north of Newport, Ore. Other areas on
the Oregon coast with vast rocky intertidal areas were
searched repeatedly but no Cryptochiton were found. These
areas include: Seal Rock, Cape Perpetua, Strawberry Hill,
Heceta Head and Cascade Head. Figure 2.1 illustrates the
position of these locations on the Oregon coast and
indicates the relative abundance of Cryptochiton. These
estimates of relative abundance are subjective and are based
upon visits to the sites to search for Cryptochiton or on
visits to collect other animals during which the presence of
Cryptochiton was noted. Table 2.2 gives the approximate
number of visits to the intertidal and subtidal zones at
each site.

Several intertidal sites in northern and central
California were searched for Cryptochiton. Chitons were
found only at the northern sites. In the intertidal zone of
Indian Beach at Trinidad Head, a thorough search during the
low low tide of 12/13/85 yielded 35 chitons in 30 x 45 m
area, or .03 chitons/m^2. The same size rectangle was
searched at Shell Cove (Sonoma County) on the low low tide
of 12/15/85 and only 7 chitons (.01 chitons/m^2) were found.
No Cryptochiton were found during a

Figure 2.1. The distribution and abundance of _Cryptochiton_ _stelleri_ in intertidal and subtidal zones at sites along the Oregon coast. If relative abundance is not indicated for a zone at a site, that zone was not explored at that site.

FIGURE 2.1

OCCURRENCE

	a-I	Cascade Head—
c-S	c-I	Boiler Bay
u-S	u-I	Pirates Cove—
c-S	u-I	Whale Cove—
u-S	u-I	Yaquina Head—
c-S		South Jetty, Newport
	a-I	Seal Rock—
	a-I	Cape Perpetua—
	a-I	Strawberry Hill
	a-I	Heceta Head—

Key

S = Subtidal
I = Intertidal
a = absent
u = uncommon
c = common

c-S c-I	Cape Arago—

OREGON

N
W———E
S

c-S	Port Orford—
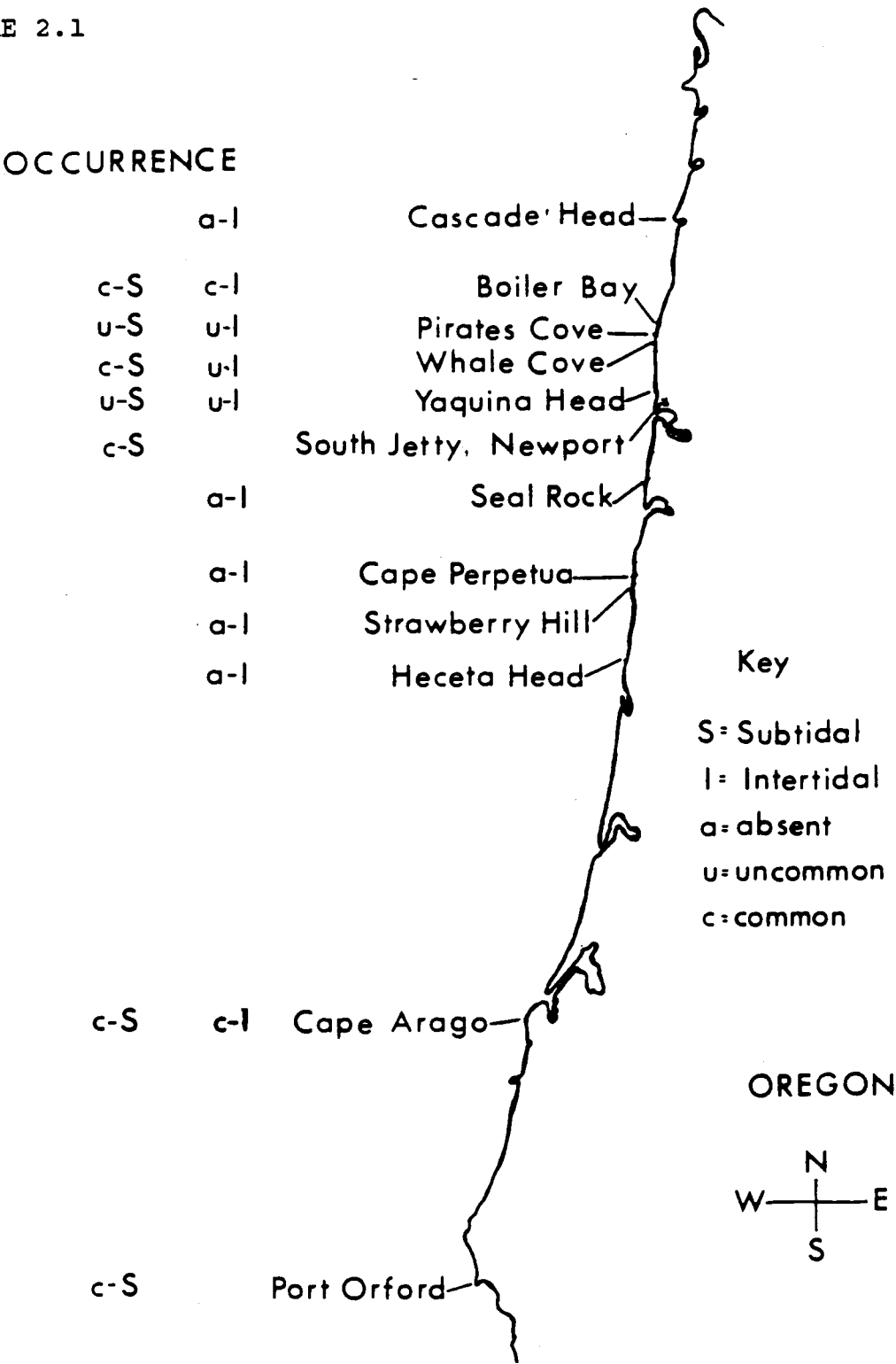
Table 2.2. Basis for subjective estimates of abundance of
Cryptochiton in the intertidal and subtidal zones of sites
along the coast of Oregon. The numbers represent
conservative and approximate visits to the zones at each
site.

Site	Number of Visits	
	Intertidal Zone	Subtidal Zone
Cascade Head	2	0
Boiler Bay	230	5
Pirates Cove	3	10
Whale Cove	20	50
Yaquina Head	50	5
South Jetty, Newport	0	30
Seal Rock	30	0
Cape Perpetua	4	0
Strawberry Hill	10	0
Heceta Head	1	0
Cape Arago	1	1
Port Orford	0	4

thorough search of the entire Biological Preserve at the Bodega Marine Laboratory, approximately 32 kilometers south of Shell Cove. Cryptochiton is said to be rare or absent at this site (Victor Chow, pers. communication.). These chitons are also rare or absent in the intertidal zone of sites farther to the south (Dr. James Watanabe, The Monterey Bay Aquarium, personal communication based on 12 years of experience in these areas).

Methods

The population size of chitons found in Chiton Cove of Boiler Bay was estimated by mark-recapture methods. Chitons were marked by inserting numbered "spaghetti tags" (Floy Tag Co., Seattle, Washington) through the edge of the girdle with a hollow stainless steel dart. The girdle consists of muscle and connective tissue. Although chitons reacted to the insertion of the tag by rolling up into a ball, they usually would unroll and reattach to the substratum in a matter of minutes. Unrolling could be hastened by holding the chitons inverted. Tagged chitons were observed until they had unrolled and then encouraged to reattach to the substratum. Tag loss was not observed during the mark-recapture study, but several animals were observed several months after the four day study with tags that were pulling out of the girdle or with raw grooves where tags had pulled out of the girdle.

Two different methods were used to estimate the population size. One method involved a single marking date and a consecutive recapture date. The Lincoln Index was used to calculate population size from these data (Southwood 1978). The second method, the Jolly-Seber method, involves a series of at least two dates on which animals are marked and subsequently recaptured. On the first date, all animals are marked and released. After the first date, any unmarked animals that are captured are marked and released. This method also involves at least a third date when animals are captured or recaptured. The advantages of the Jolly-Seber method are that it is based on a stochastic model, which may better correspond to natural phenomena than a deterministic model, and that the assumptions of a closed population and no births or deaths may be relaxed (Southwood 1978).

These methods were used on data gathered from a 522 m^2 area in Chiton Cove in which chitons were marked and then searched for recaptures. Animals were first marked at low tide on 7/19/82 and recaptured on 7/20/82. Any unmarked animals found on 7/20/82 were marked. This procedure was repeated on 7/21/82 and on 7/22/82. The Lincoln Index was used on the data from 7/19/82 and 7/20/82 and yielded an estimate of 51 chitons or a density of .10 chitons per m^2 in this area. The Jolly-Seber method was used to calculate a population estimate of 62.35 chitons for 7/20/82, which is a density of .12 chitons per m^2.

Subtidal Distribution

The actual abundance of chitons in the intertidal zone
appears to decrease toward the southern parts of its range,
where the animal is found primarily in subtidal areas
(Palmer and Frank 1974, personal observations).
Cryptochiton is found rarely in the intertidal zone south of
Shell Cove, California. In Oregon, Cryptochiton are common
in the shallow subtidal areas (5-8m) of Boiler Bay, Whale
Cove, Pirates Cove, the South Jetty of Yaquina Bay, Cape
Arago and the Harbor Jetty of Port Orford (Figure 2.1).
They occur but are uncommon in the subtidal zone of Yaquina
Head, Pirates Cove (just north of Depoe Bay) and the North
Point Cove of Depoe Bay. Several dives at Hopkins Marine
Laboratory at Monterey Bay indicate that Cryptochiton is
common in the subtidal zone at that site.   At the northern
California sites subtidal areas were not examined due to
logistic difficulties.

   Possible Causes of Patterns

    In general, the distribution and abundance of
Cryptochiton stelleri appears to be affected by latitude,
the presence of submergent substratum and wave shock. The
effects of latitude on the abundance of intertidal chitons
may be connected to the higher temperatures experienced at
low tide toward the southern part of its range. During
laboratory experiments on the respiratory physiology of
Cryptochiton, Petersen and Johansen (1973) found that oxygen
uptake decreased and the animals became sluggish and

distressed at water temperatures above 15 C. When chitons
were exposed to air at temperatures of 20 C and 21 C, they
became "quite flaccid and appeared unable to move" (Petersen
and Johansen 1973). I have also observed that when chitons
are exposed to air at higher temperatures (20-30 degrees C)
they will actually hang off of the substratum, lose their
hold and drop, often into a tidepool. This behavior may
allow chitons to escape to the lower temperatures of
tidepools, surge channels or shaded substratum. The
presence of constantly submerged substratum appears to be
important to these chitons because they rarely move or
exhibit active behaviors when on completely emerged
substratum (Petersen and Johansen 1973, personal
observations). Wave shock may affect distribution and
abundance through chiton mortality or recruitment. Little
is known of the recruitment of Cryptochiton, but wave shock
is definitely a source of mortality (Palmer and Frank 1974;
Petersen and Johansen 1973; personal observations). Wave
shock also inhibits chiton activity and feeding (see Chapter
5).

The intertidal sites that had high densities of
Cryptochiton share some common habitat characteristics. All
are relatively heterogeneous, including abundant tidepools
and surge channels; i.e., substratum that is submerged at
low tide. At Chiton Cove of Boiler Bay I estimated the
percent of submerged substratum by placing randomly a .0625
m quadrat along transect lines that were parallel to the

shoreline. This quadrat was divided into 100 squares and the percent of the substratum that was submerged was estimated by counting the number of squares that were over submerged substratum. Transect lines were placed every meter, starting at the seaward edge of the chiton search area and working back toward the shore. Overlap of consecutive transect lines was avoided by orienting the transects along a compass sighting. A total of 260 quadrats over 36 transects yielded an average percent cover of submergent substratum of 28.47%. The amount of submergent substratum appeared to be similar at other intertidal sites where Cryptochiton were common such as Cape Arago, Indian Beach, and Shell Cove, but this was not measured quantitatively.

Cryptochiton may be excluded at some intertidal sites by one or more factors. Seal Rock and Strawberry Hill have numerous tidepools but Cryptochiton does not occur at either site. A characteristic common to both sites is a high degree of sand scour or burial (C. Trowbridge, personal communication; K. Yates, personal observation). Cryptochiton may be intolerant of sand effects, or the abundance of its food may be affected. I have observed high density patches of Iridaea cordata, one of the preferred foods of Cryptochiton, at Seal Rock, but these patches were on emergent substratum in areas with little sand. Coincidentally, Strongylocentrotus purpuratus, which occurs at all sites where Cryptochiton is found, is also absent

from Strawberry Hill and Seal Rock. Other intertidal sites
such as Heceta Head, Cascade Head, and the Bodega Bay Marine
Laboratory Biological Preserve, are exposed to heavy wave
action and the small amount of tidepool substratum occurs at
relatively high tide levels.

Wave action may also be a factor in determining the
distribution of Cryptochiton (Morris et al. 1981, personal
observations). All of the intertidal sites where chitons
are common are relatively protected from wave action but
still receive some wave shock and surge. Chiton Cove at
Boiler Bay is protected from the prevailing southwesterly
swell by two points of basaltic rock to the south. North
Cove and South Cove of Cape Arago are protected by the wave
dampening properties of the head of the Cape, and North Cove
is further protected by Stimpson's Reef. Central Cove of
Cape Arago is fully exposed to wave action and Cryptochiton
is rare at that site. Indian Beach is protected by Trinidad
Head and a large outcropping of basaltic rock seaward.
Shell Cove has a similar outcropping. The sites where
Cryptochiton are common at both Indian Beach and Shell Cove
are nestled behind very large projections of basalt that
block virtually all direct wave shock.

Interactions With Other Species

Understanding the nature and magnitude of interactions
of Cryptochiton with other species is necessary to determine
its community effects and role. Limited information exists

on predators, commensals and prey species but nothing has
been published on competitors. The observations that have
contributed to the understanding of predators, commensals
and competitors are summarized below. Chapter 4 focuses on
the interactions between Cryptochiton and its prey.

Predation

Only two predators of Cryptochiton have been reported
in the literature. In northern California the neogastropod
Ocenebra lurida rasps the flesh, creating pits up to a
centimeter in diameter and 3-4 mm deep (Talmage 1975).
Although this may expose the chiton to infection, it does
not directly affect survivorship. Such attacks were never
observed during my research. The presence of the valves of
Cryptochiton in the kitchen middens of coastal Indians
suggests that they were eaten by humans in the past, but
they are not consumed in any appreciable quantities at
present (Morris et al., personal observations - Whale Cove
Indian Middens).

Although this has not been reported previously, I have
observed numerous instances of Cryptochiton being eaten by
Pycnopodia helianthoides, a large (up to 1 m in diameter)
predatory asteroid. This phenomenon was first observed at
Whale Cove in the subtidal zone at depths of 5-10 m. On two
separate dives, over half of the feeding Pycnopodia were
consuming Cryptochiton. On 8/17/82, 10 Pycnopodia
helianthoides were observed on a shallow (5m depth) bench

during a dive at Whale Cove. 5 of the 7 feeding seastars
were eating Cryptochiton. Observations during at least 7
other dives at Whale Cove and 2 dives at Boiler Bay suggest
that these chitons are a common prey item of Pycnopodia in
Oregon. All of the seastars observed eating Cryptochiton
were relatively large, ranging from approximately 60cm to
90cm in diameter. The approximate size range of the chitons
that were eaten were 20cm to 30cm length. The seastars eat
the chitons by everting their cardiac stomach over the
animal, which appears to clamp itself very tightly to the
substratum in response. Escape or running responses were
not observed. Sometime during the procedure the chiton is
flipped over and the foot and viscera are consumed. The
girdle is apparently resistant to digestion, as this was not
digested by the seastar in all feeding observations.
Although this chiton and seastar co-occur in many areas,
this chiton has never been reported to be a food item of
Pycnopodia (Mauzey et al. 1968). For example, Cryptochiton
and Pycnopodia both are common in the heavily studied
subtidal areas off of the Hopkins Marine Laboratory of
Stanford University, but consumption of the chiton by the
seastar has never been observed at this site (Dr. James
Watanabe, personal communication). On one occasion I
observed a Cryptochiton being eaten by Pisaster ochraceus in
the intertidal zone at Boiler Bay, but the animal was
partially decomposed and may have been dead before the
seastar found it. Fish such as the rock greenling

(Hexagrammos superciliosus) and the cabezon (Scorpaenichthys marmoratus) may be occasional predators on Cryptochiton. A small (2.3 cm) Cryptochiton was found in a gut of a rock greenling caught on the South Jetty of Yaquina Bay, Ore. I have also observed large (up to 10 cm) Katharina tunicata (another chiton) in the gut of cabezon, so this fish may be capable of eating small Cryptochiton.

Some obvious predators in the intertidal and subtidal zone do not eat Cryptochiton. Sea otters apparently ignore Cryptochiton, which is surprising given the voraciousness and general diet of this mammal (Morris et al. 1980). Crabs such as the antenna crab (Cancer antennarius) and the red rock crab, (Cancer productus) co-occur with Cryptochiton but were never observed feeding on it (K. Yates, personal observations). Birds such as gulls (Larus spp.) and the black oystercatcher (Haematopus bachmani), which eat other large intertidal invertebrates, apparently ignore Cryptochiton. The paucity of predators on this chiton may be due to a size escape, the toughness of the foot and girdle, or toxins. The sizes of Cryptochiton that are usually observed, and thus may be available to predators, range between 15cm and 33 cm; small chitons are rarely seen. The larger sizes may be difficult for most predators to consume but sea otters and gulls might be able to consume these sizes. Although the foot of Cryptochiton is tough, the similar foot of the abalone (Haliotus sp.) does not deter sea otters. Pycnopodia helianthoides appears to be

unable to digest the tough girdle, which may be a factor in deterring other predators. Toxins may be sequestered from the algal food of this chiton, but no evidence exists for this.

Competition

The distribution of Cryptochiton overlaps with several other intertidal and subtidal herbivores who may thus compete with this chiton for food. Two potential competitors of Cryptochiton are Strongylocentrotus purpuratus, the purple urchin, and Strongylocentrotus franciscanus, the red urchin. S. purpuratus is often very abundant in the shallow tide pools where the chiton forages and feeds in the low intertidal zone. When these urchins are present in high enough numbers, the only algae present are crustose or upright coralline algae, which Cryptochiton does not eat. Under these conditions the chitons often can be observed feeding on algae that are hanging down from the emergent substratum surrounding the tidepools. These algal species are often either Odonthalia floccosa or Hedophyllum sessile, which are low on the preference hierarchy of Cryptochiton (Chapter 3). Although the purple urchin may decrease the abundance of fleshy algae growing in tidepools, they also counteract this effect partially by seizing and holding drift algae that has been washed into the tidepool. I have observed Cryptochiton eating drift algae held by purple urchins on 5 separate occasions. Red urchins, which

occur in the same shallow subtidal areas as Cryptochiton, also decrease the abundance of algae when their densities are high. In addition, S. franciscanus may exclude these chitons merely by their physical presence. It is highly unlikely that Cryptochiton would move over the wall of long, sharp spines formed by a high density of these urchins.

Commensalism

Several species have commensalistic relationships with Cryptochiton. The polynoid polychaete (scale worm), Arctonoe vittata, occupies the chiton's pallial groove and may occur in 22-60% of the chitons examined (Webster 1968, personal observations). Another occupant of the pallial groove is the pea crab, Opisthopus transversus, which may occur in 20-40 percent of the chitons observed in Monterey Bay (Webster 1968). I never observed this pea crab as a commensal with Cryptochiton in hundreds of observations of this chiton in Oregon. Both of these commensals appear to feed on materials brought in by the respiratory currents in the pallial groove and do not appear to harm the host (Webster 1968). 24 species of algae also occur as epibionts on the girdle of subtidal specimens (Morris et al. 1980). I also have observed algae such as diatoms, Ectocarpus spp. and Iridaea sp. growing on the dorsal surface of the girdle of Cryptochiton. These epibionts appear to be most abundant on subtidal chitons during the summer months.

Cryptochiton also may be an indirect commensal in what could be a consumer- and disturbance-mediated coexistence between fleshy red algae and upright coralline algae. On a shallow subtidal bench at Whale Cove fleshy red algae such as Cryptopleura ruprectiana, Cryptopleura sp., Ptilota filicina, and Plocamium cartilagineum overgrow Bossiella sp. and Corallina officinalis. When specimens of the fleshy algae are collected from this bench and dissected, they are usually growing around a core of whitened intergenicula of the coralline algae. In addition to the negative effects of this overgrowth, the extra drag created by the epiphytic fleshy algae may cause the host to be dislodged by wave action. Following the first winter storms the beach at Whale Cove is often littered by these fleshy algae attached to their coralline hosts. Fortunately for the host, this disturbance appears to remove only the parts of the coralline that the fleshy algae are growing on. Cryptochiton may reduce these negative effects of overgrowth and disturbance by eating the fleshy algae and not the coralline. This chiton has never been observed to eat corallines in the field, and when starved chitons were given these algae in the laboratory none were eaten (personal observations, Chapter 4). In contrast, both of the Cryptopleura species and Ptilota are preferred by Cryptochiton (Chapter 4). This phenomenon has not been investigated and would be a fruitful area for further research.

Literature Cited

Fretter, V. and A. Graham. 1962. British prosobranch
    molluscs, their functional anatomy and ecology. Ray
    Society, London, 548 pp.

Greer, M. L., and A. L. Lawrence. 1967. The active
    transport of selected amino acids across the gut of the
    chiton (Cryptochiton stelleri). 1. Mapping
    determinations and effects of anaerobic conditions.
    Comp. Biochem. Physiol. 22:665-74.

Harrison, J. T. 1975. Isometric responses of somatic
    musculature of Cryptochiton stelleri (Mollusca:
    Polyplacophora). Veliger 18 (Suppl.): 79-82.

Lawrence, A. L., and D. C. Lawrence. 1967. Sugar absorption
    in the intestine of the chiton, Cryptochiton stelleri.
    Comp. Biochem. Physiol. 22:341-57.

Lowenstam, H. A. 1962. Magnetite in denticle capping in
    Recent chitons (Polyplacophora) Bull. Geol. Soc. Amer.
    73:435-38.

Lubchenco, J. and S. D. Gaines. 1981. A unified approach to
    marine plant-herbivore interactions. I. Populations and
    communities. Ann. Rev. Ecol. Syst. 12:405-37.

MacGinitie, G. E., and N. MacGinitie. 1968. Notes on
    Cryptochiton stelleri (Middendorff, 1846). Veliger

11:59-61.

Mauzy, K. P., C. E. Birkeland, and P. K. Dayton. 1968.
Feeding behavior of asteroids and escape responses of
their prey in the Puget Sound region. Ecology
49:603-619.

Michael, P. F. 1975. Blood glucose concentration and
regulation in Cryptochiton stelleri (Mollusca:
Polyplacophora). Veliger 18 (Suppl.):117-21.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980.
Intertidal Invertebrates of California. Stanford
University Press, Stanford, CA. 690 pp.

Palmer, J. B., and P. W. Frank. 1974. Estimates of growth of
Cryptochiton stelleri (Middendorff, 1846). Veliger
16:301-4.

Petersen, J. A., and K. Johansen. 1973. Gas exchange in the
giant sea cradle Cryptochiton stelleri (Middendorff).
J. Exper. Mar. Biol. Ecol. 12:27-43.

Robbins, K. B. 1975. Active absorption of D-glucose and
D-galactose by intestinal tissue of the chiton
Cryptochiton stelleri (Middendorff, 1846). Veliger 18
(Suppl.):122-27.

Southwood, T. R. E. 1978. Ecological methods with particular
reference to insect populations. John Wiley and Sons,
New York,

Talmadge, R. T. 1975. A note on <u>Oceanebra</u> <u>lurida</u>
(Middendorff). Veliger 17:414.

Tucker, J. S., and A. C. Giese. 1962. Reproductive cycle of
<u>Cryptochiton</u> <u>stelleri</u> (Middendorff). J. Exper. Zool.
150:33-43.

Webster, S. K. 1968. An investigation of the commensals of
<u>Cryptochiton</u> <u>stelleri</u> (Middendorff, 1846) in the
Monterey Peninsula area, California. Veliger 11:121-25.

CHAPTER 3: Movements and Home Range of the Gumboot
Chiton, <u>Cryptochiton</u> <u>stelleri</u>, in intertidal and
subtidal habitats.

ABSTRACT

The movements of an organism can reveal important
information about its home range, site fidelity, prey
availability and the patchiness of its impact on prey. Very
little is known about the movements of any species of
chiton, including the gumboot chiton, <u>Cryptochiton</u> <u>stelleri</u>.
The movements of this chiton were observed by tagging 252
individuals and measuring their positions relative to fixed
anchor points in the substratum. Periods between position
observations ranged from 1 day to 512 days. Movements over
1 and 2 days were observed for intertidal and subtidal
chitons to permit comparison between animals subjected to
two radically different physical regimes. Movements of
intertidal chitons on emergent and submergent substrata were
compared. Home ranges were calculated by digitizing the
area within the shape defined by connecting at least three
sequential points of observation with straight lines.

The results of this research indicate six basic
patterns. 1) For intertidal <u>Cryptochiton</u>, the distance
between two positions is significantly correlated with the
time between observations (correlation coefficient = .498).
2) The means of 1-day movements of intertidal chitons were
not significantly different between late summer and middle
winter (1.23 m in summer vs. .61 m in winter). 3) At
intertidal study sites, the average distance that emerged
chitons (out of pools) move in one day is not significantly
different from submerged chitons (in pools) (1.33 m for

emerged chitons vs. 1.30 m for submerged chitons). 4) Cryptochiton moves significantly more in subtidal habitats than intertidal habitats over the same length of time (7.35 m in subtidal habitats vs 1.13 m in intertidal habitats). 5) The home ranges of intertidal chitons are restricted relative to those of subtidal chitons. 6) The chitons that were recaptured remained within 21 m of initial capture point over periods greater than 1 year. Cryptochiton does not appear to home to a specific site or scar as occurs with several species of limpets and chitons.

These movement patterns suggest that the impact of chitons on macroalgae will be more restricted in intertidal areas than at subtidal sites. Assuming that consumption rates are the same, the impact of an intertidal chiton would be more concentrated, thus causing a more patchy effect. Of course, many factors that were not examined in this research will affect consumption rates and the concentration of the impacts of a consumer.

The relatively limited home ranges and movements of intertidal chitons also indicate that fewer types of algae may be available to chitons in the intertidal zone than in the subtidal zone. This prediction assumes that the patch size of the maximum algal species number is greater than the home range of intertidal chitons.

INTRODUCTION

The movements of individuals of a species can provide insight into several aspects of its population dynamics and interactions with other species. The range of movements of an individual provides information about the range of impact that a consumer may have on its prey. A restricted range of movements suggests very concentrated effects and a wide range of movements suggests more diffuse effects. When the movements of a consumer are related to foraging, the effects of that individual will be concentrated within the range of its movements. Assuming even distribution of prey items and a constant feeding rate of the consumer, a wider foraging range will result in more diffuse effects of an individual consumer. The effects of a consumer population will also be dependent on the density of the consumer and the degree of overlap of foraging ranges of individuals.

Foraging range also indicates the scale of prey availability. Measurements of the abundance of prey items will be unrelated to availability if taken on a scale greater that the foraging range of an individual consumer. Prey species or individuals that occur in habitats outside of the consumer's foraging range will be unavailable during its food selection process.

The movements of a consumer may be affected by physical factors such as wave action, desiccation and temperature stress. These physical factors may restrict the foraging activities to refuge habitats with physically benign

conditions. Conversely, these habitats will be more biologically harsh for the prey of the consumer. Comparison of movements under different physical conditions can suggest how physical factors affect the movements of a consumer and thus its range of effects.

Movement studies of marine invertebrate herbivores have focused primarily on limpets (Branch 1981, Underwood 1979), but limited information also exists on the movements of several species of chitons (Boyle 1977, Glynn 1970, Palmer and Frank 1974). An extensive study by Glynn (1970) on two species of Caribbean chitons, Acanthopleura granulata and Chiton tuberculatus, produced extensive information on movements. Both species live on boulders on wave-swept shores in Puerto Rico. Chiton could reposition itself on the undersurface of an overturned rock in under one minute. This behavior may decrease desiccation and heat stress, and avoid predation by fishes (Glynn 1970). Both species would forage primarily at night during excursions from refuges underneath boulders. Homing was observed in both species but was best developed in Acanthopleura. These chitons would return to a spot within several centimeters of the previous position, often with a different orientation. Chiton would range over an area with a mean radius of 45 cm and Acanthopleura ranged over a mean radius of 30 cm.

Homing behavior also appears to be well developed in the Australian chiton, Acanthozostera gemmata (Boyle 1977). When displaced up to 60 cm from the home site, 50% of these

chitons returned to the same site with an orientation in the same direction as the initial position or 180 degrees rotated. This chiton would not home when a sheet of glass was placed between them and the home site. Displaced individuals would also avoid and circumvent experimentally damaged strips of rock between them and the home site.

Other information on chiton movements is much less detailed. During a mark-recapture study on growth of Cryptochiton stelleri, Palmer and Frank (1974) noted that most animals were found within 20m of release after 2 years. Himmelman and Carefoot (1975) noted that Katharina tunicata appeared to adopt homing depressions within feeding enclosures. Duggins and Dethier (1985) state that K. tunicata moves very slowly, but provide little information about their range of movements. This species appears to form deep scars in soft substratum at Whale Cove on the Oregon coast (K. Yates, personal observations), but no data have been gathered on possible homing to these scars. Nuttallina californica may home to pits that they apparently form in soft substratum along the coastline of Palos Verdes, California, but nothing is known about movements away from these pits or whether each individual returns to the same pit (Ricketts and Calvin 1968, K. Yates, personal observations).

Homing, territorial and migratory movements of limpets have been studied extensively (Branch 1971, 1981; Hawkins and Hartnoll 1983; Stimpson 1970, 1973; Underwood 1979).

Limpets such as _Lottia scabra_, _L. digitalis_, _L. gigantea_ and
several _Patella_ spp. will return to a homing scar following
foraging excursions (Branch 1981). Others exhibit short-
term movements up and down the shore in response to
desiccation stress. Seasonal migrations occur in several
species such as _L. digitalis_, _L. strigatella_, _Patella
vulgata_, and _P. granularis_ (Branch 1971). _L. gigantea_ has
well developed territorial behavior and restricts its
movements to a relatively small area from which it excludes
other mobile organisms (Stimson 1970, 1973).

There are few studies of urchin movements (Lawrence
1975), which is probably due to the difficulty of tagging
individuals. In the intertidal zone _Strongylocentrotus
purpuratus_ is usually very sedentary and forms cup-shaped
depressions in the rock. However, these animals will
occasionally move out of these cups, often in response to
the presence of _Pycnopodia helianthoides_, a seastar which is
one of the major predators on these urchins (Dayton 1973,
1975). The large red urchin, _Strongylocentrotus
franciscanus_, is more mobile than _S. purpuratus_ and has a
similar, but more rapid response to _P. helianthoides_.

An organism can receive several potential benefits from
limited movements such as homing or a restricted home range
(Hawkins and Hartnoll 1983, Branch 1981, Underwood, 1979).
Restricted movements allow easier relocation of preferred
feeding areas or preferred foods. A limited home range can
ensure that an animal remains at a level on the shore or

within habitats where the ability to survive the stress of emersion has been demonstrated. In addition, the availability of suitable refuges from physical factors or predators may be limited, and staying near these refuges may enhance survivorship.

The gumboot chiton, Cryptochiton stelleri, is an excellent organism to use in movement studies because of its large size, relative ease of relocation and insensitivity to the presence of an observer. Since this animal is often seen in an inactive state during low tide, observers often question whether Cryptochiton moves extensively. Preliminary observations on Cryptochiton revealed several patterns regarding movements. These chitons can be seen moving primarily when submerged, either in tidepools at low tide or in subtidal habitats (K. Yates, personal observations). In general, Cryptochiton does not move when exposed at low tide. Intertidal Cryptochiton individuals were often found very close to the same site on consecutive low tides. In addition, moving chitons are loosely attached to the substratum and can be dislodged easily by wave surge.

These observations suggested several predictions about the movements of Cryptochiton. 1) Intertidal chitons will move less than subtidal chitons over the same period because these chitons remain stationary when exposed at low tide. 2) The home range of intertidal chitons is relatively restricted due to the disjointed distribution of tidepools, the impact of wave surge at high tide, and, perhaps, the

advantages of homing for an intertidal mollusc. The
validity of these predictions was tested by observing the
movements of individually tagged chitons at intertidal and
subtidal study sites.

MATERIALS AND METHODS

Study Site Description

Observations were made in the low intertidal zones of
two sites and the subtidal zone of one site on the central
coast of Oregon from 1980 - 1982. Movement observations
were made at two intertidal sites in the complex of coves
that comprises Boiler Bay and at one subtidal site at Whale
Cove (Chapter 4, Fig.4.1). The substrata at these sites are
mixtures of mudstone, sandstone, volcanic conglomerate and
basalt. These complex substrata produce a very
heterogeneous habitat at Boiler Bay. The sites have many
tidepools, surge channels and benches that result in a
variety of microhabitats.

Movement Observation Techniques

Movements of Cryptochiton were determined by
calculating the distance between observed positions of
individually marked chitons on consecutive observation
dates. Positions were recorded relative to set reference
points at the study sites. Intertidal study sites were
searched for tagged chitons starting at the upper limit of

their range and moving back and forth across the site to the shoreward edge of the study site. Searching movements were parallel to shore, and local landmarks were used to assure an overlapping search pattern. The subtidal site was searched by attaching a polypropylene rope and a measuring tape to the central observation point and moving in concentric circles while looking for tagged chitons. When a chiton was found, and a tag could be observed, the position relative to a set point was recorded. On several occasions chitons with hidden tags or partially hidden bodies were not recorded because disturbing the animal to observe the tag number may have affected its subsequent movements.

Chitons were marked with numbered "spaghetti tags" (Floy Tag Co., Seattle, Washington) in the girdle using methods identical to those described for a mark-recapture study in Chapter 2. This method is similar to that used by Palmer and Frank (1974) in their study on growth of Cryptochiton. These workers marked chitons by threading beaded monofilament loops through the girdle. In several animals observed during the subsequent 17 months tags were pulling out of the girdle, or there were raw grooves where tags had pulled out. Urchins contributed to tag loss by holding on to the tags with their tube feet while the chiton moved away and by eating the tags. This phenomenon was also reported by Palmer and Frank (1974) during a tagging study of Cryptochiton .

After tagging, <u>Cryptochiton</u> were given a "rest" period
prior to position observations to avoid possible effects of
tagging trauma on movement or behavior. This period was 30
days or more for chitons that were tagged at Boiler Bay and
23 days or more for chitons tagged at Whale Cove.

The position of a chiton on a particular date was
measured relative to reference points in the study sites.
The reference points at intertidal sites were either masonry
nails or stainless steel expander bolts that were pounded
and glued (Z-Spar Splash-Zone compound, an epoxy putty) into
pre-drilled holes in the substratum, and were set into the
rock in lines that were close to areas at the study site
that were observed to have high concentrations of
<u>Cryptochiton</u>. Reference points at the subtidal Whale Cove
site were 1/2 inch threaded brass rods that were anchored
into the rock at the four corners of a 20m square on a
subtidal bench where many chitons had been observed. The
rods were anchored using methods similar to intertidal
reference points.

Chiton position was determined by stretching a
fiberglass tape from the closest reference point to the
girdle edge of the head region of the chiton. The angle of
this line relative to magnetic north was determined by using
a compass with an accuracy of .5 degrees. This pair of
measurements yielded polar coordinates relative to the
reference point. The position of each point relative to an
arbitrarily chosen zero point was measured using the same

method. Polar coordinates for each point were then
converted to Cartesian coordinates using a simple computer
program. A similar program was used to convert the polar
coordinates of a chiton position relative to one of the
reference points into Cartesian coordinates with the same
zero point as the reference points.

The minimum distance that a chiton moved between
position observations was determined by computing the length
of the line between the two points. Although the same area
was searched, the same individuals were not always found on
consecutive observation sessions. This was probably due to
several factors, including concealment of chitons or tags in
the heterogeneous habitat of the study sites, tag loss, and
possible dislodgment. 252 chitons were tagged, 160 at
Boiler Bay and 92 at Whale Cove. Movement data for >= 1 day
(2 or more position observations) were obtained for 47
chitons at Boiler Bay and 9 chitons at Whale Cove. These
data reflect a total of 292 chiton-days of observation at
Boiler Bay and 44 chiton-days of observation at Whale Cove.
The data group into movements over time periods ranging from
1 day to 519 days. Periodicity of movement was judged from
natural breaks in the data. These groupings were 1 day, 2
days, 30-31 days, 77-84 days, 160-166 days, 246-278 days and
354-519 days. 1 day and 2 day movements were compared
between Whale Cove and Boiler Bay study sites with a t-test.
Distance moved was plotted against time between positions
for chitons at Boiler Bay and regression analysis was

performed on these data. The data allowed some grouping into seasonal movements for late summer (August 1982, August 1983) and middle winter (November 1982, December 1983 and January 1984). 1 and 2 day movements were compared between seasons with a t-test.

An alternate method for analyzing movement data is to compare the observed movement to that predicted from a correlated random walk. This method requires consistent criteria for determining endpoints of movement such as a consistent time period and involves the plotting of the mean squared distance a animal is displaced versus the number of consecutive moves between endpoints (Kareiva and Shigesada 1983). This plot is compared to an expected curve that is calculated assuming the movements are a correlated random walk. Unfortunately, the movement data that were obtained in this study do not lend themselves well to this analysis. Data are available for only 2 and 3 consecutive moves for intertidal habitats and 2 consecutive moves for subtidal habitats. Thus the curve that could be plotted would be limited and comparison of observed to expected would be trivial.

Home range was computed for chitons with at least 3 position observations by measuring the area within the shape formed by connecting the consecutive plotted positions of an individual chiton with straight lines. The requirement of at least 3 position observations was necessary to obtain an area measurement. Data meeting this requirement were

obtained for 29 chitons, 24 at Boiler Bay and 5 at Whale
Cove. Home range data reflect a total of 252 chiton-days of
observation at Boiler Bay and 36 chiton-days at Whale Cove.
Area measurements were done by digitizing the position
points and using a program to compute the area. The
perimeter of the home range was also obtained in this
manner.

RESULTS AND DISCUSSION

Chiton movement observations reveal six basic patterns.
1) At intertidal study sites, the distance between two
chiton observation positions is significantly correlated
with the time between observations. 2) 1 day movements of
intertidal chitons were not significantly different between
late summer and middle winter. 3) At intertidal study
sites, the average distance that chitons on emergent
substrata (out of pools) move in one day is not
significantly different from submerged chitons (in pools).
4) Cryptochiton moves significantly more in subtidal
habitats than intertidal habitats over the same length of
time. 5) The home range of intertidal chitons is
restricted relative to subtidal chitons. 6) Intertidal
chitons remain within 21 meters of initial capture point
over periods greater than 1 year.

The distance moved by intertidal chitons at Boiler Bay
increased significantly with the amount of time between
observations. A plot of distance moved versus time between

observations yields a correlation coefficient of .498, which is significantly different from 0 (p<<.005) (see Figure 3.1). With one exception, for the time period 160-166 days, the mean distance moved appears to increase as time periods increase (Table 3.1). These data suggest that Cryptochiton moves within its habitat over time and does not home in the strict sense to a single position.

Seasonality apparently has little effect on the short-term (1 and 2 day) movements of intertidal Cryptochiton at Boiler Bay. 1 day movements were not significantly different between late summer observations and middle winter observations (t-test, p=.268). Cryptochiton moved an average of .61 m +/- .14 (n=12) over 1 day in winter versus 1.23 m +/- .29 (n=47) in late summer. 2 day movements were also analyzed but the sample size of winter observations was very small (n = 2). One of these values appeared to be aberrant because it was so high (21 m) relative to other 2 day movement observations regardless of season (maximum value = 10.89 m). This value was probably due to dislodgment of the chiton by wave action, which often occurs during the winter months. When the aberrant value is included, 2 day movements in winter are significantly higher than in summer (winter mean = 11.18 m +/- 7.09; summer mean = 2.28 m +/- .62, n = 22). When this value is rejected, no analyses of these data are meaningful.

One-day movements of intertidal chitons that were found on

Figure 3.1. The distance moved by <u>Cryptochiton</u> between position observations plotted against the time in days between observation dates. These data represent 148 pairs of observations.
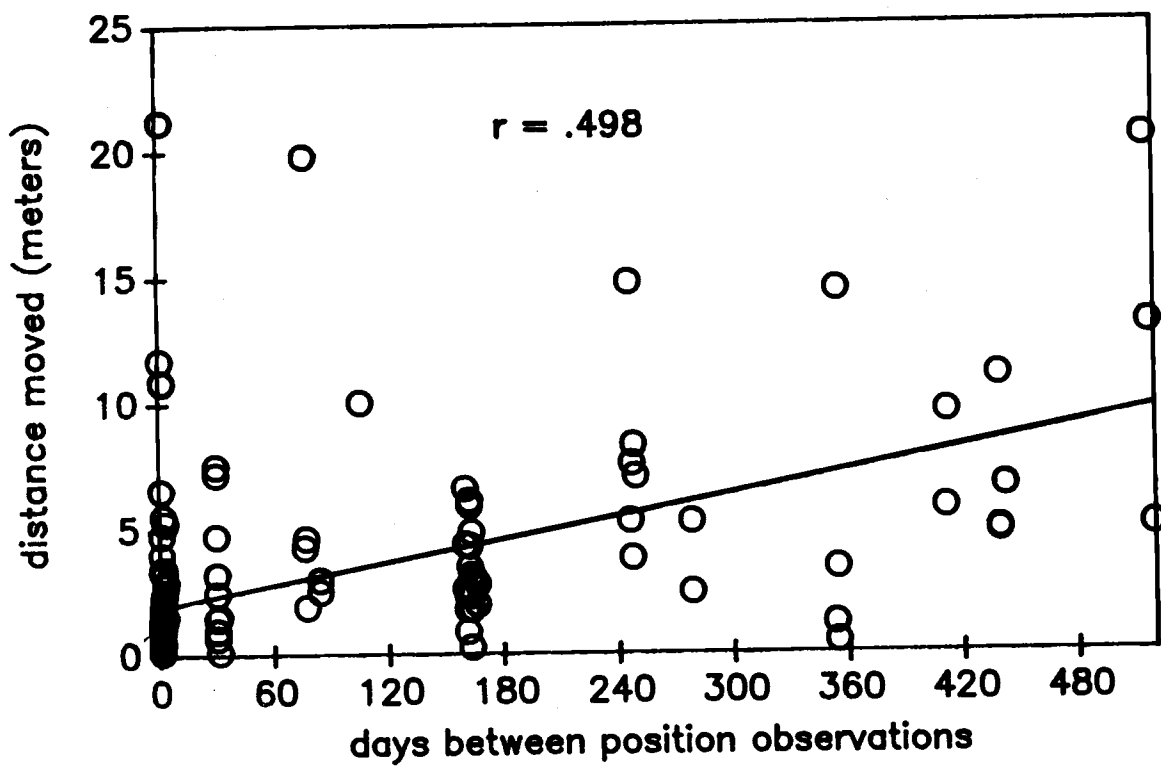
FIGURE 3.1

Table 3.1. Movements of _Cryptochiton_ over different time periods (days) at Boiler Bay and Whale Cove. Time periods were based on obvious groupings in the data.

		Distance Moved		
Study Site	Time Period (days)	Mean	Sample Size	Variance
Boiler Bay	1	1.10	59	3.28
Whale Cove	1	7.35	14	33.38
Boiler Bay	2	3.02	24	22.59
Whale Cove	2	9.77	5	34.77
Boiler Bay	30-31	2.99	10	6.33
Boiler Bay	77-84	6.37	5	45.95
Boiler Bay	160-166	3.26	18	2.98
Boiler Bay	246-278	6.80	8	12.31
Boiler Bay	354-519	9.56	10	24.38

emergent substrata during consecutive position observations
were very similar to those of chitons found on submergent
intertidal substrata during consecutive position
observations.   Analyses were performed only on data from
observations where an animal was observed on emergent or on
submergent substrata during both of the consecutive position
observations.   "Emergent chitons" moved an average of 1.33
meters and "submergent chitons" moved 1.30 meters between
consecutive low tide observations.   These results are
somewhat puzzling as submerged chitons exhibit more active
behaviors than emerged chitons (Yates, Chapter 4).   One
possible explanation is that the relatively higher activity
of submerged chitons consists primarily of feeding and
foraging instead of much movement.

The average distance moved over one day by a chiton at
Whale Cove was 7.4 m +/- 1.54 versus 1.1 m +/- .24 by an
intertidal chiton at Boiler Bay.   This difference was highly
significant (t-test, p<<.005).   In addition, the average
distance moved by a chiton over 2 days was significantly
greater at Whale Cove than at Boiler Bay (9.8 m +/- 2.64;
versus 3.02m +/- .97; t-test, p=.013).   The original
prediction of differences in movement distances between
subtidal and intertidal habitats is strongly supported by
these data.

The causes of these differences may be due to several
factors.   In general, physical factors are less stressful in
subtidal habitats.   The subtidal habitats at Whale Cove,

although relatively shallow at a depth of 5 meters, are well protected from the prevailing wave surge by a point of land that projects out from the north side of the cove. Chitons in these habitats experience no desiccation stress and little variation in temperature.

In contrast, physical factors at the intertidal sites at Boiler Bay are more stressful. Chitons on emergent substrata experience desiccation stress and temperature stress, both of which can affect metabolic rate (Peterson and Johansen 1973). Chitons in tidepools may also experience temperature stress, depending on the volume of the pool. Large bodies of water (large tidepools) will change temperature more slowly than small bodies of water (small tidepools). Wave action is relatively high at the Boiler Bay sites due to both the shallow nature of the habitat and the exposure of these habitats to the prevailing wave action. Subjective observations indicate that wave action is higher at the Boiler Bay sites than the Whale Cove site under similar ocean swell conditions.

Biological factors which may affect movements include competition and predation. Little is known about potential competitors of Cryptochiton, although purple urchins, Strongylocentrotus purpuratus, may affect food availability in tidepools that chitons share with a high urchin population. The only known natural predator on Cryptochiton in Oregon is the sunflower star, Pycnopodia helianthoides (K. Yates, Chapter 2). These seastars can be found in areas

surrounding the subtidal bench at Whale Cove, but were never observed at the Boiler Bay sites. The effects of Pycnopodia on the movements of Cryptochiton are unknown.

Home range comparisons must be standardized for the length of time over which the home range was measured. Comparisons of the home ranges of subtidal chitons at the Whale Cove study site with intertidal chitons from the Boiler Bay study sites were limited to movements occurring over periods of 2 and 3 days because movements were measured at the Whale Cove study site over a maximum of three days.

Although the mean home range for subtidal chitons observed at Whale Cove was much higher than the mean for intertidal chitons at Boiler Bay (Table 3.2), this difference was not significant (t-test, $p<.05$). Examination of the data revealed one extremely aberrant value in the home ranges of Whale Cove chitons. When this data point is removed, the differences between means is significant ($p=.006$). This aberrant value may be due to several factors: the chiton may have been dislodged by wave action and been rolled farther than it normally would have moved; the distances that chitons move vary greatly; or this individual chiton may have been avoiding a predator by moving at top speed.

The perimeter of the home range is an interesting measurement because it indicates the degree of site fidelity of a chiton. The area of a home range may be small but the perimeter

TABLE 3.2. Mean home range parameters for tagged chitons at Boiler Bay and Whale Cove. Units of area are in square meters, perimeter values are in meters, and the perimeter/area ratio is in the inverse of meters.

| Study Site	Time(days)	Sample Size	Mean Home Range Parameters		
			area	perimeter	per./area
Whale Cove	<=3	n=5	7.45	10.76	2.79
Boiler Bay	<=3	n=4	.35	7.58	86.78
Boiler Bay	>100<=200	n=8	2.34	10.06	7.20
Boiler Bay	>200<=300	n=3	5.97	11.32	3.82
Boiler Bay	>300	n=9	5.96	11.60	2.82

may be large because the shape of the range is long and narrow, thus indicating more linear movement than restriction to a particular area. Hence, the ratio of the perimeter to the area of a home range gives a useful measure of the shape of the home range. The greater the ratio, the more linear the shape of the home range. A circular home range would have the lowest ratio. The means of these ratios suggest that subtidal chitons at Whale Cove have a more compact home range than intertidal chitons at Boiler Bay (Table 3.2). However, these differences are not significant (t-test, p<.05). Examination of the data reveals a high variance of this value for both sites.

Home ranges for chitons observed over longer times indicate a trend of increasing home range area and perimeter over time (Fig. 3.2). In addition, distances between initial and final capture points for the eight chitons that were tracked for the longest time indicate that these animals stay within a maximum of 21m (mean = 9.53 +/- 1.88; n = 8) of initial capture over periods greater than 1 year (Table 3.3). These data are similar to those of Palmer and Frank (1974), who found most chitons within a maximum of 20m of the point of release after 2 years. Examples of paths of an intertidal Boiler Bay chiton and a subtidal Whale Cove chiton are given in Figure 3.3. All of this information indicates that the range of movements of Cryptochiton is

Figure 3.2. The relationship between home range parameters and time between initial and final position of chitons. A.) Home range area versus time. B.) Home range perimeter versus time.

FIGURE 3.2

A. HOME RANGE AREA OVER TIME

r = .159

home range area (squ. m)

# of days between initial and final positions
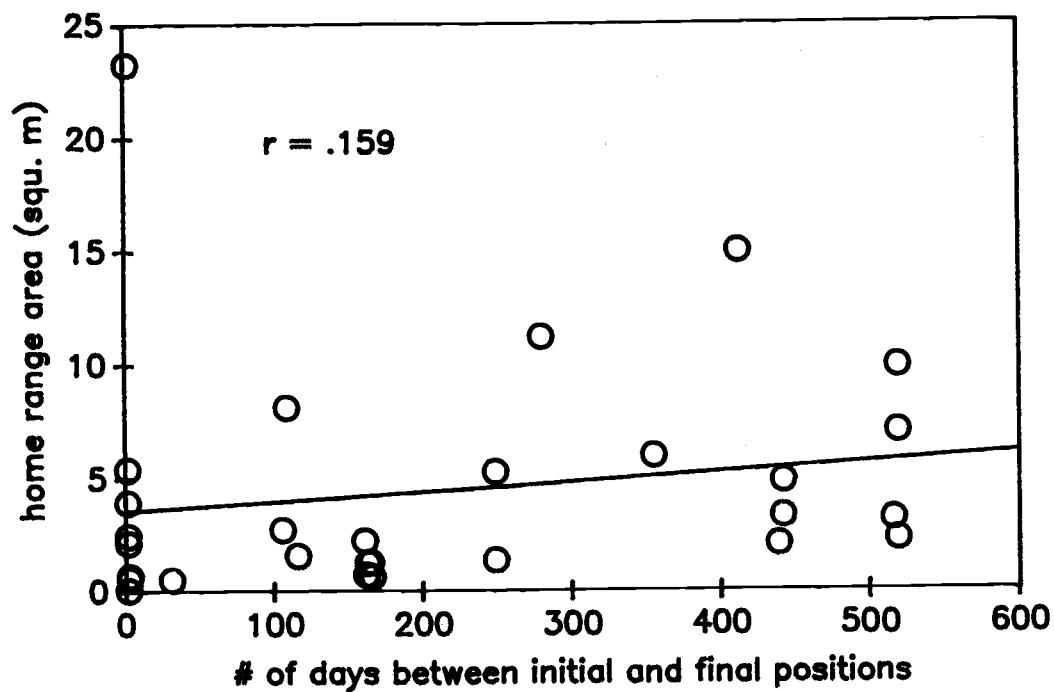
B. HOME RANGE PERIMETER OVER TIME

r = .372

home range perimeter (m)

days between initial and final position
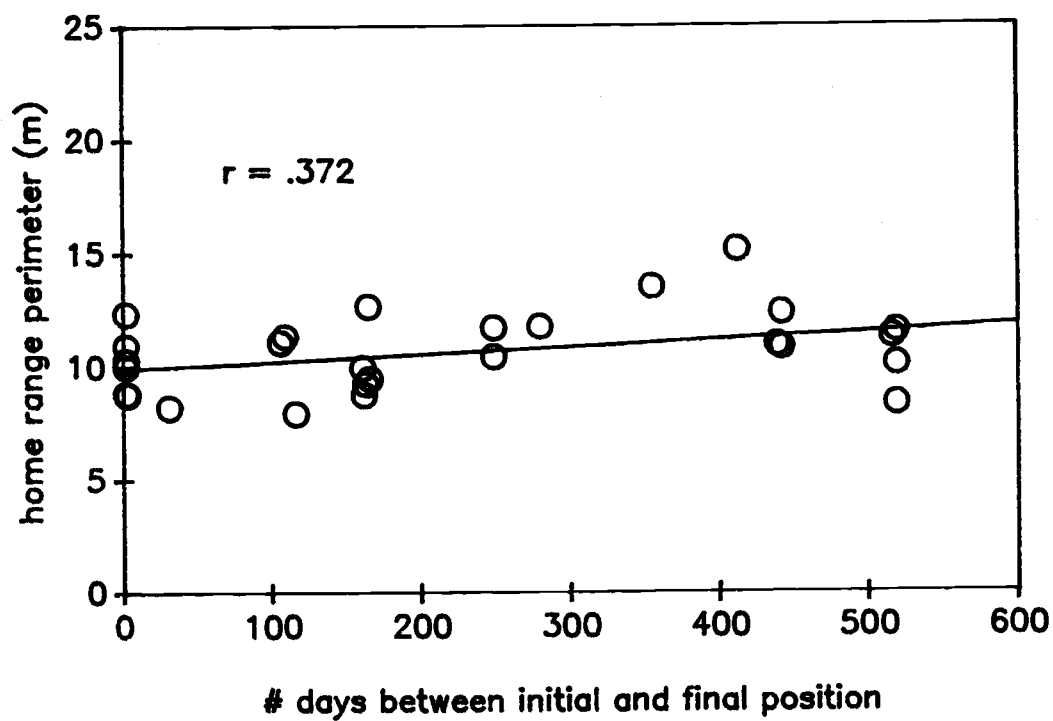
Table 3.3. Distance between initial capture and final recapture for the eight chitons that were recaptured >400 days after initial capture.

Chiton #	Initial Date	Final Date	#Days	Range (m)
26	11/4/82	1/17/84	439	4.83
30	12/4/82	1/20/84	412	9.58
33	8/18/82	1/19/84	519	5.01
80	12/4/82	1/19/84	411	5.77
84	11/3/82	1/19/84	442	6.63
91	8/20/82	1/19/84	517	13.01
106	8/20/82	1/17/84	515	20.43
210	11/4/82	1/17/84	439	10.99

mean = 9.53
standard error = 1.88

Figure 3.3. Examples of movement paths of A) an intertidal chiton from Boiler Bay (#84) and B) a subtidal chiton from Whale Cove (#135). Numbers by plot points represent the sequence of position observations over time.

FIGURE 3.3

A. MOVEMENT PATH OF INTERTIDAL CHITON #84
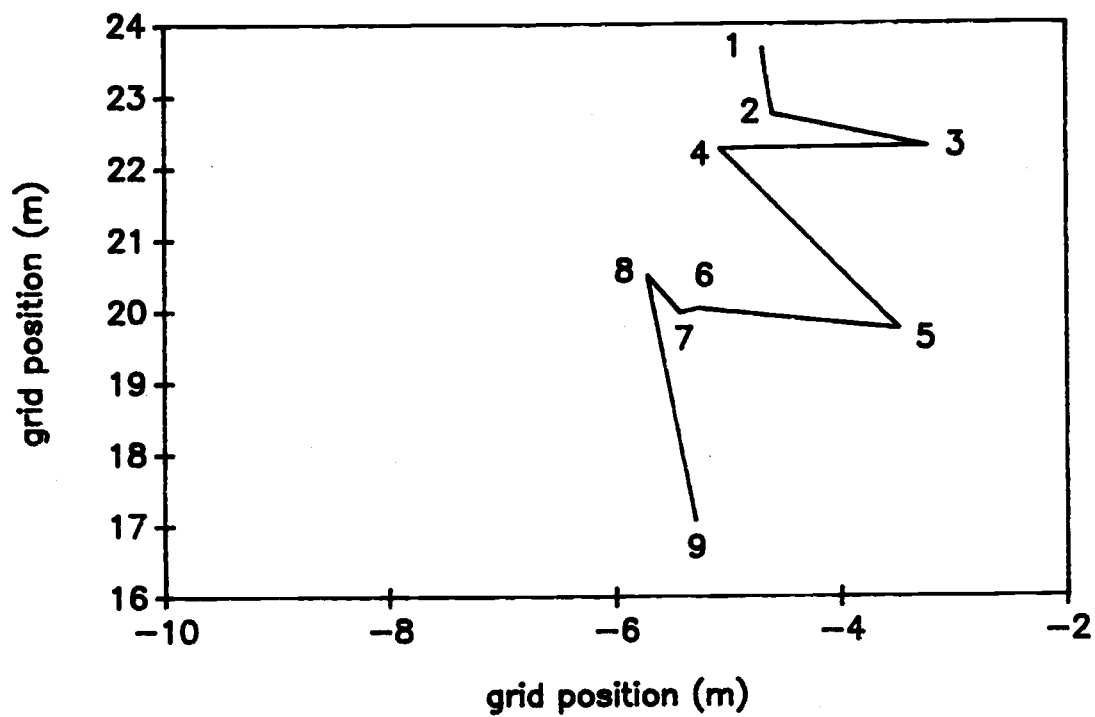
B. MOVEMENT PATH OF SUBTIDAL CHITON #135

restricted over long periods but that these animals do not home to a specific site as is known for several species of limpets.

CONCLUSION

This research suggests that <u>Cryptochiton</u> can move considerable distances but that its home range may be relatively limited over long periods of time. These chitons do not home to a specific site or scar as occurs with several species of limpets and chitons. Comparison of movements of subtidal chitons at Whale Cove and intertidal chitons at Boiler Bay s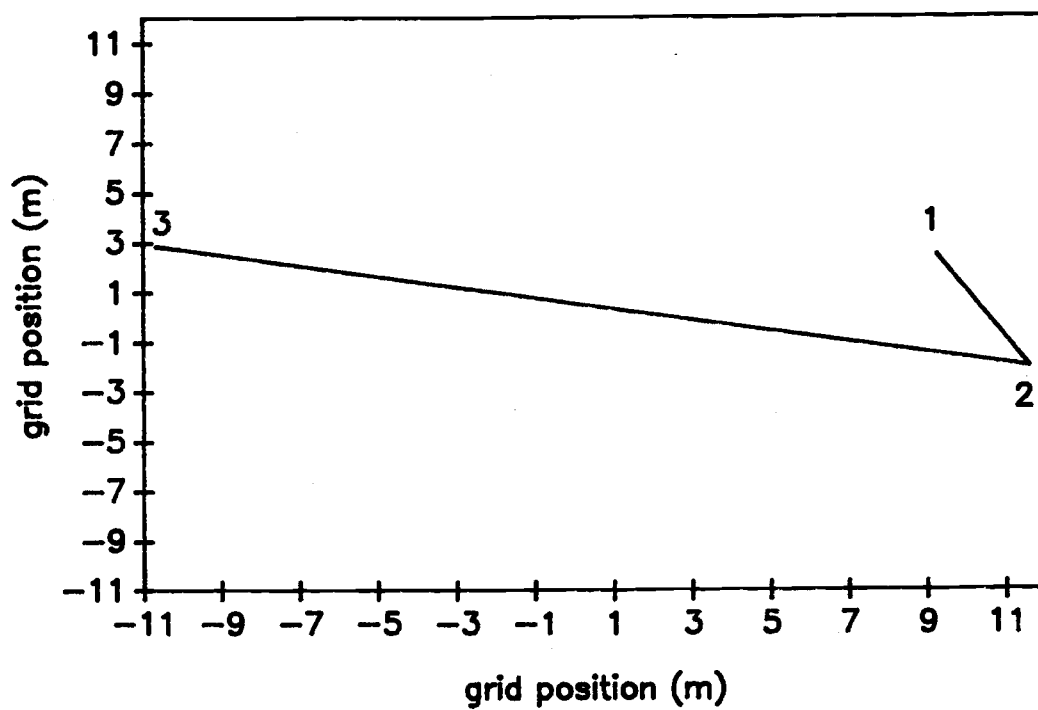uggest that chitons move less and have more restricted home ranges in intertidal habitats. This suggests that the impact of chitons on macroalgae will be more restricted in intertidal areas than at subtidal sites. Assuming that consumption rates are the same, the impact of an intertidal chiton would be more concentrated, thus causing a more patchy effect. Of course, many factors that were not examined in this research will affect consumption rates and the concentration of the impacts of a consumer.

The relatively limited home ranges and movements of intertidal chitons also indicate that fewer types of algae may be available to chitons in the intertidal zone than in the subtidal zone. This prediction assumes that the patch size of the maximum species number is greater than the home range of intertidal chitons.

Literature Cited

Branch, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. Oceanogr. Mar. Biol. Ann. Rev. 19:235-380.

Branch, G. M. 1971. The ecology of *Patella linnaeus* from the Cape Peninsula, South Africa. I. Zonation, movements, and feeding. Zool. Afr. 6:1-38.

Boyle, P. R. 1977. The physiology and behavior of chitons (Mollusca: Polyplacophora). Oceanogr. Mar. Bio. Ann. Rev. 15:461-509.

Dayton, P. K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. Am. Nat. 107:662-70.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137-59.

Dethier, M. N. and D. O. Duggins, 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. Oecologia 67:183-191.

Glynn, P. W. 1970. On the ecology of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linne: density, mortality, feeding, reproduction and growth. Smith. Contrib. Zool. 66:1-21.

Hawkins, S. J. and R. G. Hartnoll. 1983. Grazing of
intertidal benthic algae by marine invertebrates.
Oceanogr. Mar. Biol. Ann. Rev 21:195-282.

Himmelman, J. H. and T. H. Carefoot. 1975. Seasonal changes
in calorific value of three Pacific coast seaweeds and
their significance to some marine invertebrate
herbivores. J. Exp. Mar. Biol. Ecol. 18:139-51.

Kareiva, P. M. and N. Shigesada. 1983. Analyzing insect
movement as a correlated random walk. Oecologia
56:234-38

Lawrence, J. M. 1975. On the relationship between marine
plants and sea urchins. Oceanogr. Mar. Bio. Ann. Rev.
13:213-286.

Palmer, J. B., and P. W. Frank. 1974. Estimates of growth of
Cryptochiton stelleri (Middendorff, 1846). Veliger
16:301-4.

Petersen, J. A. and K. Johansen. 1973. Gas exchange in the
giant sea cradle Cryptochiton stelleri(Middendorff). J.
Exp. Biol. Ecol. 12:27-43.

Ricketts, E. F., and J. Calvin. 1968. Between Pacific
Tides. Revised by J. W. Hedgpeth. Fourth Edition.
Stanford University Press, Stanford, California, USA.

Stimpson, J. 1970. Territorial behavior of the owl limpet,
Lottia gigantea. Ecology 51:114-118.

Stimpson, J. 1973. The role of the territory in the ecology
of the intertidal limpet *Lottia gigantea* (Gray).
Ecology 54:1020-1030.

Underwood, A. J. 1979. The ecology of intertidal
gastropods. Adv. Mar. Biol. 16:111-210.

CHAPTER 4: The Interaction of Food Availability and Preference in the Field Diet of the Gumboot Chiton, Cryptochiton Stelleri.

ABSTRACT

Feeding preferences are a critical component of the information needed to predict the relative impact of a consumer on its prey. Most studies assume that preferences that are determined in the laboratory will be expressed under field conditions of fluctuating availability of prey or that selectivity determined from field data represent preferences. In this study I examined the feeding behavior of the giant chiton, *Cryptochiton stelleri*, by comparing laboratory preferences to selectivity calculated from actual availability and feeding observations in the field.

In general, preference interacted with availability to yield a diet that was different from that expected due to either factor by itself. For example, if preference alone determined the diet of *Cryptochiton*, its diet would consist primarily of *Iridaea cordata*, *Cryptopleura* spp., and ulvoids. In contrast, if the availability of algae was the sole factor determining diet, these chitons would eat primarily *Hedophyllum sessile*, *Odonthalia floccosa* and ulvoids because these species are, on the average, the most abundant. The actual field diet is a mixture of all of these species, which suggests that both factors are important. The selectivity of *Cryptochiton* in the field reflects the preferences determined by laboratory experiments but the relative proportion of an algal type in the diet is correlated with the relative availability of that type.

In addition, feeding preferences of <u>Cryptochiton</u> were very different from what is known for other chitons and most marine herbivores. Most other marine herbivores whose preferences have been investigated prefer kelps, ephemeral green algae or ephemeral red algae. <u>Cryptochiton</u> chiefly prefers perennial red algae such as <u>Iridaea</u> <u>cordata</u> and <u>Cryptopleura</u> spp. Other chitons that have been studied prefer either microphytes or kelp.

INTRODUCTION

Determining the factors governing food choice in animals has been one of the primary concerns of ecologists for several decades (Ebert 1968, Lubchenco 1978, Paine 1968, Steinberg 1985, Nicotri 1980, Vadas 1977, Leighton 1966, Leighton and Boolootian 1963, Schoener 1971, Watanabe 1984). Consumers usually discriminate among the potential prey in their environment, avoiding some species and seeking others. Knowledge of this behavior and the conditions under which it changes can help ecologists predict the impact of a consumer on the potential prey species within a community (Lubchenco and Gaines, 1981). In addition, study of the characteristics of the preferred and avoided prey can contribute toward the understanding of how prey can escape consumption.

Much of the information on feeding preferences comes from studies done either in the laboratory, where prey availability is controlled but conditions are artificial, or in the field, where prey availability varies but conditions are natural. In both cases, one measures what a consumer eats relative to what is available. Both approaches have limitations, however. In the laboratory, the innate preference of a consumer for potential prey species can be studied but whether or not this behavior is exhibited under field conditions cannot. In the field, electivity indices can be calculated from estimates of the availability and dietary proportion of prey species but determination of

actual preference is difficult. Further, estimates of the "availability" of prey to a consumer may be in reality merely measures of abundance (Menge 1972, Strauss 1979). Organisms that are assumed to be available prey items may be inaccessible or essentially inedible to the consumer. Physical or biological factors such as desiccation, wave action, predation or competition may exclude either the consumer or the prey items from certain microhabitats (Dayton 1971, 1975, Connell 1961, Paine 1966, Menge 1972, Menge 1974, Lubchenco 1983, Menge and Sutherland 1987). Estimates of the proportion of a prey item in the diet that are derived from gut samples can be biased due to variation in the rate of digestion between different prey items (Peterson and Bradley 1978, Fairweather and Underwood 1983). Problems with estimating actual availability may be minimized by restricting measurements to those species which are actually consumed and at the time and place that an animal is feeding (Menge 1972). Biases in the estimation of the proportion of prey in the diet can be avoided by direct observation of feeding on prey species.

A combination of laboratory and field approaches will yield the most detailed information on the food electivity of a consumer. Integrated study permits investigation of both the relative importance of preference behavior and prey availability. Indices of electivity indicate whether a prey item is eaten in greater, less, or equal proportions to its availability, but yield little information about how a

consumer responds to changes in availability over time. Correlations between the proportion of a prey item in the diet and the proportion available will indicate whether a consumer is changing its diet in response to changes in availability or is actually searching for a particular prey item.

The ideal consumer (1) behaves naturally in the laboratory, (2) can be observed feeding in the field without being disturbed, and (3) feeds on prey that can be sampled immediately following a feeding observation. Marine invertebrate macro-herbivores tend to fit these requirements well. They usually have little or no visual acuity, so the movements or presence of a human observer should have minimal effect on the consumer's behavior. These animals often behave naturally under laboratory conditions. The availability of the prey of many benthic marine herbivores can be estimated following a feeding observation because adult macrophytic algae are sessile and large enough to observe easily.

The herbivore that I used in this study of selectivity and preference was the gumboot chiton, _Cryptochiton stelleri_ (Middendorff, 1846). This is the largest polyplacophoran mollusc in the world, reaching lengths of 33 cm. It occurs from the low intertidal zone to depths of 20 m and ranges from the Aleutian Islands in Alaska to the Channel Islands in California but also can be found off northern Hokkaido Island in Japan and in the Kurile Islands of Kamchatka

(Morris et al. 1980). Very little is known about the autecology of Cryptochiton, which is probably due to the relative inaccessibility of its natural habitat, the low intertidal and subtidal zones. In addition, this animal is relatively rare and is patchily distributed (personal observations). Most of the work done on this chiton involved either respiratory or digestive physiology (Greer and Lawrence 1967, Harrison 1975, Lawrence and Lawrence 1967, Lawrence et al. 1965, Lawrence and Mailman 1967, Lawrence et al. 1972, Michael 1975, Peterson and Johansen 1973, Robbins 1975, but see MacGinitie and MacGinitie 1968, Palmer and Frank 1974, and Webster 1968). Preliminary observations indicate that this herbivore feeds mainly on macroalgae in submergent microhabitats (Yates Chapter 2). Their behavior is very limited and the presence of a human observer appears to have little effect on their foraging and feeding behavior (personal observations). Cryptochiton is an ideal animal to use in laboratory studies as it will forage and feed easily in the laboratory.

The purposes of this study were to (1) determine the preference of Cryptochiton stelleri for selected species of algae in the laboratory; (2) estimate the field electivity of chitons for all species of algae that are observed to be eaten; (3) compare laboratory preference to field selectivity; and (4) compare seasonal patterns of availability and algal utilization to preferences to

determine the relative importance of availability and preference behavior in the field diet of Cryptochiton.

STUDY SITES

Field observations of chiton feeding and measurements of algal availability were taken from the intertidal zone of several sites within the complex of rocky coves called Boiler Bay on the central coast of Oregon (Figure 4.1). The substratum at these sites is a mixture of mudstone, sandstone, volcanic conglomerate and various forms of basalt. This combination of substrata with different erosion rates produces a very heterogeneous habitat at Boiler Bay. The sites used in this research have many tidepools, surge channels, boulders and emergent benches that result in a variety of microhabitats that are emergent, partially submergent (henceforth referred to as "partial") or completely submergent (referred to as "submergent").

The chitons and algae used in laboratory experiments were collected from intertidal and/or subtidal sites at Boiler Bay, Whale Cove and the South Jetty of Yaquina Bay (Figure 4.1). The subtidal sites at Boiler Bay and Whale Cove were very similar: both were relatively flat, sloping benches with seasonal fluctuations in the abundance of several species of red algae, including Corallina officinalis, Botryoglossum farlowianum, Ptilota filicina, Plocamium cartilagineum, Bossiella

Figure 4.1. The location of the sites used for field observations and organism collection for laboratory experiments. All sites are on the central coast of Oregon, USA.

79

FIGURE 4.1
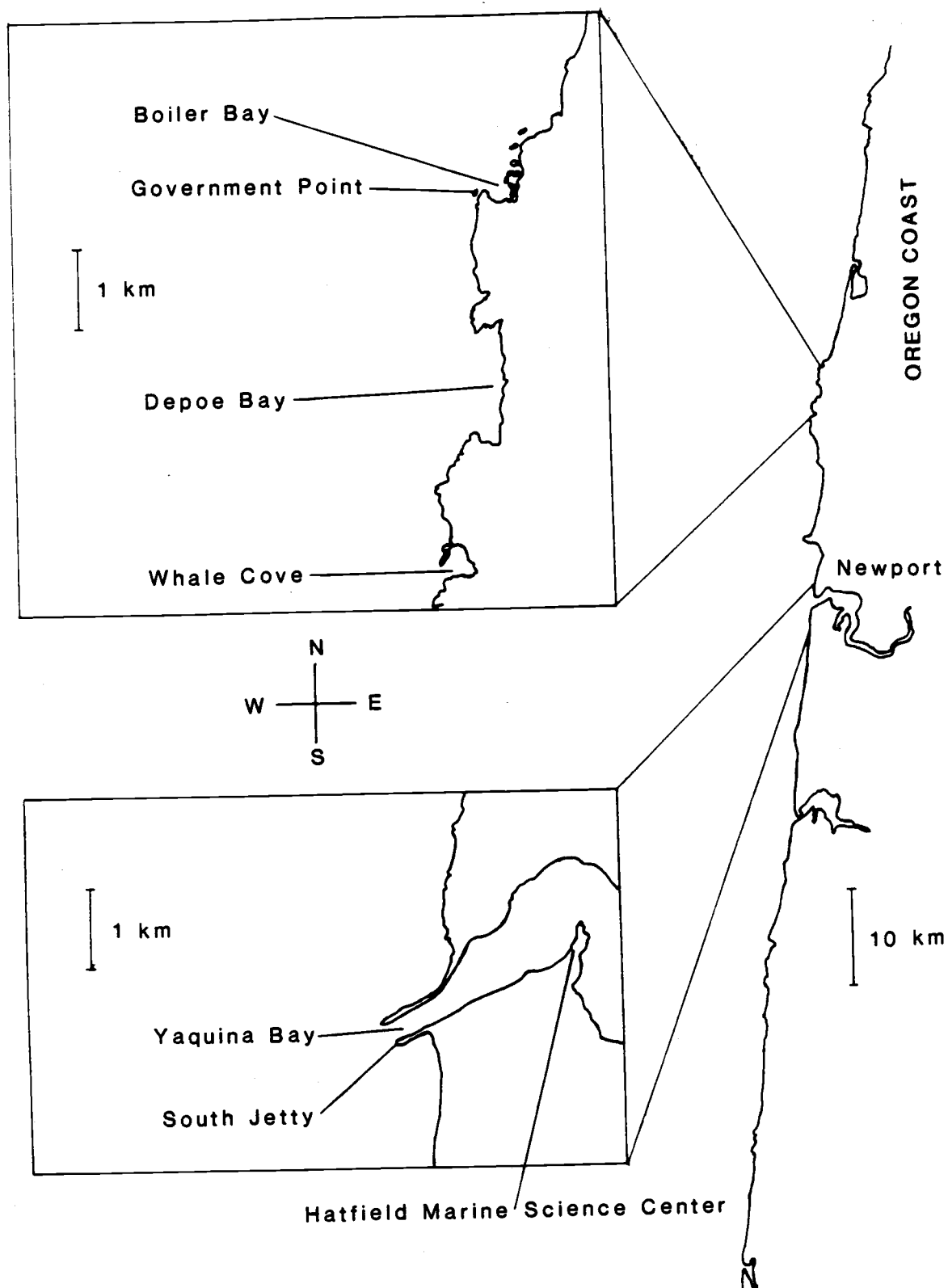
spp. and <u>Cryptopleura</u> sp. Boiler Bay is often exposed to heavy wave shock, with wave heights reaching 4+ meters (K. Yates, personal observations). The subtidal site at Whale Cove is

relatively protected from wave shock because of a protective arm of columnar basalt that forms a barrier to the prevailing winter ground swell. The subtidal collecting sites at the South Jetty of Yaquina Bay were on the large basaltic rip-rap boulders that are the main physical structures of the jetty.

MATERIALS AND METHODS

Field Electivity Observations

Attempts to measure the electivity of an actively foraging organism under field conditions usually involve some method of comparing the relative abundance of prey items in the diet to the relative availability of potential prey items in the environment. Most of the indices that are used to measure electivity have been developed for or during research on the foraging behavior of fishes (Ivlev 1961, Jacobs 1974, Chesson 1978, Strauss 1979). The utility, or biological reality, of these indices has been criticized on several bases. In most cases, the availability of prey items has been assumed to be equivalent to their abundance in the habitat of the predator. This assumption is invalid if some

prey items are actually unavailable to a predator due to temporal or spatial escapes, avoidance behavior, or inedibility caused by structural or chemical deterrents (B. Menge 1972, J. Menge 1974, Strauss 1979). An additional problem is obtaining an unbiased sample of the relative abundance of the prey as they are consumed. In studies on fish foraging behavior, the consumed prey are usually sampled by examining the gut contents of individual fish. This type of sample is unbiased only if the digestion rates for all of the prey items are equal and there is equal probability of identifying these items in a gut sample (Peterson and Bradley 1978). Unfortunately, these factors are not always equivalent for all prey items in the guts of fishes (Strauss 1979).

The techniques used in my study were designed to avoid these problems. Estimates of the availability of prey items were taken at the time and in the microhabitat in which a Cryptochiton was observed feeding. This was made possible by the insensitivity of these chitons to the close presence of an observing human. In addition, the range of potential prey items used to calculate relative availability was restricted to those algae on which Cryptochiton had actually been observed to feed. This avoids including any algae that were functionally unavailable to chitons due to structural or chemical defenses. The relative proportions of a prey item in the diet was obtained through direct observations of chitons feeding in the field. These proportions are

actually population estimates of diet, similar to the technique used by Menge (1972). Diets of individuals were not followed.

The feeding behavior of chitons and estimates of the availability of species of algae were used to calculate electivity indices for each algal species. Feeding behavior was observed in several areas of Boiler Bay. To ensure that as many chitons were observed as possible, without repeated observation of the same individual, each site was searched in a nonoverlapping manner by walking back and forth over the site. When a chiton was detected, it was observed without disturbance for 2 minutes to determine its behavior. Feeding was defined as occurring if movement of the algae was synchronized with pulling motions of the chiton. The species of algae being consumed could often be identified directly. Where this was impossible, the chiton was picked up and turned over to see if an alga was protruding from its mouth. If none of these methods were sufficient to determine the species being eaten, the algae that had been under the mouth of the chiton were examined for the characteristic grazing marks of Cryptochiton. These marks were semicircular shaped edges which are easily distinguished from the star-shaped marks of urchins. When none of these methods revealed which species was being eaten, the observation was not used in the electivity calculations.

Local availability of algae was measured by estimating the percent cover of different species of algae in a .0625

square meter quadrat (here termed "feeding observation quadrat") placed posterior to and including the area where the mouth of a feeding chiton had been present. The habitat heterogeneity of the study site required a quadrat size that would avoid sampling two different microhabitats. The size used was the largest that would fulfill these requirements. The quadrat was divided into 100 equal squares and the most abundant alga was subjectively determined for each square. Abundance (percent cover) was estimated as the number of squares in which it was most abundant. The availability of an alga was estimated by dividing the percent cover of that type of alga by the total percent cover of all algae that were present. This type of availability will be referred to as "absolute" availability. "Relative" availability was calculated by dividing the percent cover of a type of alga by the total percent cover of all algae that had been observed to be eaten; i.e., a subset of those algae present.

Estimation of prey availability in areas immediately adjacent to a feeding Cryptochiton was necessary to avoid inaccurate estimates of the proportions of prey encountered. The small scale heterogeneity of the habitat, and prey distribution, suggested that a larger sample area or randomly located quadrats may have provided an inaccurate estimate of the proportions of prey prior to feeding (Palmer 1984). Intertidal benches with a vastly different assemblage of algae were often within close proximity to the tidepools where Cryptochiton could be observed feeding.

The overall availability of algae in all habitats at the study sites was measured by estimating the percent cover of algae in quadrats placed randomly along transect (here termed "transect quadrat") lines that ran through the study site parallel to the waterline (e.g. Dayton 1971, Menge 1976). The same quadrat and technique for estimating percent cover within a quadrat described above were used in transect estimates.

The electivity index $D = (r-p)/(r+p-2rp)$ (where r = the proportion of a prey item in the diet and p = the proportion of a prey item available in the environment), recommended by Jacobs (1974), was calculated for each of the 22 algal types for each observation period. This index is similar to Ivlev's (1961) index but is modified to be independent of relative abundance and to reflect directly differential mortality rates of the prey (Jacobs 1974). D ranges from -1 to 0 for negative electivity and from 0 to 1 for positive electivity. A positive value of D indicates that a food is eaten more than it is encountered and a negative value indicates that a food is eaten less often than it is encountered (Jacobs 1974).

Mean electivities of each algal type over the entire study were calculated and tested for statistical differences using a one-way ANOVA. Where this test indicated significant differences of at least one of the means from the others, Tukey's multiple comparisons test was used to search for differences between the means of pairs of algal

types. If Bartlett's test for homogeneity of variance indicated that variances were unequal, the data were transformed by taking either the square root or the log of the indices. Transformation by one of these two methods always succeeded in producing homogeneous variances.

Laboratory Feeding Preference Experiments

Methods for determining feeding preferences can be grouped into two general categories; chemoreceptive responses and ingestion rates. Chemoreceptive methods involve an apparatus, such as a y-maze, that allows an herbivore to choose between alternate prey items based only on waterborne chemical cues. Although Himmelman and Carefoot (1975) argue that chemoreception is the best measure of preferences, the ultimate measure of preferences is whether or not, and in what quantity, a consumer will eat a prey species. Moreover, one of the primary reasons for determining preference is to predict the impact of an herbivore on the algal community (Lubchenco and Gaines 1981). Impact is best estimated by the amount of algae that is consumed, not just whether the herbivore will sample an alga once it is encountered. In addition, distance chemoreception may not be effective under conditions of extreme mixing of waterborne cues. In concurrence with the majority of other laboratory studies on preference (e.g.Leighton 1966, Vadas 1977, Watanabe 1984, Horn et al

1982, Nicotri 1980, Steinberg 1985, Lubchenco 1978), I have used relative ingestion rates as the measure of preference.

Laboratory preference experiments involved the pairwise presentation of similar weights of two species of algae to individual chitons. Two thalli of each species were clamped by attached plastic clothespins in opposite corners of approximately square water tables (Figure 4.2). These watertables are constructed of fiberglass with an internal gel coat, have inside dimensions of 96 x 91.5 x 15 cm and were filled with flowing, unfiltered seawater from Yaquina Bay to a depth of approximately 9 cm. Although the salinity of the water in the tables was not measured directly, values for the seawater system of the Hatfield Marine Science Center range between 32 and 28 0/00 during the spring and summer months, when these laboratory experiments were conducted (Physical Plant Records, Hatfield Marine Science Center; personal observations).

Experimental animals were held in flowing seawater tanks at the Hatfield Marine Science Center for a period of 3 to 6 days without food to decrease the probability that satiation would influence their feeding rates or preference. Prior to the start of a preference experiment, one chiton was placed in each of eight watertables, and allowed to acclimate for 24 hours. Algae were held in watertables with flowing seawater for a maximum of 24 hours before being used in experiments. Algae were sorted to obtain thalli that were free of macro-epiphytes.

Figure 4.2. The experimental tanks, apparatus and algal thalli arrangement used in laboratory preference experiments.

FIGURE 4.2
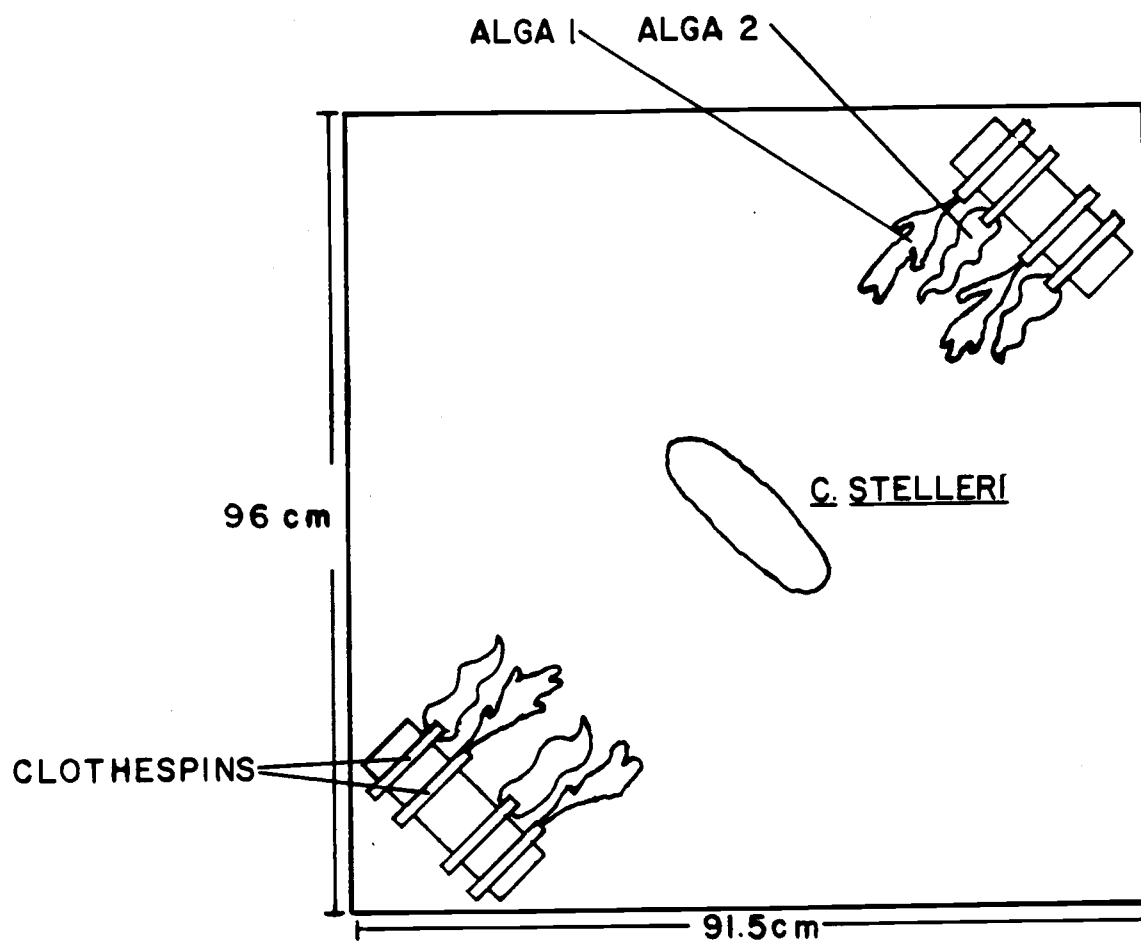
To initiate an experiment, excess water was removed from the thalli by spinning in a hand-operated centrifuge and blotting dry on paper towels until no moisture was visible on the towels. Pieces of algae were then weighed on an electronic balance to 4 decimal places. To reduce differences in the availability of algae between species and replicates, approximately the same weights of each species were used in each replicate. For each algal species the weighed thalli were divided into four approximately equal pieces, two of which were clamped in clothes pins at each of two opposite corners of the experimental water tables (Figure 4.2). This resulted in similar availability of both algal species in each of the corners of the water tables. Thus, a replicate consisted of four thalli each of two species presented to one chiton. In most cases, there were eight replicates of each experiment, but occasionally, a chiton would not eat any algae. When this occurred, and other chitons were eating the algae presented in the experiment, it was assumed that the refractory chiton was inactive due to some factor other than the palatability of the algae and that replicate was not included in the experimental results. The maximum number of chitons not eating during an experiment was 2, and in all cases these chitons were totally inactive (i.e., not moving).

Experiments were terminated according to one of the following criteria: either (1) after 50% of the thalli of one species of algae were eaten in 50% or more of the

replicates; or (2) 3 days had lapsed since the beginning of the experiment. Termination involved weighing the uneaten thalli of each species as described above for each replicate, including unattached pieces.

Although I attempted to present the chitons with equal amounts by weight of the two algae used in a trial, there were weight differences between the thalli used in an experiment. These slight differences in availability were adjusted by calculating the weight loss of each species for each replicate as a percentage of the initial weight. In addition, if weight loss or gain of the control thalli (those without chitons) indicated that the two species of algae responded significantly differently to laboratory conditions (paired t-test, p<.05), experimental data were adjusted by the mean percent change of the control thalli. These percent weight loss data were then tested for significant differences using a paired t-test with p<.05. The most consumed alga in each pairwise experiment was judged to be preferred.

RESULTS

The field diet of Cryptochiton was composed primarily of 6 types of algae with at least one feeding observation on 17 other types (Table 4.1). Chitons were observed to feed most often on Iridaea cordata, Laurencia spectabilis, Odonthalia floccosa, Hedophyllum sessile, unidentified fleshy red blades and ulvoid

Table 4.1. Data based on 122 feeding observations from 41 field days of observation that spanned the dates 12/20/84 - 6/26/86: number of observations of chitons actually feeding, percent of total feeding observations and mean electivities using Jacobs' D index for algae in the diet of Cryptochiton stelleri.

Algal Species	Feeding Observations			
Rhodophyta	# obs.	% of obs	mean D index	mean %cover
Iridaea cordata	17	14%	.6192	2.71
Fleshy red blade	22	18%	.3964	4.08
Gigartinales	1	1%	.1198	0.01
Ceramium californicum	1	1%	.0640	0.17
Cryptopleura ruprectiana	2	2%	.0400	0.12
Mastocarpus papillatus	1	1%	-.0468	0.31
Dilsea californica	2	2%	-.0640	0.36
Odonthalia floccosa	34	27%	-.1260	9.24
Laurencia spectabilis	5	4%	-.1989	0.90
Ptilota filicina	1	1%	-.3466	0.28
Halosaccion glandiformis	1	1%	-.3529	0.04
Plocamium cartilagineum	1	1%	-.3753	0.05
Schizymenia pacifica	1	1%	-.5314	1.89
Phaeophyta				
Costaria costata	2	2%	-.1911	0.68
Hedophyllum sessile	11	9%	-.3551	7.34
Alaria marginata	1	1%	-.7456	1.80
Chlorophyta				
ulvoids	17	14%	-.4146	11.47
Acrosiphonia coalita	2	2%	-.5379	1.75

Total Observations = 122

algae. Field observations indicate that the majority (13 of 18) of types of algae eaten by Cryptochiton are in the Rhodophyta. Three species were in the Phaeophyta and two types were in the Chlorophyta.

In general, the absolute availability of all algae in the diet as measured by percent cover in feeding observation quadrats was lowest from October through February (Figure 4.3). Seasonal estimates of percent cover from transect quadrats also support this pattern (Figure 4.4). However, seasonal fluctuations in the abundance of the six main types of algae in the diet exhibit dramatically different patterns (Figure 4.5a). The abundance of O. floccosa was relatively high and constant over the observation period but the abundance of the other groups fluctuated widely. Ulvoids varied the most, reaching a peak in June 1985 and decreasing almost to zero in January 1986. Iridaea cordata also varied but was usually lower in abundance than the other four types.

The relative availability of the five important algal groups in the feeding observation quadrat followed similar seasonal patterns with the exception of O. floccosa, which peaked in winter 1986 (Figure 4.5b). Apparently, from its relatively constant percent cover and the seasonal fluctuations in other important algal types, Odonthalia floccosa is the most predictably available alga among the primary types in the diet of Cryptochiton.

Figure 4.3. Seasonal fluctuations in the mean total percent cover of all algae eaten by <u>Cryptochiton</u> <u>stelleri</u>. These data are from quadrat estimates from feeding observations at Boiler Bay, Oregon.

FIGURE 4.3
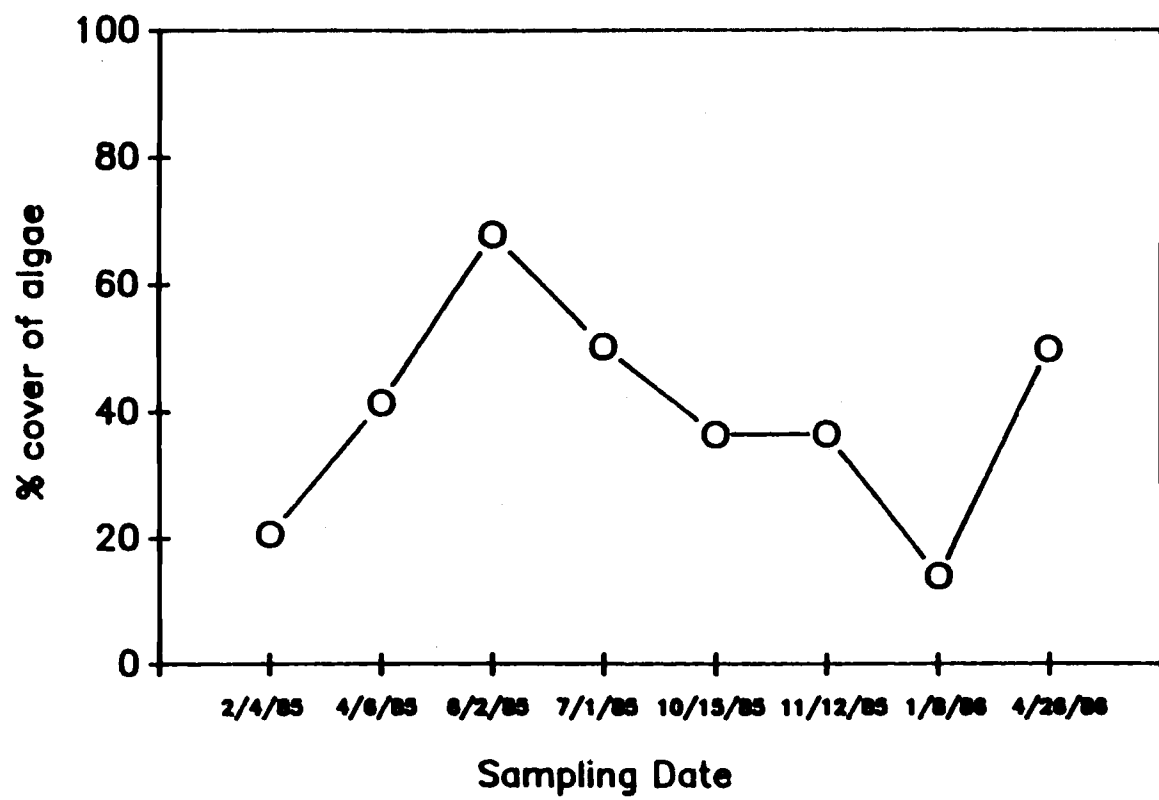
Figure 4.4. Seasonal fluctuations in the mean total percent cover of all algae known to be eaten by <u>Cryptochiton stelleri</u>. These data are from quadrat estimates from transects at Boiler Bay, Oregon.

FIGURE 4.4
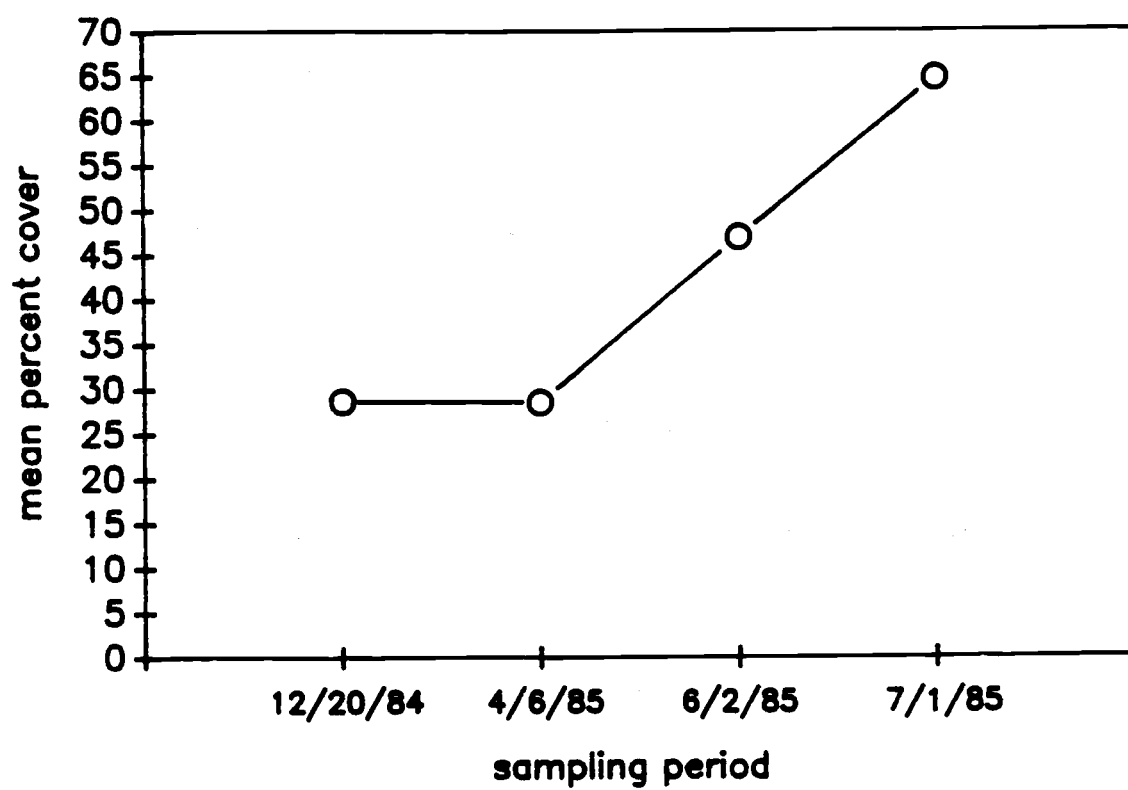
Figure 4.5. Seasonal fluctuations of the six main algal types in the diet of Cryptochiton. The left y-axis and lines with solid squares indicate mean percent cover (absolute availability). The right y-axis and lines with the open circles indicate relative availability. Relative availability is calculated by dividing the percent cover of an algal type by the total percent cover of all algae that are known to be in the diet of Cryptochiton. Note that scales on right axes may vary among panels. The numbers on the x-axis correspond to the following dates:

1 - 2/4/85

2 - 4/8/85

3 - 6/2/85

4 - 7/1/85

5 - 10/15/85

6 - 11/12/85

7 - 1/9/86

8 - 4/26/86

FIGURE 4.5
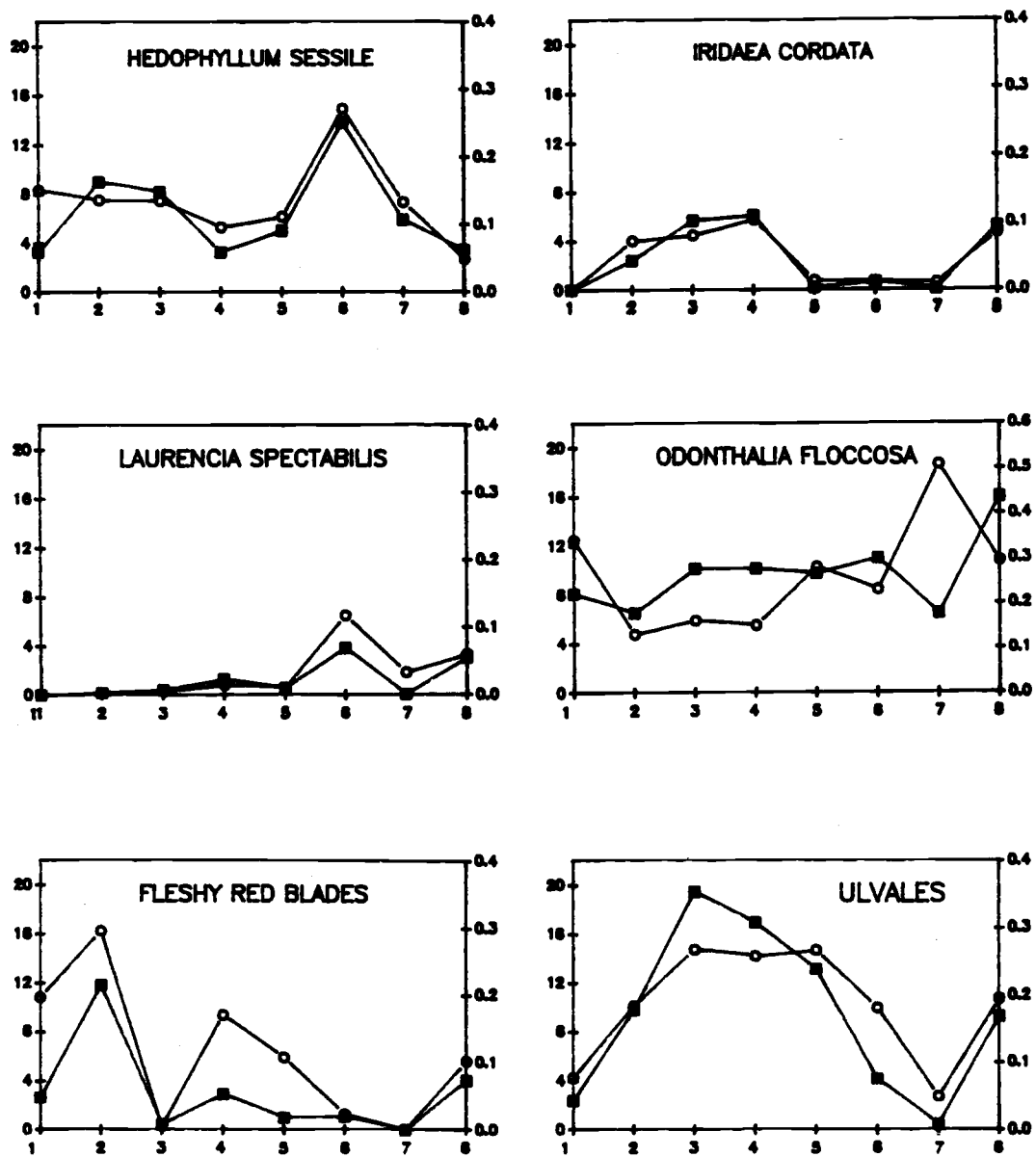
Electivity Indices Calculated From Field Observations

Of the six algal types that were eaten most frequently, only two, Iridaea cordata and red blades had positive mean electivities. ANOVA for the electivity indices indicate that at least one mean is different from the others at the .05 level of probability. Post-hoc multiple comparisons tests show significant differences between Iridaea and Hedophyllum, Ulvales, Odonthalia floccosa, and Laurencia but not between Iridaea and red blades. In similar tests, red blades were significantly different from Hedophyllum, Laurencia, Odonthalia floccosa, and Ulvales. These results are summarized in Table 4.2. The electivity hierarchy of Cryptochiton suggested by these data is:

Iridaea cordata= fleshy red blades > Hedophyllum sessile = Laurencia spectabilis = Odonthalia floccosa = Ulvales.

Seasonal variation and trends of electivities are illustrated in Figure 4.6. Iridaea cordata was always selected while Hedophyllum and ulvoids were always avoided. Fleshy red blades was chosen in six and avoided in 2 of the sampling periods of the study. Odonthalia floccosa was selected on three and avoided on five of the sampling periods. Although D for this species was often negative, it never fell to -1. This means that Odonthalia was available and always eaten during each of the

Table 4.2. Mean electivity indices for 6 most frequently eaten algae. * - Different letters indicate significantly different means.

Species	Mean Electivity	Significance *
Iridaea cordata	.6192	A
Red blades	.3964	A
Odonthalia floccosa	-.1260	B
Laurencia spectabilis	-.1989	B
Hedophyllum sessile	-.3551	B
Ulvales	-.4146	B

Figure 4.6. Temporal changes in the electivity indices of
the 6 algal groups that are most important in the diet of
Cryptochiton. These indices are calculated from a formula
developed by Jacobs (1974). $D = r - p\ /\ r + p - 2rp$, where
r is the proportion of a prey species in the diet of the
consumer and p is the proportion of that food that is
available in the environment. Positive values of D indicate
that a food is eaten more often than it is encountered and
negative values indicate that a food is eaten less often
than it is encountered. Estimates of r and p were taken
from field feeding observation data at Boiler Bay, Oregon.

FIGURE 4.6

Electivity Index vs. Sampling Date

KEY

— Iridaea cordata

— fleshy red blades

— Odonthalia floccosa

— Laurencia spectabilis

— Hedophyllum sessile

— ulvoids
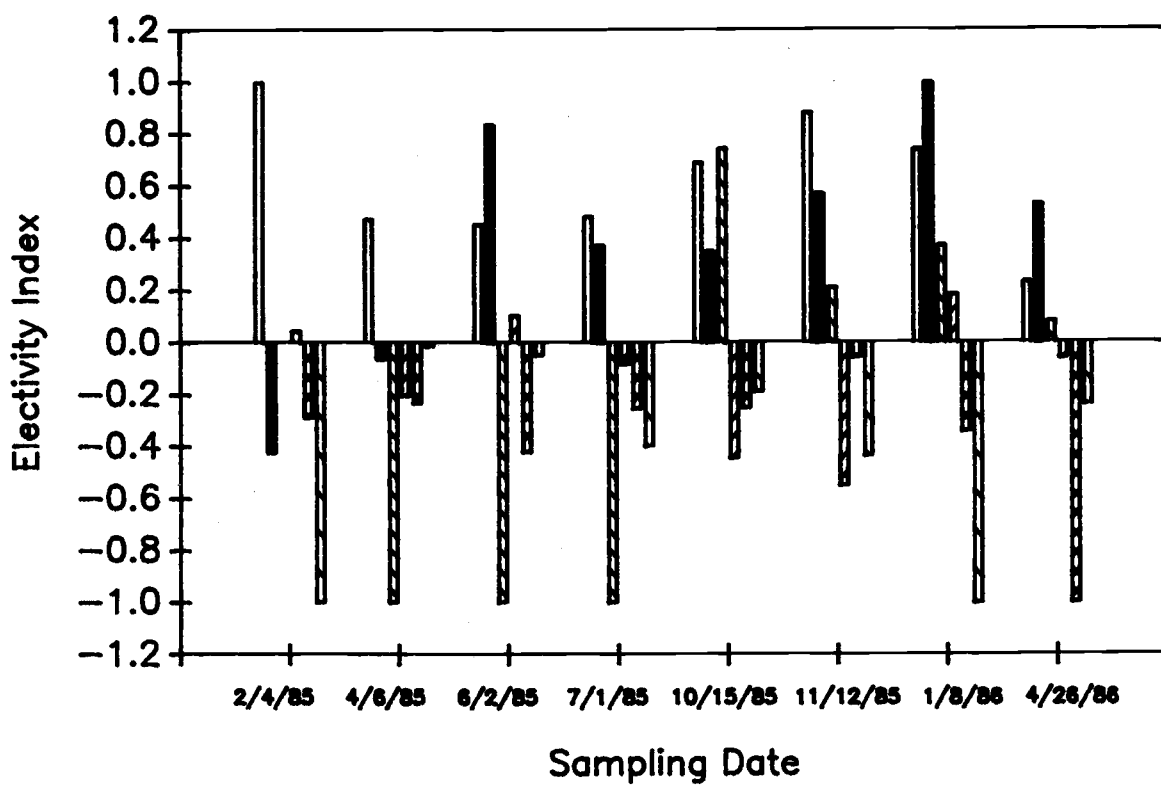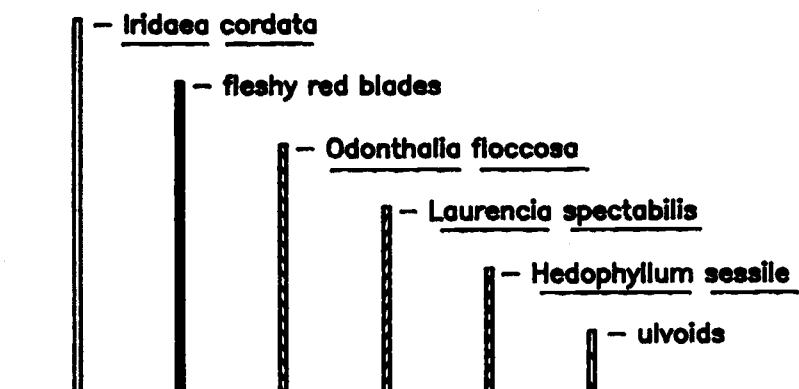
sampling periods, a characteristic shared with only one other species of alga, Iridaea cordata.

A comparison of the patterns of temporal variation of r and p for an algal type reveals some interesting relationships. When r and p for an algal type are plotted together against time, they follow the same pattern of variation (see Figure 4.7 for an example). A plot of r against p reveals a positive correlation, at least for all of the 6 algal types that are most important in the diet of Cryptochiton. The Spearman correlation coefficients for these plots are significant at $p < .05$ for Hedophyllum sessile, Laurencia spectabilis, Odonthalia floccosa, Ulvales and for fleshy red blades but not for Iridaea cordata (Table 4.2). This suggests that Cryptochiton actively searches for Iridaea.

Laboratory Feeding Preference Experiments

In contrast to the field feeding observations, these experiments were designed to assess the relative preferences of Cryptochiton under conditions of equal availability. Analyses of these experiments (Figure 4.8) indicate that there are four levels in the preference hierarchy of Cryptochiton. The percent weight loss data for the species of algae paired in an experiment were tested for significant difference using a paired t-test with $p<.05$. The most consumed alga (the one with the highest percent weight loss) in each pairwise experiment was judged to be

Figure 4.7. Seasonal fluctuations of r, the proportion of a prey species in the diet of a consumer, and p, the proportion of that food that is available in the environment, for the alga _Hedophyllum sessile_. These data were calculated from feeding observations of _Cryptochiton_ at Boiler Bay, Oregon.
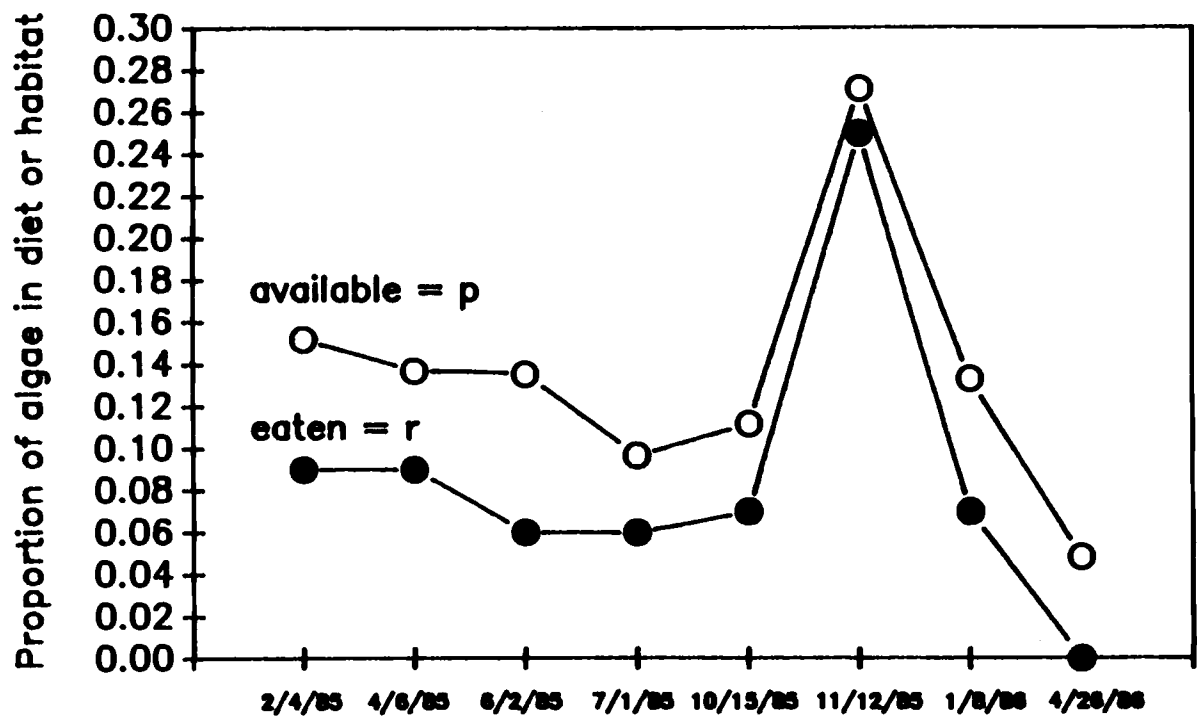
FIGURE 4.7

Figure 4.7. Values of p = proportion in environment and r = proportion in diet against time for the algae Hedophyllum sessile
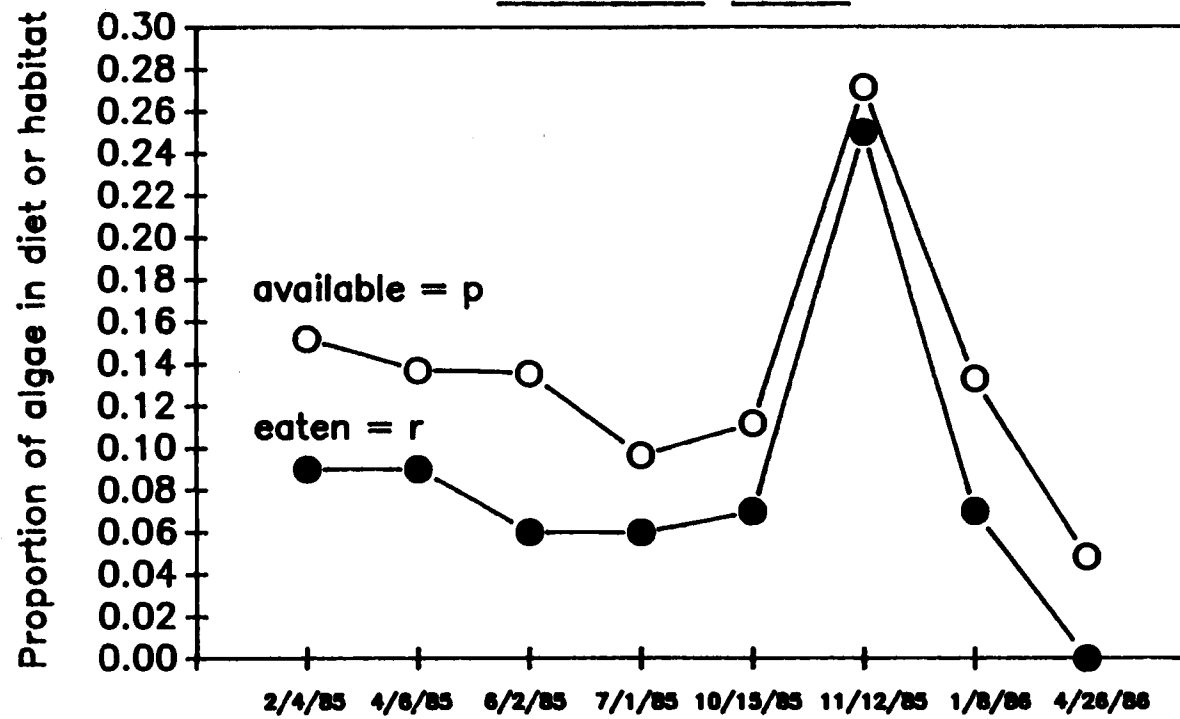
Figure 4.8. Results of the laboratory feeding preference experiments. The top right half of the figure shows which alga was preferred of the pair used in that particular experiment. The arrows indicate that a significantly higher percent (by weight) of the alga on the left was eaten than the species on top (paired t- test, p<.05). Open circles indicate that neither alga was preferred.

The lower left half of the figure gives the mean percent eaten of the two algae used in that experiment. The top number in each box is for the species at the head of the column and bottom number is for the species on the left.

FIGURE 4.8

	Ic	Cs	Ul	Cr	Ls	Of	Pf	Em	Ow	Cc	Hs	Ac	Co	Pc	Am
Iridaea cordata			○	←	←	←		←	←	←	←	←			
Cryptopleura sp.				←											
Ulvales	54/59										←				
Cryptopleura ruprechtiana	69/20	65/43					○		←					←	
Laurencia spectabilis	45/37							←							
Odonthalia floccosa	62/28										←				
Ptilota filicina				61/59					←			←			
Egregia menziesii	50/23				67/5						←				
Odonthalia washingtoniensis	82/26			58/9			74/18						←	←	
Costaria costata	54/28														
Hedophyllum sessile	58/5		51/4			35/8		36/0							←
Acrosiphonia coalita	71/19						63/20								
Corallina officinalis									40/3						
Plocamium cartilagineum				58/0					48/0						
Alaria marginata											36/10				

	Ic	Cs	Ul	Cr	Ls	Of	Pf	Em	Ow	Cc	Hs	Ac	Co	Pc	Am
Iridaea cordata			○	←	←	←		←	←	←	←	←			
Cryptopleura sp.				←											
Ulvales	54/59										←				
Cryptopleura ruprechtiana	69/20	65/43					○		←					←	
Laurencia spectabilis	45/37							←							
Odonthalia floccosa	62/28										←				
Ptilota filicina				61/59					←			←			
Egregia menziesii	50/23				67/5						←				
Odonthalia washingtoniensis	82/26			58/9			74/18						←	←	
Costaria costata	54/28														
Hedophyllum sessile	58/5		51/4			35/8		36/0							←
Acrosiphonia coalita	71/19						63/20								
Corallina officinalis									40/3						
Plocamium cartilagineum				58/0					48/0						
Alaria marginata											36/10				

preferred. The position of an alga in the preference
hierarchy was determined by placing it above species that
were less preferred and on the same level with species that
were preferred equally (i.e., had similar weight losses).
The species tested and their appropriate levels are
illustrated below:

LEVEL 1   _Iridaea_ _cordata_ = _Cryptopleura_ sp. = _Ulvales_ >

LEVEL 2   _Odonthalia_ _floccosa_ = _Laurencia_ _spectabilis_

               = _Botryoglossum_ _farlowianum_ = _Ptilota_ _filicina_

               = _Egregia_ _laevigata_ >

LEVEL 3   _Hedophyllum_ _sessile_ = _Costaria_ _costata_

               = _Acrosiphonia_ = _Odonthalia_ _washingtoniensis_ >

LEVEL 4   _Alaria_ _marginata_ = _Plocamium_ _cartilagineum_ =

               Corallina _officinalis_

Preference groups were statistically different with the
exception of the comparison between _Iridaea_ _cordata_ and
Laurencia _spectabilis_. The first set of experiments
suggested a trend of differences in preference but these
differences were not significant. This suggested that the
sample size of replicates may have been insufficient to
detect real differences that were being obscured by natural
variation. All of the other comparisons had been quite
distinctly different so this comparison was run again with
eight more replicates, thus doubling the number of

replicates for this comparison. When the data from all replicates are pooled, the analysis indicates significant differences in preference, so the hierarchy was constructed based on the pooled data.

Transitive preferences, i.e. sp. A > sp. B > sp. C but sp. C > sp. A, did not occur. However, only 23 of the 105 possible permutations of pair-wise comparisons of preference were run due to time limitations. Figure 4.8 shows the species that were compared and the results of those comparisons.

If feeding preferences are expressed in the field, the preference rank of an alga should correlate positively with the mean values of the selectivity indices for that alga. When the preference ranks of all algal groups used in preference experiments are plotted against their electivities, the correlation is not significant (Spearman correlation coefficient = - .552, Figure 4.9). However, when the Ulvales are removed from the analysis the Spearman correlation coefficient is -.833, which is significant at p < .01 (Figure 9). The D index of the Ulvales is unexpectedly low (-.4146), given their high preference rank (1). Thus, excepting the Ulvales, highly preferred species are selectively taken in the field over species of low preference. Possible explanations for the Ulvales outlier will be discussed later.

Figure 4.9. Scatterplots of the preference rank of all the algae used in laboratory feeding preference experiments and their corresponding mean electivity (Table 4.1). The upper graph, a., shows the plot when the ulvoids are removed from the analysis. The lower graph, b. shows all points.

FIGURE 4.9

A. Ulvales excluded

B. Ulvales included
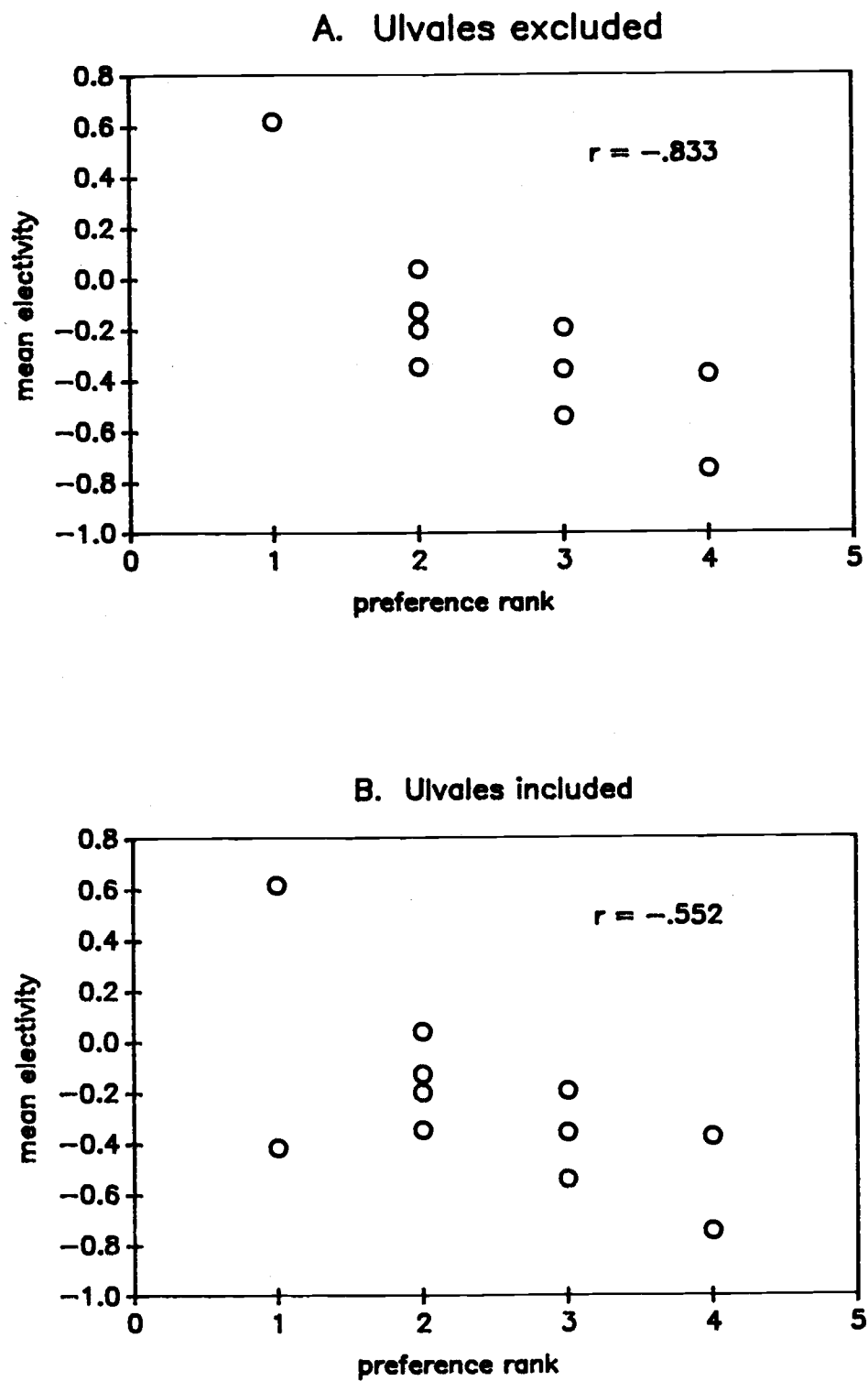
DISCUSSION

The results of this study indicate that although
Cryptochiton stelleri eats at least 18 types of algae, there
are clear preferences. Furthermore, these preferences
interact with the relative availability of potential prey
algae under field conditions to produce a diet that is
different from that expected due to either factor alone.
For example, if preference alone determined the diet of
Cryptochiton, its diet would consist primarily of Iridaea,
Cryptopleura spp. and ulvoids. In contrast, if the
availability of algae was the sole factor determining diet,
these chitons would eat primarily Hedophyllum sessile,
Odonthalia floccossa and ulvoids because these species are,
on the average, the most predictably abundant (Table 4.1).
The actual field diet is a mixture of all of these species,
which suggests that both factors are important (Table 4.1).
In general, the selectivity of Cryptochiton in the field
reflects the preferences determined by laboratory
experiments but, when high preference foods are rare or
unavailable, low preference foods are eaten.

Few studies have attempted to examine whether an
actively foraging herbivore can actually express
laboratory-determined preference behavior under field
conditions. Most existing studies have determined the
preference of an herbivore through laboratory experiments
(Nicotri 1980, Lubchenco 1978, Watanabe 1984, Anderson and
Velimirov 1982, Steinberg 1985) or by experiments conducted

in the field under conditions of controlled availability (Himmelman and Carefoot 1975, Steinberg 1985). Notable exceptions are the research of Vadas (1977) and Horn et al. (1982), which combined laboratory preference experiments with estimates of selectivity from field sites. Results from both studies suggest that food preferences interact with the availability of potential prey items to determine the observed diet of the herbivore under field conditions. Under conditions of low availability of preferred food items, preferences are less important, but are still expressed. These results are in general agreement with optimal foraging theory, which predicts that the abundance of potential prey will affect the range of prey items in the diet (Schoener 1971). Cryptochiton exhibits similar behavior: although the abundance of the highly preferred Iridaea cordata fluctuates seasonally and is always low relative to other algae, chitons consistently eat this species much more than would be predicted by simple probability of encounter. In fact, the lack of correlation between the proportion of Iridaea in the diet and the proportion available in the environment suggests that Cryptochiton actively searches for this alga (Table 4.3). Conversely, Hedophyllum sessile, a low preference but abundant alga, is always eaten less than it is encountered. The data for Odonthalia floccosa, which is on the second level of the

Table 4.3. Spearmans rank correlation coefficients and
significance level for correlations between r and p for the
six algal types that are most important in the diet of
Cryptochiton stelleri. r is the proportion of a prey species
in the diet of a consumer and p is the proportion of that
food that is available in the environment.

Algal Type	correlation coefficient	significance level
Iridaea cordata	.695	P>.05
Fleshy red blades	.719	P<.05
Odonthalia floccosa	.778	P<.05
Laurencia spectabilis	.822	P<.05
Hedophyllum sessile	.885	P<.01
Ulvales	.916	P<.01

preference hierarchy, is consistent with these patterns.
Selectivity values for this species are intermediate, and
fluctuate around zero over time.

An interesting exception to the correspondence of
selectivity and preference data is for the ulvoids.
Preference experiments indicate that these algae are highly
preferred, but field feeding observations suggest that
chitons eat this type much less often that it is
encountered. The correlation between preference rank and
mean field selectivity values is high and significant when
the ulvoids are removed from the analysis but when included,
the correlation is nonsignificant (Figure 4.9). This
discrepancy is most likely an artifact of lumping ulvoids
into a single category. The ulvoids were lumped instead of
identified to species because of both the difficulty of
determining species in the field and the general taxonomic
confusion of the group. Thus, comparison of field and
laboratory data is in this case difficult and possibly
inappropriate. The ulvoids used in the laboratory
experiments were collected in Yaquina Bay and were chosen
for their large, intact thalli. The thalli that were
grouped as ulvoids in estimates of availability from field
feeding observations were usually small and short. Hence,
ulvoids encountered by chitons in the field may have been a
different species with different chemical or nutritional
characteristics than those used in laboratory experiments.
In addition, the smaller thalli found in the field may have

been more difficult to consume or detect than the larger thalli used in the preference experiments.

One of the problems involved with any field study of food selectivity is the determination of the actual availability of potential prey items (Strauss 1979, Menge 1972). Relative abundance may not accurately reflect the availability to a predator due to prey characteristics such as structural or chemical defenses, behavioral avoidance, and escapes in size, time or space (Menge 1972). Although some prey characteristics are not normally possible in plant-herbivore systems, such as active avoidance or escape behavior, other characteristics may limit the potential prey items to a subset of all the algae that occur at a site. Algae can be considered be available if they are eaten by the herbivore, and if they occur when and where an herbivore is known to be foraging and/or eating. This was the approach used in my study to determine the actual availability of potential prey algae. Algal abundance was estimated in the microhabitat and at the time that a Cryptochiton was observed to be feeding. The subset of algae that was considered to be potential prey to chitons was limited to those that had been observed to be fed upon by Cryptochiton. The previous studies by Vadas (1977) and Horn et al. (1982) did not address the problems of determining actual availability as estimated abundance was equated with availability in both of these studies. Specifically, the transect method used by Horn et al. may

have included many microhabitats in which fish, which were the herbivores in their study, would not feed or forage.

Several models of optimal foraging behavior predict that the range of prey items consumed by the optimal predator will increase as the absolute and relative abundance of potential prey decreases (Schoener 1971). The feeding observation data do not show any patterns of increasing range of algae eaten as the average percent cover of edible algae decreases (Figure 4.10). In addition, a food-item diversity index (Simpson's Index) shows little fluctuation over time (Figure 4.10). Both the range of food items and the diversity index remain remarkably constant relative to the total availability of edible algae. This constancy may be due to a need of Cryptochiton to maintain a mixed diet, as has been suggested by Kitting (1980) for a limpet species. Theoretically, herbivores may maintain mixed diets due to a need to balance nutrients or minimize toxin intake (Kitting 1980).

Alternatively, the differences between the biology of herbivores and the assumptions of some models of optimal foraging behavior may make these predictions inappropriate for Cryptochiton. For example, many models assume that energy (calories) is the currency that should be maximized, but herbivores may be more limited by nutrients or by the need to avoid excessive toxins. The prey of carnivores are relatively

Figure 4.10. Seasonal fluctuations in the Simpson's species diversity index (a) and species richness (b) of the diet of Cryptochiton as determined by feeding observations at Boiler Bay, Oregon. Lines with open circles correspond to the y-axis on the left. Lines with solid squares correspond the y-axis on the right and plot the seasonal fluctuations of the total percent cover of the diet of Cryptochiton determined from feeding observations.

FIGURE 4.10

A.

B.
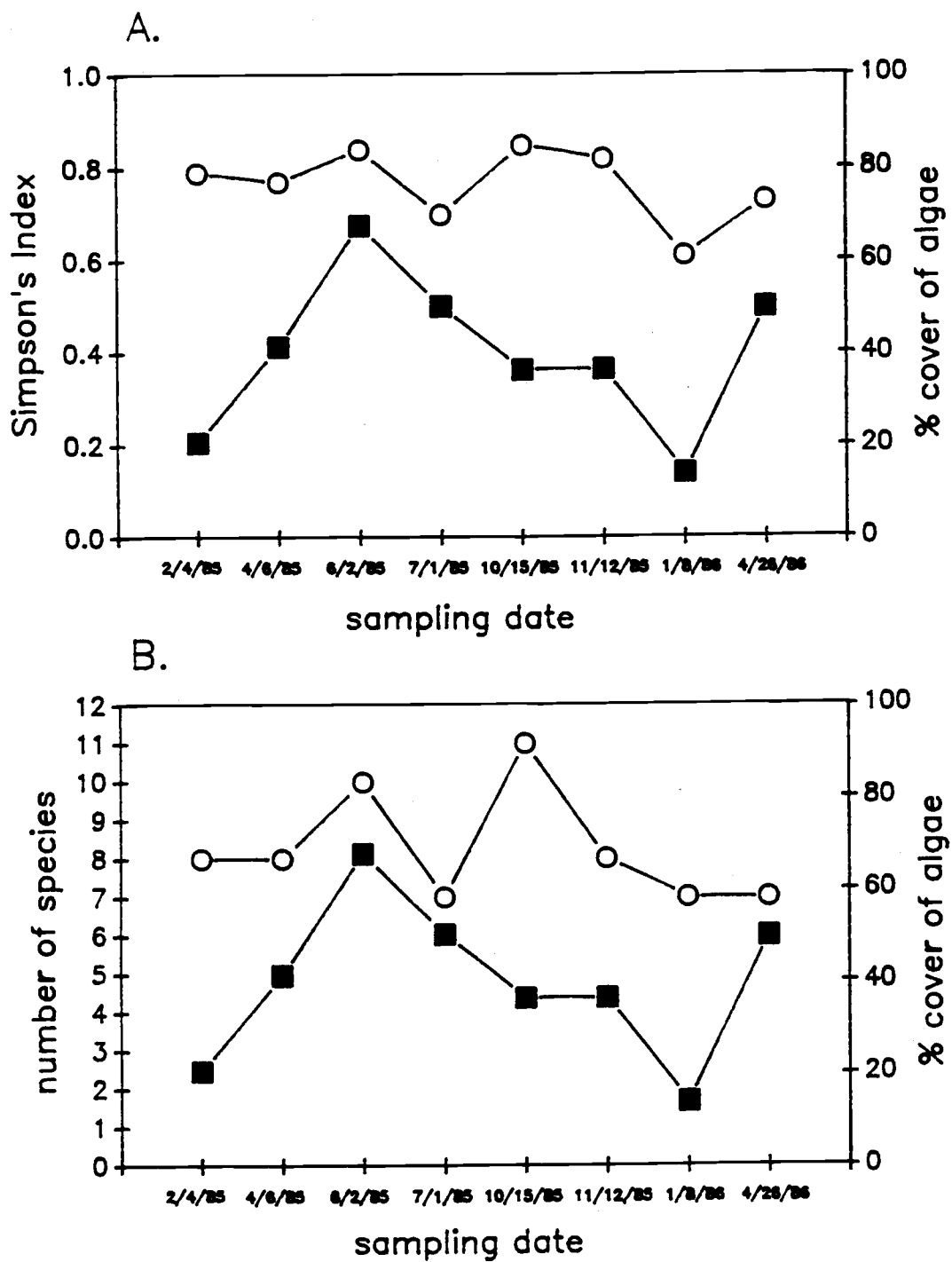
balanced food packets, but plants are usually rich in
energy,
poor in nutrients and sometimes high in toxins (Stephens and
Krebs 1986). Attempts to relax these assumptions result in
qualitatively different predictions, such as the expectation
of partial preferences for nutrient or toxin-constrained
herbivores versus the "all or none" rule for food choice in
the diet of carnivores (Stephens and Krebs 1986). Another
constraint of optimal foraging models is the assumption of
sequential encounter of prey items. Different species of
algae often grow so close together that chitons may
effectively encounter both species simultaneously (personal
observations). When assumptions have not been explicitly
verified, tests of the predictions of a model should be
viewed cautiously.

The actual preference hierarchy of Cryptochiton is much
different than what has been reported for any chiton and
most other marine herbivores (Anderson and Velimirov 1982,
Gaines 1985, Himmelman and Carefoot 1975, Steinberg 1985,
Vadas 1977, Nicotri 1980, Watanabe 1984, Lubchenco 1978,
Leighton 1966, Leighton and Boolootian 1963, but see Horn et
al. 1982). In general, molluscan herbivores which feed on
macroalgae tend to prefer brown algae (kelps) or ephemeral
green algae (Gaines 1985, Himmelman and Carefoot 1975,
Steinberg 1985, Nicotri 1980, Watanabe 1984, Lubchenco 1978,
Leighton 1966, Leighton and Boolootian 1963, but see Shepard
1973). As a group, sea urchins have preferences similar to

molluscs (Anderson and Velimirov 1982, Lawrence 1975, Vadas 1977). The herbivorous fishes studied by Horn and his co-workers (1982) preferred annual red and green algae most highly. Perennial rhodophytes, such as _Iridaea cordata_ var _splendens_, _I. flaccida_, _Gelidium coulteri_, and _Gigartina canaliculata_ were important in the diets of the fish but selectivity was always relatively low for these species (Horn et al. 1982). Therefore, the preference of _Cryptochiton_ for perennial rhodophytes is unusual and suggests that the feeding biology of this chiton is somehow different than that of most of the other marine herbivores for which preferences have been determined.

What is the basis for this difference? The research in the present study was focused on chitons found in the intertidal zone, but a larger proportion of the population in Oregon, Washington and California occurs in subtidal habitats (Chapter 2). At Whale Cove on the central Oregon coast, perennial red algae such as _Botryoglossum farlowianum_, _Ptilota filicina_, _Cryptopleura_ spp. and _Plocamium cartilagineum_, are the most abundant fleshy algae in the shallow subtidal habitats that have the highest densities of _Cryptochiton_. Perennial red algae also appear to be the most abundant algal type at other subtidal Oregon sites with high densities of _Cryptochiton_ (personal observations). The feeding model of Emlen (1966) predicts that food availability should be more important than food quality in the evolution of food preference. Paine and

Vadas (1969) make the same prediction based on data that compare food value and preference by several marine herbivores. Perhaps Cryptochiton has evolved a general preference for perennial rhodophytes because those types are the most abundant edible algae in the habitat where this chiton is most abundant.

Cryptochiton's preferences are much different than what is known for other species of chitons (Steneck and Watling 1982). Katharina tunicata, the black leather chiton, is found at the same sites as Cryptochiton but at a higher tide level. Some species of algae, specifically Iridaea cordata and Hedophyllum sessile, co-occur with both chiton species. However, Hedophyllum, which is low on the preference hierarchy of Cryptochiton, is preferred by Katharina over Iridaea, which is the most preferred species of Cryptochiton (Himmelman and Carefoot 1975, present study). These two chiton species have radulae which are very similar in form but differ greatly in size. Hedophyllum is much more difficult to tear than Iridaea (personal observations). From this observation one would expect that Katharina, with the smaller radula, would be able to eat Iridaea much more easily than Hedophyllum. This suggests that factors other than toughness must be affecting the preferences of these two chiton species.

Data compiled by Steneck and Watling (1982) indicate that chitons with known diets consume four different functional groups of algae: 1.) microscopic diatoms and blue

green algae; 2.) filamentous red and green algae; 3.) leathery phaeophytes such as Hedophyllum; and 4.) crustose coralline algae. They attribute this pattern to the multi-purpose radula of chitons which can either 'sweep' microscopic and filamentous algae with the marginal teeth or excavate deeply into leathery macrophytes or crustose corallines. Steneck and Watling (1982) suggest that intermediate sized corticated macrophytes may have a coexistence escape (sensu Menge 1982) because few molluscs are known to feed on this functional group. Intermediate sized macrophytes, such as the perennial rhodophytes, appear to be too small to provide suitable habitat for small herbivores and are too large to be trampled down and grazed by larger molluscs without risk of dislodgment by waves or predators.

This explanation appears to be dependent on the size of the herbivore relative to the alga and thus might explain the preference of Cryptochiton for intermediate-sized perennial rhodophytes. Cryptochiton, with a maximum size of 33 cm, is larger than any other chiton and most molluscan herbivores. Intermediate-sized rhodophytes are small relative to Cryptochiton and can be held down and eaten more easily than for other molluscan herbivores (K. Yates, personal observations). However, eating these types of algae still involves some risk of dislodgment by wave action. When feeding, a portion of the anterior section of the foot is usually detached from the substratum.

Cryptochiton appears to be more prone to dislodgment in this condition than when clamped fully to the substratum (K. Yates, personal observations). Although most generalizations have exceptions, it appears that intermediate sized corticated macrophytes do not have an escape from at least one large marine herbivore. Preferences are well known for only a small proportion of all marine herbivores, so generalizations about coexistence escapes of marine algae are premature. The apparent escape of intermediate sized algae may be an artifact of the pragmatic focus of most marine ecologists on the intertidal zone. Much less is known about subtidal herbivores, which is where the majority of the intermediate sized perennial rhodophytes occur.

The functional groups of molluscs and methods of eating assigned to radular types described by Steneck and Watling (1982) may have been overly simplified. Numerous observations of the feeding behavior of Cryptochiton indicate that the primary method used by this chiton is to grip the algal thallus with the mouth and tear off a piece by using the radula (K. Yates, personal observations). The thallus that was being eaten was often observed to be brought under tension and then jerk as a piece was torn off. Many of the perennial rhodophytes, such as Iridaea have the property of stretching up to a point and then suddenly tearing. Iridaea is apparently resistant to tearing until a small nick is made in the epicuticle (A. Miller, personal

communication). These insights, combined with the observed feeding behavior of <u>Cryptochiton</u>, suggest the following mechanism of feeding. The chiton grips the alga with its mouth, pulls on the thallus by contracting its body musculature, and then cuts the surface of the thallus with its sharply cusped median radular teeth, thus causing a piece to be torn off. This scenario involves a much different use of the radula than the sweeping or excavating motions suggested by Steneck and Watling (1982). The radulae of molluscs may be used in many different ways, and that of a single species may function differently depending on the type of feeding behavior is exhibited in a particular instance.

Information on food preferences and how they are expressed under field conditions can help predict the potential community effects of <u>Cryptochiton</u>. Other considerations include the ability of prey algae to recover from damage, consumer density and the effects of physical and biological forces on the grazing rate of these chitons. Where and when these factors are equal, this study suggests that <u>Cryptochiton</u> <u>stelleri</u> will have the greatest effects on algae in the division Rhodophyta and especially on the species <u>Iridaea</u> <u>cordata</u>.

Literature Cited

Anderson, R. J., and B. Velimirov. 1982. An experimental investigation of the palatability of kelp bed algae to the sea urchin Parechinus angulosus Leske. Mar. Ecol. 3:357-73.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-15.

Connell, J. H. 1961. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Monogr. 31:61-104.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137-159.

Ebert, T. A. 1968. Growth rates of the sea urchin Strongylocentrotus purpuratus related to food availability and spine abrasion. Ecology 49:1075-1091.

Emlen, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611-17.

Fairweather, P.G., and A.J. Underwood. 1983. The apparent diet of predators and biases due to different handling times of their prey. Oecologia 56:169-79.

Gaines, S. D. 1985. Herbivory and between-habitat diversity: The differential effectiveness of defenses in a marine plant. Ecology 66:473-85.

Greer, M. L., and A. L. Lawrence. 1967. The active transport of selected amino acids across the gut of the gumboot chiton (Cryptochiton stelleri). 1. Mapping determinations and effects of anaerobic conditions. Comp. Biochem. Physiol. 22:665-74.

Harrison, J. T. 1975. Isometric responses of somatic musculature of Cryptochiton stelleri(Mollusca: Polyplacophora). Veliger 18(Suppl.):79-82.

Himmelman, J. H., and T. H. Carefoot. 1975. Seasonal changes in calorific value of three Pacific coast seaweeds and their significance to some marine invertebrate herbivores. J. Exp. Mar. Biol. Ecol. 9:315-22.

Horn, M. H., S. N. Murray, and T. W. Edwards. 1982. Dietary selectivity in the field and food preferences in the laboratory for two herbivorous fishes (Cebidichthys violaceus and Xiphister mucosus) from a temperate intertidal zone. Mar. Biol. 67:237-46.

Ivlev, V. S. 1961. Experimental ecology of the feeding of
     fishes. Yale University Press, Newhaven, Connecticut,
     USA 302pp.

Jacobs, J. 1974. Quantitative measurement of food
     selection: a modification of the forage ratio and
     Ivlev's electivity index. Oecologia 14:413-17.

Kitting, C. L. 1980. Herbivore-plant interactions of
     individual limpets maintaining a mixed diet of
     intertidal marine algae. Ecol. Monogr. 50:527-50.

Lawrence, J. M. 1975. On the relationship between marine
     plants and sea urchins. Oceanogr. Mar. biol. Annu.
     Rev. 13:213-86.

Lawrence, A. L., and D. C. Lawrence. 1967. Sugar
     absorption in the intestine of the chiton,
     Cryptochiton stelleri. Comp. Biochem. Physiol.
     22:341-57.

Lawrence, A. L., J. M. Lawrence, and A. C. Giese. 1965.
     Cyclic variations in the digestive gland and glandular
     oviduct of chitons (Mollusca). Science 147:508-10.

Lawrence, A. L., and D. S. Mailman. 1967. Electrical
     potentials and ion concentrations across the gut of
     Cryptochiton stelleri. J. Physiol. 193:535-45.

Lawrence, A. L., D. S. Mailman, and R. E. Puddy. 1972. The
     effect of carbohydrates on the intestinal potentials of

Cryptochiton *stelleri*. J. Physiol. 225:515-27.

Leighton, D. L. 1966. Studies of food preference in algivorous invertebrates of Southern California kelp beds. Pac. Sci. 20:104-13.

Leighton, D. L., and R. A. Boolootian. 1963. Diet and growth in the black abalone, *Haliotis* *cracherodii*. Ecology 44:227-38.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116-1123.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. 12:405-37.

MacGinitie, G. E., and N. MacGinitie. 1968. Note on *Cryptochiton* *stelleri* (Middendorff, 1846). Veliger 11:59-61.

Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual food availability and environmental predictability. Ecol. Monogr. 42:25-50.

Menge, B. A. 1982. The effects of feeding on the environment: Asteroidea. Pages 521-551 in M. Jangoux and J. M. Lawrence, eds. Echinoderm nutrition. Balkema Rotterdam, The Netherlands.

Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, Acanthina punctulata. Oecologia 17:293-316.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130:730-757.

Michael, P. F. 1975. Blood glucose concentration and regulation in Cryptochiton stelleri (Mollusca: Polyplacophora). Veliger 18 (Suppl.):117-21.

Nicotri, M. E. 1980. Factors involved in herbivore food preference. J. Exp. Mar. Biol. Ecol. 42:13-26.

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

Paine, R. T. 1969. The Pisaster-Tegula interaction: prey patches, predator food preference and intertidal community structure. Ecology 50:950-961.

Paine, R. T., and R. L. Vadas. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Mar. Biol. 4:79-86.

Palmer, R. A. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia 62:162-172.

Palmer, J. B., and P. W. Frank. 1974. Estimates of growth of Cryptochiton stelleri (Middendorff, 1846). Veliger 16:301-4.

Peterson, C.H., and B.P. Bradley. 1978. Estimating the diet of sluggish predator from field observations. J. Fish. Res. Bd. Can. 35:136-40.

Peterson, J. A., and K. Johansen. 1973. Gas exchange in the giant sea cradle Cryptochiton stelleri (Middendorff). J. Exper. Mar. Biol. Ecol. 12:27-43.

Robbins, K. B. 1975. Active absorption of D-glucose and D-galactose by intestinal tissue of the chiton Cryptochiton stelleri (Middendorff, 1846). Veliger 18 (Suppl.):122-27.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-403.

Shepherd, S. A. 1973. Studies on southern Australian abalone (genus Haliotis) I. Ecology of five sympatric species. Aust. J. mar. Freshwat. Res. 24:217-57.

Steinberg, P. D. 1985. Feeding preferences of Tegula funebralis and chemical defenses of marine brown algae. Ecol. Monogr. 55:333-49.

Stenek, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Mar. Biol. 68:299-318.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index the forage ratio and a proposed linear index of food selection. Tran. Am. Fish. Soc. 108:344-52.

Vadas, R. L. 1977. Preferential feeding: An optimization strategy in sea urchins. Ecol. Monogr. 46:337-71.

Watanabe, J. M. 1984. Food preference, food quality and diets of three herbivorous gastropods (Trochidae: Tegula) in a temperate kelp forest habitat. Oecologia 62:47-52.

Webster, S. K. 1968. An investigation of the commensals of Cryptochiton stelleri (Middendorff, 1846) in the Monterey Peninsula area, California. Veliger 11:121-25.

CHAPTER 5: The Effects of Environmental Harshness on the Foraging Ecology of the Gumboot Chiton, _Cryptochiton Stelleri_.

ABSTRACT

The effects of periodic exposure to air during low tides and water turbulence on the feeding behavior and consumption rates of the gumboot chiton, Cryptochiton stelleri, were studied on the central coast of Oregon. This chiton eats fleshy macroalgae in the low intertidal and shallow subtidal zones of the Pacific Coast of North America north of San Nicholas Island. Cryptochiton is less active on substrata that are exposed to air at low tide than they are on adjacent tidepool substrata, indicating that exposure to air inhibits foraging activity. Intertidal chitons were much more active on low tides following heavy and medium wave action than following calm waves. These observations and experiments suggest that their activities were restricted to low tide periods when waves were large and distributed over the whole tide cycle when waves were small. Chitons are also significantly less active in subtidal regions when wave action increases. Grazing rates of chitons in enclosures were lower at a wave-exposed than at an adjacent wave-protected site, indicating that the actual grazing rate of these chitons on a preferred alga was inhibited by high wave action.

I conclude that the feeding rates and foraging activity of Cryptochiton are decreased by increased harshness, specifically, wave action and exposure to air. Other intertidal invertebrate consumers may be affected in a similar manner but further study is needed to generalize.

INTRODUCTION

Predation is considered to be one of the primary factors regulating patterns of community structure (Paine 1966, 1971, 1974, 1976; Dayton 1971; Connell, 1975; MacArthur 1972; Harper 1969; Sprules 1972; Dodson 1970, 1974a,b; Janzen 1970; Menge 1976a,b, 1978a,b, 1983; Menge and Sutherland 1976, 1987; Lubchenco 1978). Recent theory suggests that the species diversity observed in a community may be a result of the interactions between consumer pressure, environmental harshness and competition (Connell 1975, Huston 1979, Lubchenco 1978, Menge and Sutherland 1976, 1987). In benign environments consumers may control prey populations at levels where competitive exclusion is prevented, thus producing high diversity. Intermediate levels of environmental harshness may reduce consumer effectiveness and allow few prey species to dominate the community, resulting in decreased diversity. In severe environments consumers are either absent or ineffective and competition among prey is prevented by the direct effects of environmental stress.

Although one of the central assumptions of this theory is that consumer pressure is affected by the physical environment, little empirical work has specifically addressed this problem (but see Menge 1978a,b, 1983). In addition, little attention has been directed to sublethal effects of physical and physiological stresses (sensu Menge and Sutherland 1987) such as those on consumer foraging

behavior or feeding rates. Most research on ecological

disturbance has focused on lethal effects such as

dislodgment by waves, bashing by logs, freezing

and lethal desiccation. Many ecologists assume that

sublethal effects occur, and are important, but rarely has

this assumption been tested. A better understanding of the

role of environmental stress in community dynamics is

dependent on the empirical quantification of these effects.

The size and mobility of organisms appear to be

important factors affecting their response to environmental

stress (Denny et al. 1985, Menge and Sutherland 1987).

Large organisms may have more difficulty finding

appropriately sized refuge microhabitats and are more likely

to be dislodged by wave shock (Denny et al. 1985). If this

larger size is not offset by a correspondingly higher

mobility, escape from the stressful habitat is less

possible, and the survivorship or behavior of the organism

will be more likely to be affected by the stress. Many of

the major invertebrate consumers in marine rocky intertidal

communities are large but relatively immobile. Examples of

these types of consumers are seastars, urchins, abalone and

chitons. From the above argument, these animals are most

likely to be affected by environmental stress such as wave

action or desiccation.

Theoretical considerations and preliminary observations

suggested that the gumboot chiton, Cryptochiton stelleri,

would be adversely affected by wave action and desiccation.

This is the largest chiton in the world, reaching lengths of 33cm. It is found on rocky shores in the low intertidal and shallow subtidal zones from the Aleutian Islands (Alaska) to the Channel Islands (California) (Morris et al. 1980). During foraging and feeding behavior it is very loosely attached to the substratum and can be easily dislodged by wave action or a human observer (K. Yates, personal observations). Dislodgment is definitely a source of mortality; battered and dead chitons can be found in the high intertidal zone following heavy wave action. Contrary to the information in Morris et al. (1980), this chiton can clamp down and attach very firmly to rocks when disturbed, but this behavior precludes foraging and feeding (K. Yates, personal observations). Preliminary observations suggested that subtidal chitons were less active when wave action increased and that intertidal chitons were more active at low tide on submergent than emergent substratum. These animals are ideal subjects for behavior observations in the field. Their limited perceptive abilities allow the observer to approach a chiton quite closely without affecting its behavior (K. Yates, personal observations).

The goal of this paper is to determine the effects of environmental stress on the foraging of Cryptochiton stelleri. Specifically, I examine (1) the effect of wave shock on the activity of subtidal chitons, (2) the influence of emergence and previous wave shock on the behavior of

intertidal chitons, and (3) the effect of wave exposure on the feeding rates of intertidal chitons.

MATERIALS AND METHODS

Study Site Description

Experiments and observations were made in the low intertidal zones of four sites and the subtidal zones of two sites on the central Oregon coast from 1982 - 1986. Behavioral observations were made at three intertidal sites in the complex of coves that comprises Boiler Bay and at one subtidal site at Whale Cove (see Figure 4.1, Chapter 4). Grazing rate experiments were conducted at an exposed and a protected site along a pair of relatively flat, sloping benches close to the boiler at Boiler Bay. The substrata at these sites is a mixture of mudstone, sandstone, volcanic conglomerate and basalt. This combination of substrata produces a very heterogeneous habitat at Boiler Bay. The sites at which behavioral observations were made have many tidepools, surge channels and benches that result in a variety of microhabitats.

Behavioral Observations

The behavior of Cryptochiton was observed by locating a chiton, observing it for 2 minutes, and scoring that individual as exhibiting one of five different behaviors.

Only chitons that were clearly in view were observed, as removing obstructing algae or other material would alter their behavior. Intertidal sites were searched at low tide for chitons by starting at the highest level of the site and working down toward the waterline. This search pattern was used to minimize differences in emersion time between chiton individuals during one observation period. Subtidal observations at Whale Cove were conducted by attaching a yellow polypropylene line to anchor bolts that had been secured previously in the rock and swimming a circle to locate chitons. The radius of this circle was expanded by one or two meters (depending on visibility) after each full revolution until a radius of 20 meters was reached.

The behavioral repertoire of <u>Cryptochiton</u> is relatively limited so each individual could easily be scored as exhibiting one of five behaviors. These are (1) clamped, (2) exposed gills, (3) moving, (4) foraging, and (5) feeding. Clamped chitons were inactive and firmly attached. "Exposed gill" chitons observed had their girdle edge curled back to expose the gills in the groove between their foot and girdle. "Moving" chitons were actively moving ahead without swinging their anterior end from side to side. Moving chitons were very loosely attached to the substratum and often had an elongated body shape. Foraging chitons were swinging the anterior end from side to side or were applying their mouth to the substratum but were not eating. Such animals were also loosely attached, usually

with at least the anterior fourth of their feet detached from the substratum. Feeding chitons were either directly observed tearing pieces of algae from attached thalli, or they were foraging individuals found with algae in their mouths when turned over. Feeding chitons were also loosely attached.

At intertidal sites the microhabitat occupied by the chiton was recorded at the same time as its behavior. The complex mixture of tidepools, surge channels, benches, cobbles and boulders provided three basic types of microhabitat for chitons at low tide. "Partial" chitons had up to 75% of their body covered by water. "Submergent" chitons were > 75% underwater. Together, submergent and partial chitons are termed "wet". Animals that were totally out of water were termed "emergent".

Climatic conditions were recorded for most observation periods. These included estimates of wave height, wind velocity and direction, precipitation, the temperature of the ocean, substratum and air, and whether it was sunny, cloudy or foggy.

Behavioral data were analyzed by calculating proportions of chitons exhibiting specific behaviors within each microhabitat for each observation period and using each period as a replicate. Mean proportions of behaviors in a microhabitat and/or under specific climatic conditions were compared using a Mann-Whitney test with a critical value of .05. A nonparametric procedure was chosen because the data

were in the form of proportions and multiple comparisons
were being made.

Grazing Rate Experiments

Grazing rates of individual Cryptochiton were
determined in field experiments conducted at two sites on
neighboring benches at Boiler Bay (Figure 4.1, Chapter 4).
These two benches ran roughly parallel to each other and
were sloped toward the south at similar angle. The main
difference between these two benches was in wave exposure.
The eastern bench was partially protected from the full
force of incoming waves by the western bench, which was
relatively exposed to wave shock. This subjectively
determined difference was subsequently quantified with
wave-force dynamometers (see below).

The experiments were designed to compare the grazing
rates of Cryptochiton at a wave-exposed site to those at a
wave-protected site. Iridaea cordata was chosen as the alga
to be grazed because it is highly preferred by these chitons
(Yates, Chapter 4). Chitons collected from adjacent habitats
were isolated in cages and provided with pre-weighed pieces
of algae placed in clamps. Similar pieces of algae were
clamped nearby in identical cages with no chitons to serve
as controls for growth or deterioration of the algae. All
algae were retrieved on the following lower low tide and
replaced with fresh pre- weighed pieces. Cage attachment
sites were arranged in four pairs on each bench. One of the

cages of each pair was randomly designated as the experimental cage and the other was used as a control.

Cages were bolted to concrete platforms constructed on the substratum of the benches. The cage attachment platforms were prepared by first removing as many organisms as possible from the rock surface with scrapers and wire brushes. Stainless steel bolts were then glued into previously drilled holes with a marine epoxy, Z-Spar splash-zone compound. These bolts served also as anchors for a layer of quick-set concrete which was poured over the attachment areas to smooth out the surface and equalize the substratum texture and heterogeneity between the two benches. Holes were then drilled into the concrete and substratum and stainless steel bolts were glued into the attachment platforms to anchor both the inclusion cages and the algae clamps within the cages. The cages were made by modifying plastic laundry baskets. These baskets were 45.5 x 45.5 x 26.5 cm, had solid bottoms, and were perforated on the sides by holes that were approximately 4 x 2 cm. Part of the bottoms were cut out and replaced by black plastic netting with .25 inch mesh. This was secured with plastic cable ties. Holes were cut into the four thickened handles on the upper lip. The baskets were inverted and anchored to the attachment platform bolts with plastic washers and stainless steel nuts and locknuts.

Thalli of _Iridaea cordata_ were collected from the protected (east) bench on the day before an experiment and

taken back to flowing seawater tanks at the HMSC, where
approximately equal pieces were cut from thalli. These
pieces were then spun in a hand-operated centrifuge and
blotted with paper towels to remove excess water. The algae
were weighed on an electronic balance and placed in a
flowing seawater tank until the following morning, when they
were taken to the experimental sites and clamped in the
cages. Square Plexiglas washers and stainless steel nuts
were used to secure two algal thalli to stainless steel
bolts in opposite corners of each cage. After one tidal
cycle, thalli were removed, taken back to the HMSC and
reweighed.

The data generated by these experiments were converted
from weight lost to a grazing rate and then analyzed
statistically. Since the exposed site was at a slightly
higher tidal height than the protected site the difference
in emergence time for the two sites was approximately 1.5
hours on calm days (estimated wave heights of approximately
1'-3', personal observation). Increased wave action reduced
this difference considerably and when heavy wave action
occurred (up to 8') the emergence time differential was
essentially zero because of the difference in exposure of
the two benches. Estimated wave height, predicted low tide
level and observations of emergence time were used to
estimate total emergence time for each site. This time was
subtracted from 24 hours to arrive at a total submergence
time during which it was assumed that chitons could

potentially feed if not inhibited by wave action. Grazing rates were calculated for each replicate at each site by dividing weight change of the thalli by the total submergence time. The means rate of change of control thalli were compared between the two sites with a paired t-test using a critical value of .05. If controls were not significantly different between sites, the mean grazing rates for experimental plots were compared using the same statistical procedure. Rates from consecutive days during a spring tide series using the same chitons were pooled to facilitate analysis.

A potential problem with these measures of grazing rates is that some of the weight loss of the algae may have been due to the sloppy eating habits of chitons. Pieces of algae may be transported outside of the cages if chitons do not eat every piece that they detach from the main algal thallus. The amount that may have been lost in this manner was estimated in laboratory feeding experiments conducted at the HMSC. Chitons were collected from Boiler Bay and placed in 91.5 X 96 X 15 cm fiberglass water tables supplied with flowing seawater. _Iridaea_ _cordata_ was collected from the protected bench at Boiler Bay, treated and weighed as for field experiments and clamped to the tables with clothespins. After approximately 50% of the algae was consumed, loose pieces and clamped pieces were weighed separately.

Maximum wave force was estimated for the grazing experiment sites by using simple wave-force measuring devices (dynamometers). These dynamometers, which are described by Palumbi (1984), are made of severed cable ties, stainless steel wire, half ping-pong balls and elastic surgical tubing. Wave force acts on the half ball (drogue) which slides the one-way ratcheting end of the cable tie along the strap of the cable tie. This force is opposed by a section of elastic surgical tubing which is attached between the ratcheting end and strap of the cable tie. Basically, this device sets itself at the maximum wave force that the drogue experienced. An investigator can then measure this force at low tide by attaching a Pesola spring-scale to the drogue, pulling on the scale until the dynamometer moves one notch and noting the force on the scale. The device can be reset by detaching the surgical tubing and strap from their mutual clamping mechanism, sliding the ratcheting head all the way off the strap, and sliding it back on the clamping end of the strap.

Dynamometers were secured to one algae clamping bolt of each cage platform at the exposed and the protected site. To investigate possible cage effects on wave force, the cage was left off of one of each pair of the attachment platforms at each site. This arrangement resulted in 2 dynamometers in each of two cages and 2 dynamometers on each of two cage platforms without the cage at each site. During estimation of wave force, neither algae nor chitons were present in the

cages or on the platforms. The dynamometers were measured and reset at low tide for as many tidal cycles as possible within a series.

RESULTS

Intertidal Behavior Observations

In the intertidal zone of Boiler Bay, 65% of Cryptochiton were completely (45%) or partially submerged (20%) at low tide (Figure 5.1a). Combined behavior data from all habitats suggest that chitons spend most of their time either clamped to the substratum or foraging (see Figures 5.1b and 5.2a). Clamped and exposed-gill chitons will be referred to subsequently as "inactive", while moving, foraging and feeding will be defined as "active". Chitons exhibited progressively more active behaviors in more moist habitats (Figure 5.2b). Feeding activity increased in a similar manner (see Figure 5.3).

To determine the relation between chiton activity and water turbulence, observation periods were grouped into 3 wave height classes: calm, with estimated wave height from 0' to 4'(1.22 m); medium, with wave height from 4' to 6' (1.83 m); and heavy, with wave heights from 6' to 10' (3.05 m). Combined data from all habitats suggest that chitons were least active at low tide

Figure 5.1. a) Histogram of average proportions of total chitons observed in emergent, partially submergent and submergent habitat. Error bars in this and all subsequent figures are for the standard error of the mean. b) Histogram of the proportions of all chitons observed in all habitats that were exhibiting a particular behavior. Behaviors are defined in the text. Data are from 31 observation periods and a total of 989 chiton sightings.

FIGURE 5.1

A.

Proportion of chitons found in habitat — Habitats (emergent, partial, submergent)

B.

Proportion of chitons found in habitat — Behavior (clamped, exposed gills, moving, foraging, feeding)
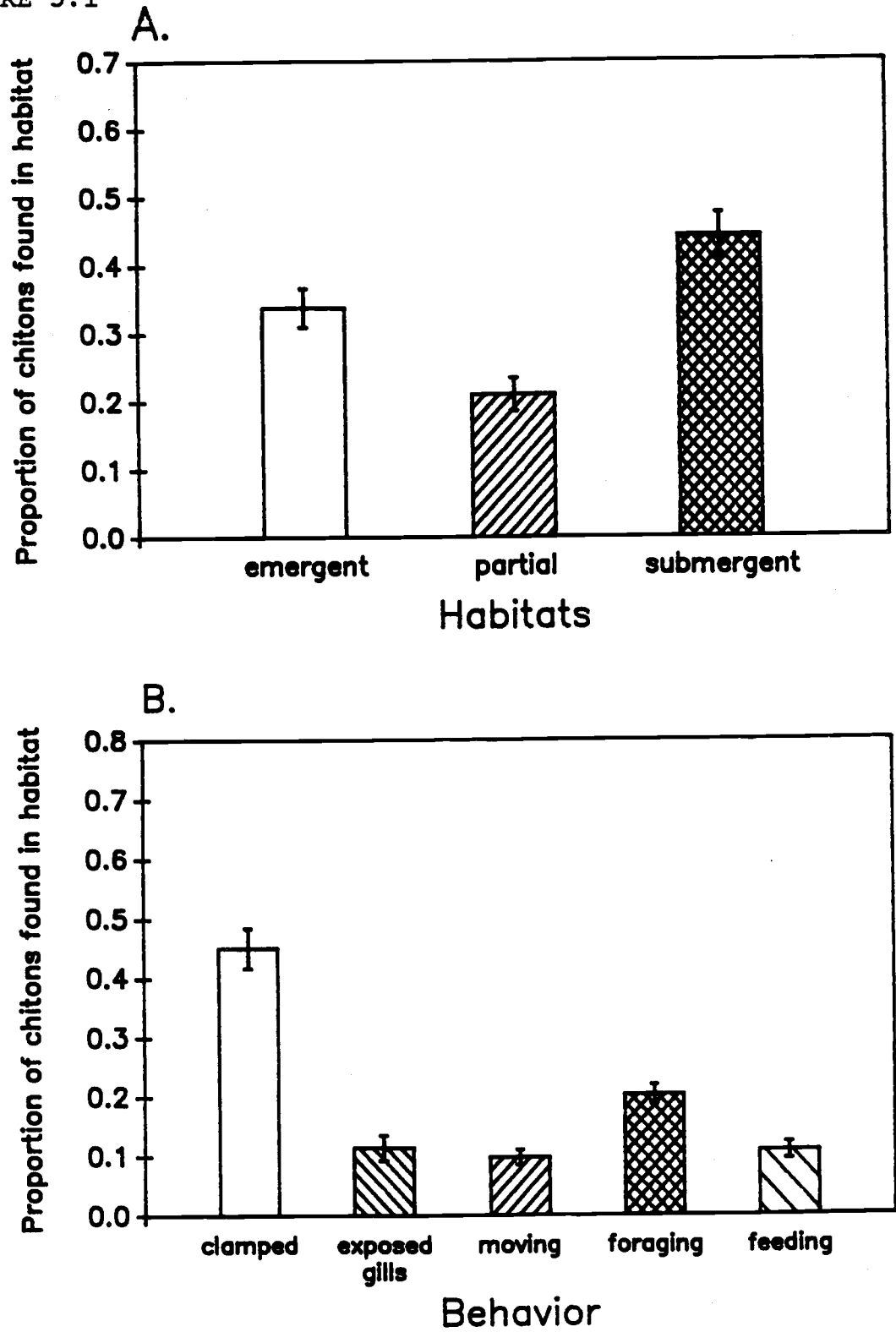
Figure 5.2. a) Histogram of the proportions of active and inactive chitons observed in all habitats. Active behaviors included moving, foraging and feeding. b) Histogram of the proportions of chitons that were observed in all habitats (pooled), and in emergent, partial and submergent habitats. Habitats and behaviors are defined in the text. Data are from 31 observation periods and a total of 989 chiton sightings.

FIGURE 5.2

A.

Proportion of chitons observed (y-axis, 0.0 to 0.8)

Chiton Behavior (x-axis: Inactive, Active)

B.

Proportion of chitons active (y-axis, 0.0 to 1.0)

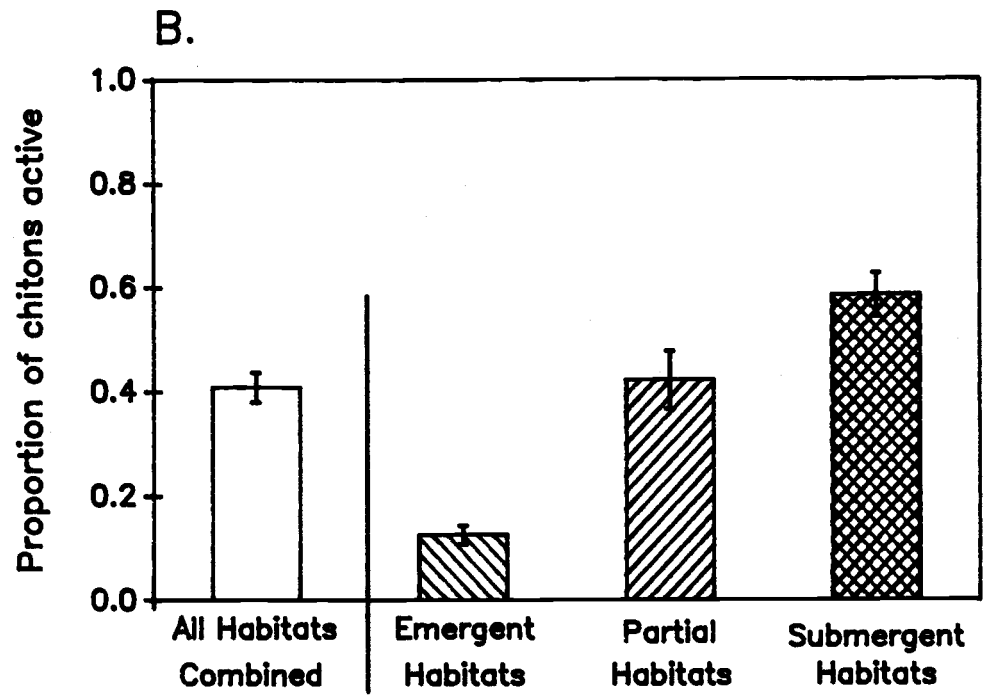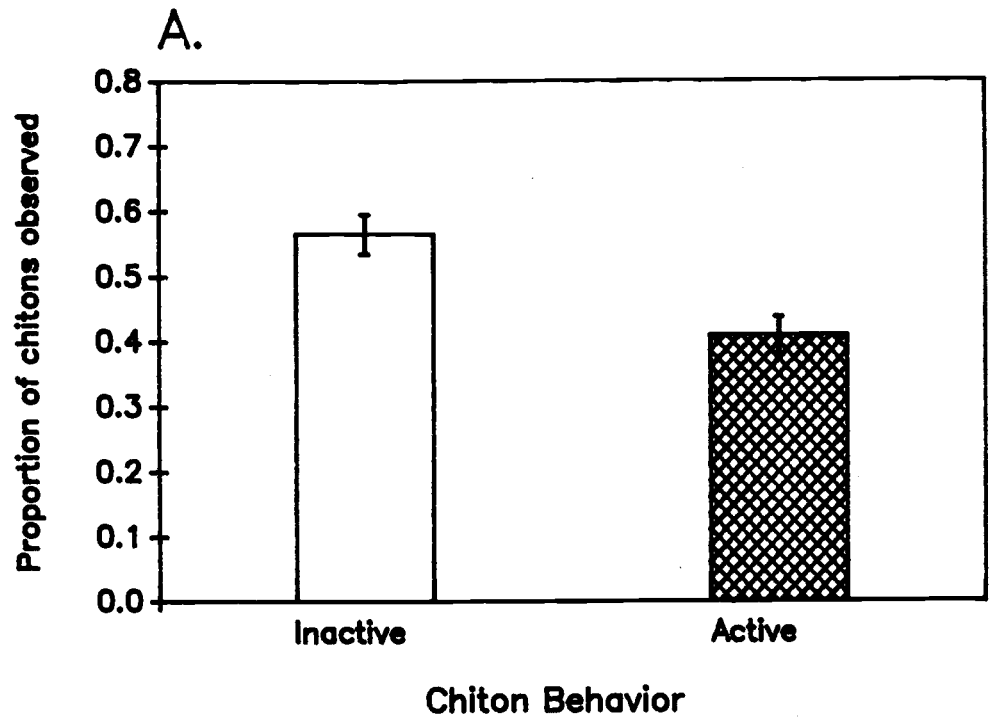x-axis: All Habitats Combined, Emergent Habitats, Partial Habitats, Submergent Habitats

Figure 5.3. Proportions of chitons observed feeding in emergent, partial and submergent habitats pooled over all observation periods.
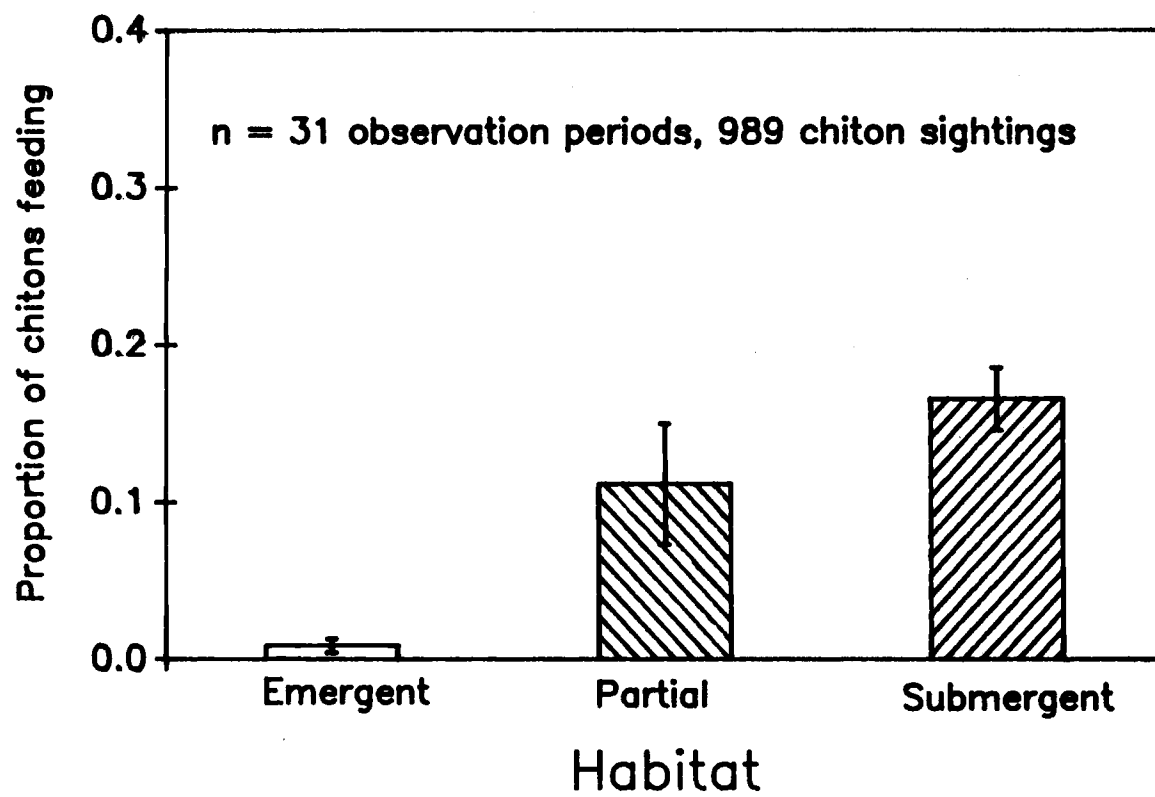
FIGURE 5.3

n = 31 observation periods, 989 chiton sightings

following calm waves and most active following either medium or heavy wave action. The mean proportion of active chitons is higher following medium than heavy wave action, but this trend is not significant (see Figure 5.4a). When the data are analyzed by habitat the differences in the mean proportion of active chitons between calm and higher (medium + high) wave action are significant only for completely submerged habitats. However, the trends in the data remain the same regardless of habitat, i. e. chiton activity decreases from medium to heavy to calm wave action (Figure 5.4b).

Comparison of data from observation periods with high and low desiccation potential suggest that when on emergent substratum, Cryptochiton is less stressed during wet, nighttime lowtides than dry, daytime lowtides. During respiratory distress Cryptochiton curls back its girdle to expose the gills in the groove around its foot (Peterson and Johansen 1973). A significantly lower proportion of emergent chitons expose their gills during foggy or rainy night low tides than during daytime lowtides (Mann-Whitney U test, $p < .05$, see Figure 5.5a). Although it might be expected that emergent chitons would also be more active under these conditions, the slight differences in the mean proportion of active chitons observed on wet nights were not significantly different from those observed on dry days. (see Figure 5.5b).

Figure 5.4. a) Proportions of chitons observed displaying active behaviors during observation periods that followed calm, medium and heavy wave action. These proportions are for pooled data from all habitats. Active behaviors include moving, foraging and feeding. Wave action classification criteria are described in the text. b) Proportion of active chitons observed following calm, medium and heavy wave action broken down by the habitat in which the chitons were found.

FIGURE 5.4

A. Proportion of chitons active vs Wave Action (Calm, Medium, Heavy). n = 10, n = 7, n = 10.

B. Proportion of chitons active vs Wave Action (calm, medium, heavy) for Emergent, Partial, and Submergent conditions.
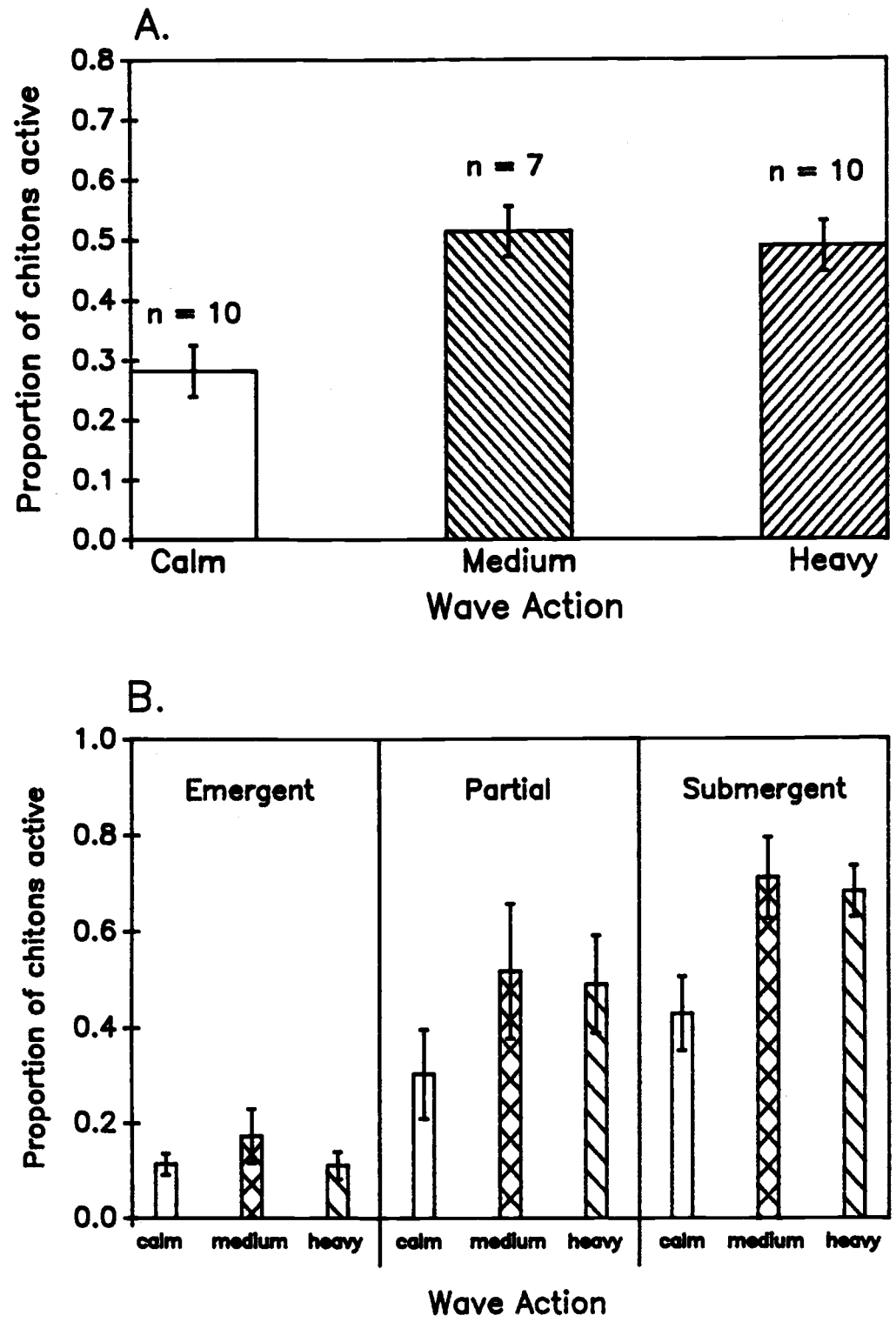
Figure 5.5. a) Mean proportions of chitons displaying exposed gills on emergent substrata under the climatic conditions wet, dry, night, day and at the extremes of combined conditions (i.e. wet, night and dry, day). Climatic conditions are described in the text. b) Mean proportion of chitons found in emergent and "wet" habitats on wet nights, and dry days. "t" represents the total number of chiton sightings contributing to the mean proportion and "n" is the number of observation periods during the specified climatic condition.

FIGURE 5.5
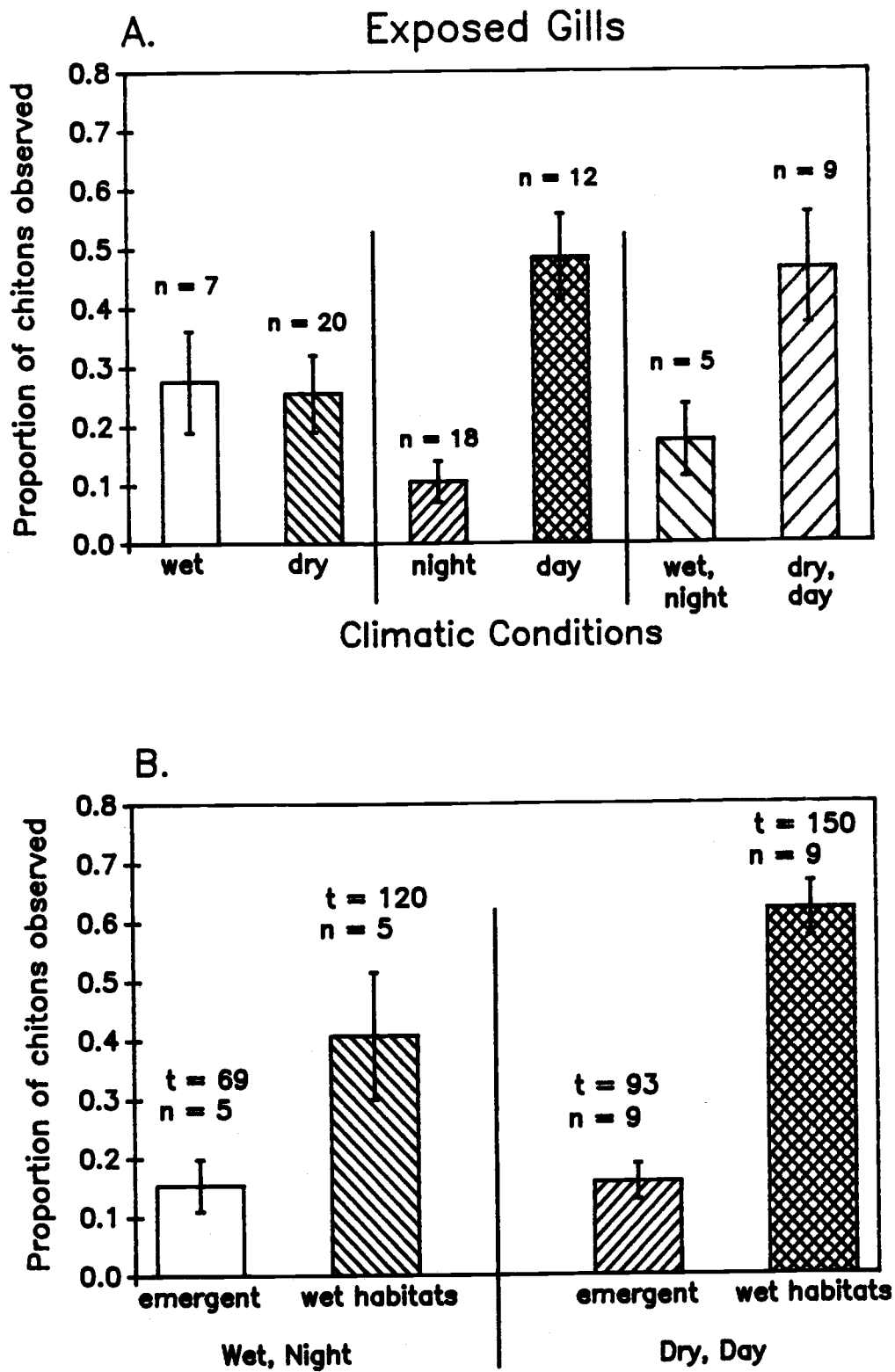
Observations from a shallow subtidal bench at Whale Cove suggest that although Cryptochiton forages when exposed to wave action, its activity is diminished by increased wave force. During a period of light wave action on 7/31/82 (estimated wave height 1'-3' = 0.3 - 0.9m), 15 of 19 (79%) of the subtidal chitons observed were active. On 8/5/82 the waves had increased considerably (estimated wave height 5'-8' = 1.5 - 2.4m), and significantly fewer (4 of 23 or 17.4%; X^2 = ?, p << 0.001) of the chitons on the same subtidal bench were active. The estimated height of waves at the mouth of Whale Cove on 7/31/82 were 1-3'(.3-.91m) and on 8/5/82 were 5-8'(1.52-2.44m). Although heavily weighted, I was moved by underwater wave surge as much as 2-3'(.6-.91m) in either direction on 8/5/82 but was not moved more than several centimeters on 7/31/82. Although this sequence of observations could not be repeated these results, and the observations reported earlier, suggested that experiments should be conducted to investigate the effects of wave action on feeding rates.

Grazing Rate Experiments

In two of three experiments, the grazing rates of Cryptochiton on Iridaea cordata were significantly higher in the protected experimental plots than in the exposed plots (Table 5.1). Significant differences in grazing rates occurred during ^KR 65,T 5,spacing 1

TABLE 5.1. Daily means, pooled means and estimated wave heights for grazing rate experiments at Boiler Bay. Rates are in units of grams of _Iridaea_ per hour. Wave heights were estimated by eye at the exposed bench. Pooled means combined data from consecutive days of experiments.

Exp.		Mean Grazing Rate				Estimated Wave Height	Pooled Mean Grazing Rate	
	Date	exposed		protected			exp.	prot.
		(n)		(n)				
1	7/24/86	.12	(4)	.23	(4)	3'-5',Oc. 7'*	.12	.23
	8/6/86	.02		.21		1'-2'		
2	8/7/86	.09		.22		1'-3'		
	8/8/86	.08		.31		3'-5',Oc. 7'*	.08	.25
	8/19/86	.35		.46		1'-3'		
3	8/20/86	.18		.34		2'-4'		
	8/21/86	.08		.25		1'-3'	.21	.35

* - occassional 7' waves were seen

both of the spring tide series of August, 1986. Although the mean of the grazing rate was higher at the protected than at the exposed site for the experiments run at the end of July, 1986, this difference was not significant. Two factors were different between the August and July experiments. The sample size was lower for the July data (6 replicates versus 12 for both of the August series) because the experiment was run for only two days, and because one chiton at each of the exposures failed to eat on both days. In addition, the wave action was much higher during the July series than either of the two in August. During the July experiment wave height was estimated at 3'-5' (1.0-1.5 m) with an occasional 7' (2.2 m) wave for both days of the experiment. The first two days of the early August experiment were very calm, with wave heights of 1'-3' (.3-1.0 m) and the third day was rough with 3'-5' (1.0-1.5 m) and an occasional 7' (2.2 m) wave. Wave heights were estimated at no higher than 4' (1.2 m) during the experiments conducted in late August.

Weight changes of the algae in the control cages were usually positive which means the algal thalli grew during the experiment. The mean weight change of control thalli was not different between the protected and exposed plots for any of the experiments so these were not used as a correction factor for algal weight change in experimental plots.

Quantification of maximum wave force substantiated the subjective judgment of differences between the two sites in exposure to wave shock (Table 5.2). On three of four days, dynamometer force measurements were significantly higher from the plots at the exposed site than at the protected site. On the fourth day the waves were so powerful that all 4 cages and 8 wave dynamometers were gone at the exposed site, and 3 of 8 dynamometers and one of the four cages were destroyed at the protected site. Although no measurements were available, the different rates of loss of devices further substantiate my claim that wave action was greater on the west than the east bench.

Laboratory feeding experiments suggest that the amount of algae that may have been torn off but not eaten in the field grazing rate experiments was probably low. A comparison of the mean amount of Iridaea cordata consumed in 13 experiments, (65.5%), with the amount detached (0.9%) suggests that little of the weight change of thalli in field experiments was due to unconsumed thalli loss.

DISCUSSION

The observations and experiments presented above support the hypothesis that the foraging behavior and feeding rates of Cryptochiton are affected by environmental harshness. When

TABLE 5.2. Mean dynamometer wave force data from the
exposed and protected experimental sites used in chiton
grazing rate experiments. Forces were measured using wave
force dynamometers Palumbi(1984) and spring scales (Pesola
brand).

	Mean Dynamometer Force		
Date	exposed	protected	Estimated Wave Height
2/26/87	.92 kg	.69 kg	1'-3'
2/27/87	1.17 kg	.64 kg	3'-5', Oc. 8'*
6/12/87	1.11 kg	.62 kg	3'-5'
6/13/87	all devices destroyed	.70 kg	5'-8', Oc. 9'*

* = Occasional Waves

exposed to air at low tide these chitons are relatively inactive and were rarely observed moving, foraging or feeding on emergent substrata. In contrast, approximately 65% of chitons occupying submerged or partially submerged intertidal habitats where observed to be active. The proportion of chitons observed in active behaviors appears to increase as their habitat becomes more "wet". Totally submerged chitons are more active than partially submerged and these are in turn more active than emerged chitons. The behavior that is most important in terms of consumer pressure, feeding, follows a similar pattern.

Although Petersen and Johansen (1973) describe Cryptochiton as a primarily nocturnal animal, my data showed a trend toward greater activity during the day at Boiler Bay. The proportion of active chitons was higher during daytime lowtides (45%) than nighttime tides (39%) for all microhabitats. In addition, numerous behavioral observations during the day in both intertidal and subtidal habitats confirmed that Cryptochiton is not restricted to nocturnal activity.

Since one of the physiological stresses of emergence is desiccation, the presence or absence of precipitation would be expected to affect the behavior of emergent chitons by possibly allowing them to be more active. Although the data indicated a slight trend of greater activity of emerged chitons during observation periods that were wet, this difference was not significant. In addition, the activity

of chitons appears to be virtually identical under the two extremes of desiccation stress, dry daytime lowtides and wet nighttime lowtides. Apparently, emergence alone is enough to reduce activity to a level so low that factors that might moderate the effects of emergence have little influence.

One indicator of emergence stress, gill-exposure, does appear to be affected by daylight. During daytime observation periods a significantly higher proportion of emergent chitons exposed their gills than during night periods. This difference may be a result of the higher air temperatures that occur during daytime lowtides. Petersen and Johansen (1973) reported that the tendency of Cryptochiton to curl back the edge of the mantle to expose the gills was more pronounced at higher air temperatures. Mean air temperature was higher in the day than at night for periods over which temperature was recorded, but this difference was not statistically significant. When analysis is limited to these data, there is a trend of a higher proportion of emergent chitons with exposed gills during the day but again, the difference is not significant.

The behavioral differences between subtidal and intertidal chitons during and following heavy wave shock (respectively) suggests that submerged intertidal habitats provide a refuge from wave shock when the tide is low. Subtidal Cryptochiton were much less active when experiencing heavy wave action than during calm waves. However, intertidal chitons were much more active following

heavy wave action than following calm waves. A hypothesis that would account for this difference is that chitons must curtail their foraging and feeding activities during high tide and heavy waves to avoid potentially lethal dislodgment, but that once the tide goes out and wave action is no longer being experienced, chitons become even more active to compensate for lost foraging time. During calm waves, feeding at high tide is possible and the activity of intertidal chitons would be more equally spread out during high and low tide periods. One way to test this hypothesis would be to observe chiton behavior at intertidal sites during high and low tide when waves were large and small. Unfortunately, obtaining such data directly is not feasible. The intertidal sites used in this study would be extremely hazardous to observe using scuba during high tide and heavy wave action (personal observations).

The hypothesis that the actual grazing rates of Cryptochiton are affected by wave action was supported strongly by the results of the grazing rate experiments. Grazing rates were significantly higher at protected sites than at exposed sites in August 1986. The results of the experiment conducted during the late July spring tide series indicate a similar trend.

High wave action may have produced enough dislodgment force at even the protected site to exceed the threshold that would affect the feeding behavior of Cryptochiton. In addition, since high wave action tends to negate the

differences in exposure time between the two sites, an emersion time correction factor may not be necessary for the July experiment. However, even assuming equal emersion times for both sites, the differences in July grazing rates are not significant ($p=.1$). The above comments suggest that the July results were due to either random variation, or real differences due to the exceptional wave action, or a combination of both of these factors. Overall, the results suggest that moderate to heavy wave action inhibits grazing.

In general, the quantitative measurements of wave force supported the subjective judgment of differences in exposure between the two experimental sites. Data pooled over several days of measurement demonstrate that, on the average, wave forces are higher at the exposed than at the protected site. However, the single set of measurements that were taken on a day with calm waves may indicate that there are limits to the resolution power of the type of wave force dynamometer that was used. The means of this set were different for the exposed and protected site, but not significantly so.

Several questions are raised by the behavior patterns of <u>Cryptochiton</u> that were observed in this study. First, why do these chitons spend so much of their time clamped down and inactive even when in submerged habitat at low tide? A possible explanation is that the availability of preferred food is sometimes so low as to make it nutritionally and energetically unprofitable to search for

food. However, this does not seem likely as highly preferred food items (*Iridaea* thalli) were often observed almost in contact with inactive, submerged chitons (personal observations). An alternative hypothesis is that the chitons require substantial time to simply digest the plant matter that they consume. Typically, plant matter is more difficult to digest than animal matter and herbivores have more extensive and elaborate guts to cope with the greater digestion times. *Cryptochiton* does have an extensive gut, and fecal matter often contains partially digested algae. Further investigation of this hypothesis would require a laboratory study of the assimilation efficiency and gut-passage time.

A second question concerning *Cryptochiton* behavior is if emergent habitats are so stressful and inhibit feeding behavior, why are these chitons ever found out of water? Why do they not restrict their foraging range to habitats that are submerged at low tide? It seems probable that they can not distinguish between habitats that will be emerged or submerged at low tide when they are foraging at high tide and thus are caught on emerged substrata by the receding tide. An alternative, but not necessarily mutually exclusive, explanation is that the abundance of preferred algae is so low in submerged habitats relative to emerged habitats that foraging and feeding on emerged substrata at high tide compensates for the time at low tide when foraging and feeding are apparently inhibited by physical factors.

The presence of urchins, other herbivores and cobble scour, which are often higher in submerged habitats, may affect the abundance of preferred algae. Chitons were often observed feeding at the edge of a tidepool where algae hung down from emerged substrata (personal observations).

In summary, the foraging and feeding behavior of _Cryptochiton stelleri_ are influenced by emersion, daylight and wave action. Further, during heavy wave action and low tide, submerged intertidal habitats may provide a refuge for safe foraging and feeding. Finally, feeding rates are lower at wave-exposed sites than at wave-protected sites. Similar patterns of behavior and effects can be predicted for many other sluggish intertidal consumers, which may face the same physical forces of emersion stress and dislodgment risk.

Literature Cited

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. pp. 460-490. In: M. L. Cody and J. Diamond, eds. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Mass.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. Ecol. Monogr. 55:69-102.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15:131-37.

Dodson, S. I. 1974b. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605-13.

Dodson, S. I. 1974a. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19:721-29.

Harper, J. L. 1969. The role of predation in vegetational
    diversity. Brookhaven Symp. Biol. 22:48-61.

Huston, M. 1979. A general hypothesis of species
    diversity. Am. Nat. 113:81-101.

Janzen, D. H. 1970. Herbivores and the number of tree
    species in tropical forests. Am. Nat. 104:501-528.

Lubchenco, J. 1978. Plant species diversity in a marine
    intertidal community: importance of herbivore food
    preference and algal competitive abilities. Am. Nat.
    112:23-39.

MacArthur, R. H. 1972. Geographical Ecology. Harper and
    Row, New York 269 pp.

Menge, B. A. 1976a. Ecological implications of patterns of
    rocky intertidal community structure and behavior along
    an environmental gradient. pp 155-180. In: J. D.
    Costlow, (ed) Ecology of fouling communities Office of
    Naval Research Printing Office, Washington, D. C.

Menge, B. A. 1976b. Organization of the New England rocky
    intertidal community: Role of predation, competition
    and environmental heterogeneity. Ecol. Monogr.
    46:355-393.

Menge, B. A. 1978a. Predation intensity in a rocky
    intertidal community: relation between predator
    foraging activity and environmental heterogeneity.

Oecologia 34:1-16.

Menge, B. A. 1978b. Predation intensity in a rocky
intertidal community. Effect of algal canopy, wave
action and desiccation on predator feeding rates.
Oecologia 34:17-35.

Menge, B. A. 1983. Components of predation intensity in
the low zone of the New England rocky intertidal
region. Oecologia 58:141-55.

Menge, B. A., and J. P. Sutherland. 1976. Species
diversity gradients: synthesis of the roles of
predation, competition and temporal heterogeneity. Am.
Nat. 110:351-369.

Menge, B. A., and J. P. Sutherland. 1987. Community
regulation: variation in disturbance, competition, and
predation in relation to environmental stress and
recruitment. Am. Nat. 130:730-57.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980.
Intertidal Invertebrates of California. Stanford
University Press, Stanford, Cal. 690 pp.

Paine, R. T. 1966. Food web complexity and species
diversity. Am. Nat. 100:65-75.

Paine, R. T. 1974. Intertidal community structure:
experimental studies on the relationship between a
dominant competitor and its principal predator.

Oecologia 15:93-120.

Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the _Mytilus_-_Pisaster_ interaction. Ecology 57:858-873.

Palumbi, S. R. 1984. Measuring intertidal wave forces. J. Exp. Mar. Biol. Ecol. 81:171-79.

Petersen, J. A., and K. Johansen. 1973. Gas exchange in the giant sea cradle _Cryptochiton_ _stelleri_ (Middendorff). J. Exp. Mar. Biol. Ecol. 12:27-43.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375- 86.

CHAPTER 6: CONCLUSION

The research presented in each of the previous chapters combines to give an overall picture of the behavior of Cryptochiton and its effects on algae. Each of the three key elements of the herbivore effects model (Lubchenco and Gaines 1981) are at least partially elucidated, which facilitates prediction of the community role of this chiton.

Chapter 2 suggests that the distribution and abundance of these chitons is patchy and dependent upon physical factors such as wave action, temperature extremes at low tide, and the presence of tidepool refuges. These animals are relatively long-lived (20 years or more), have sporadic, cryptic or infrequent recruitment, and have few predators. This information suggests that prey algae will be encountered by Cryptochiton in a patchy manner on a local scale, primarily in tidepools or subtidal areas, and that the encounter rate will be dependent on physical factors such as wave action and temperature.

The data presented in Chapter 3 suggest that Cryptochiton can move up to 7 m in one day but that its home range may be limited to a 6 m^2 area over 300 days. These chitons do not appear to home to a specific site or scar as occurs with several species of limpets and may occur for two other species of chitons. Comparison of movements of subtidal chitons at Whale Cove and intertidal chitons at Boiler Bay suggest that chitons move less and have more restricted home ranges in intertidal habitats. This suggests that the impact of intertidal chitons on macroalgae

will be more restricted in area than for subtidal chitons. Assuming that consumption rates are the same, the impact of an intertidal chiton would be more concentrated, thus causing a more patchy effect. Of course, many factors that were not examined in this research will affect consumption rates and the concentration of the impacts of a consumer.

The relatively limited home ranges and movements of intertidal chitons also indicate that fewer types of algae may be available to chitons in the intertidal zone than in the subtidal zone. This prediction assumes that the patch size of the maximum species number is greater than the home range of intertidal chitons. In addition, limited availability of algae may also affect the diet breadth of intertidal Cryptochiton if the availability of highly preferred species is decreased.

The information on food preferences and field selectivity presented in Chapter 4 help predict which algae will be affected most by Cryptochiton. Other considerations include the ability of prey algae to recover from damage, consumer density and the effects of physical and biological forces on the grazing rate of these chitons. Where and when these factors are equal, this study suggests that Cryptochiton will have the greatest effects on algae in the division Rhodophyta and especially on the species Iridaea cordata. In addition, the comparison of laboratory preference data and field selectivity observations suggests that preferences are expressed under conditions of variable

relative availability of algal species and that highly preferred algae are actually sought. Once encountered, many red algae and _Iridaea cordata_ in particular will be at least partially eaten. Less preferred algae will tend to escape consumption if higher preference algae are available.

The major results of Chapter 5 are first, that the foraging and feeding behaviors of _Cryptochiton stelleri_ are influenced by emersion, daylight and wave action. Second, during heavy wave action and low tide, submerged intertidal habitats may provide a refuge for safe foraging and feeding. These data suggest that intertidal algae will have a lower probability of being encountered by _Cryptochiton_ on emergent substrata than on submergent substrata. During heavy and medium wave action, intertidal algae on submergent substrata will be encountered more frequently by chitons at low tide than when wave action is calm. Because of the ease of dislodgment of a moving, foraging or feeding chiton when experiencing heavy wave action it is unlikely that chitons are active during these conditions. Animals exhibiting active behaviors during heavy wave action will likely be selected against very strongly. However, overall encounter rates during low wave action may be equal to higher wave action rates if foraging and feeding behavior is spread more equally over high and low tide. The best escape from _Cryptochiton_ for an alga that is highly preferred is on emergent substrata where or when wave action is heavy.

Finally, feeding rates are lower at wave-exposed sites than at wave-protected sites. Once a preferred alga is encountered by <u>Cryptochiton</u> and is being eaten, the alga is less likely to be heavily grazed when and where wave action is high. Assuming that all parts of the plant contribute equally to fitness, grazing rates should be a measure of herbivore damage. Therefore expected herbivore damage should be lower when and where <u>Cryptochiton</u> experiences heavy wave action.

The research presented in this thesis allows prediction of the herbivore and community effects of <u>Cryptochiton</u> and elucidates some general ecological principles of feeding behavior. The obvious next step is to test these predictions through field manipulations of chiton density.

I believe that this dissertation has advanced the state of knowledge of the ecology of this chiton significantly and that it contributes to the understanding of plant-herbivore interactions. Hopefully my research will serve as the basis for further research on many aspects of the behavior and biology of this organism, its effects, and the reasons for its preferences for certain species of algae.

BIBLIOGRAPHY

Anderson, R. J., and B. Velimirov. 1982. An experimental investigation of the palatability of kelp bed algae to the sea urchin Parechinus angulosus Leske. Mar. Ecol. 3:357-73.

Black, R. 1976. The effects of grazing by the limpet, Acmaea insessa, on the kelp, Egregia laevigata, in the intertidal zone. Ecology 57:265-77.

Branch, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. Oceanogr. Mar. Biol. Ann. Rev. 19:235-380.

Branch, G. M. 1971. The ecology of Patella linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements, and feeding. Zool. Afr. 6:1-38.

Boyle, P. R. 1977. The physiology and behavior of chitons (Mollusca: Polyplacophora). Oceanogr. Mar. Bio. Ann. Rev. 15:461-509.

Castenholz, R. W. 1961. the effect of grazing on marine littoral diatom populations. Ecology 42:783-94.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-15.

Connell, J. H. 1975. Some mechanisms producing structure

in natural communities: a model and evidence from field experiments. pp. 460-490. In: M. L. Cody and J. Diamond, eds. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Mass.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Dayton, P. K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. Am. Nat. 107:662-70.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137-59.

Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. Ecol. Monogr. 55:69-102.

Dethier, M. N. and D. O. Duggins, 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. Oecologia 67:183-191.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15:131-37.

Dodson, S. I. 1974b. Zooplankton competition and
    predation: an experimental test of the size-efficiency
    hypothesis. Ecology 55:605-13.

Dodson, S. I. 1974a. Adaptive change in plankton
    morphology in response to size-selective predation: a
    new hypothesis of cyclomorphosis. Limnol. Oceanogr.
    19:721-29.

Duggins, D. O. 1980. Kelp beds and sea otters: an
    experimental approach. Ecology 61:447-53.

Ebert, T. A. 1968. Growth rates of the sea urchin
    Strongylocentrotus purpuratus related to food
    availability and spine abrasion. Ecology 49:1075-1091.

Emlen, J. M. 1966. The role of time and energy in food
    preference. Am. Nat. 100:611-17.

Fairweather, P.G., and A.J. Underwood. 1983. The apparent
    diet of predators and biases due to different handling
    times of their prey. Oecologia 56:169-79.

Fretter, V. and A. Graham. 1962. British prosobranch
    mollusca, their functional anatomy and ecology. Ray
    Society, London, 548 pp.

Gaines, S. D. 1985. Herbivory and between-habitat
    diversity: The differential effectiveness of defenses
    in a marine plant. Ecology 66:473-85.

Glynn, P. W. 1970. On the ecology of the Caribbean chitons
Acanthopleura granulata Gmelin and Chiton tuberculatus
Linne: density, mortality, feeding, reproduction and
growth. Smith. Contrib. Zool. 66:1-21.

Greer, M. L., and A. L. Lawrence. 1967. The active
transport of selected amino acids across the gut of the
chiton (Cryptochiton stelleri). 1. Mapping
determinations and effects of anaerobic conditions.
Comp. Biochem. Physiol. 22:665-74.

Harper, J. L. 1969. The role of predation in vegetational
diversity. Brookhaven Symp. Biol. 22:48-61.

Harrison, J. T. 1975. Isometric responses of somatic
musculature of Cryptochiton stelleri (Mollusca:
Polyplacophora). Veliger 18 (Suppl.): 79-82.

Hawkins, S. J. and R. G. Hartnoll. 1983. Grazing of
intertidal benthic algae by marine invertebrates.
Oceanogr. Mar. Biol. Ann. Rev 21:195-282.

Hay, M. E. 1981. Spatial patterns of grazing intensity on a
Caribbean barrier reef: herbivory and algal
distribution. Aquat. Bot. 11:97-109.

Hay, M. E. 1985. Spatial patterns of herbivore impact and
their importance in maintaining algal species richness.
Proc. 5th Int. Coral Reef Congr. 4:29-34.

Himmelman, J. H. and T. H. Carefoot. 1975. Seasonal changes

in calorific value of three Pacific coast seaweeds and their significance to some marine invertebrate herbivores. J. Exp. Mar. Biol. Ecol. 18:139-151.

Horn, M. H., S. N. Murray, and T. W. Edwards. 1982. Dietary selectivity in the field and food preferences in the laboratory for two herbivorous fishes (Cebidichthys violaceus and Xiphister mucosus) from a temperate intertidal zone. Mar. Biol. 67:237-46.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, Newhaven, Connecticut, USA 302 pp.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413-17.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104:501-528.

Kareiva, P. M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234-38.

Kitting, C. L. 1980. Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. Ecol. Monogr. 50:527-50.

Lawrence, A. L., and D. C. Lawrence. 1967. Sugar
    absorption in the intestine of the chiton,
    Cryptochiton stelleri. Comp. Biochem. Physiol.
    22:341-57.

Lawrence, A. L., and D. S. Mailman. 1967. Electrical
    potentials and ion concentrations across the gut of
    Cryptochiton stelleri. J. Physiol. 193:535-45.

Lawrence, A. L., D. S. Mailman, and R. E. Puddy. 1972. The
    effect of carbohydrates on the intestinal potentials of
    Cryptochiton stelleri. J. Physiol. 225:515-27.

Lawrence, A. L., J. M. Lawrence, and A. C. Giese. 1965.
    Cyclic variations in the digestive gland and glandular
    oviduct of chitons (Mollusca). Science 147:508-10.

Lawrence, J. M. 1975. On the relationship between marine
    plants and sea urchins. Oceanogr. Mar. biol. Annu.
    Rev. 13:213-86.

Leighton, D. L. 1966. Studies of food preference in
    algivorous invertebrates of Southern California kelp
    beds. Pac. Sci. 20:104-13.

Leighton, D. L., and R. A. Boolootian. 1963. Diet and
    growth in the black abalone, Haliotis cracherodii.
    Ecology 44:227-38.

Lowenstam, H. A. 1962. Magnetite in denticle capping in
    Recent chitons (Polyplacophora) Bull. Geol. Soc. Amer.

73:435-38.

Lubchenco, J. 1978. Plant species diversity in a marine
    intertidal community: importance of herbivore food
    preference and algal competitive abilities. Am. Nat.
    112:23-39.

Lubchenco, J. 1980. Algal zonation in a New England rocky
    intertidal community: an experimental analysis. Ecology
    61:333-44.

Lubchenco, J. 1983. Littorina and Fucus: effects of
    herbivores, substratum heterogeneity, and plant escapes
    during succession. Ecology 64:1116-1123.

Lubchenco, J. and S. D. Gaines. 1981. A unified approach to
    marine plant-herbivore interactions. I. Populations and
    communities. Ann. Rev. Ecol. Syst. 12:405-37.

MacArthur, R. H. 1972. Geographical Ecology. Harper and
    Row, New York 269 pp.

MacGinitie, G. E., and N. MacGinitie. 1968. Notes on
    Cryptochiton stelleri (Middendorff, 1846). Veliger
    11:59-61.

Mauzy, K. P., C. E. Birkeland, and P. K. Dayton. 1968.
    Feeding behavior of asteroids and escape responses of
    their prey in the Puget Sound region. Ecology
    49:603-619.

Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual food availability and environmental predictability. Ecol. Monogr. 42:25-50.

Menge, B. A. 1976a. Ecological implications of patterns of rocky intertidal community structure and behavior along an environmental gradient. pp 155-180. In: J. D. Costlow, (ed) Ecology of fouling communities Office of Naval Research Printing Office, Washington, D. C.

Menge, B. A. 1976b. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. Ecol. Monogr. 46:355-393.

Menge, B. A. 1978a. Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental heterogeneity. Oecologia 34:1-16.

Menge, B. A. 1978b. Predation intensity in a rocky intertidal community. Effect of algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34:17-35.

Menge, B. A. 1982. The effects of feeding on the environment: Asteroidea. Pages 521-551 in M. Jangoux and J. M. Lawrence, eds. Echinoderm nutrition. Balkema Rotterdam, The Netherlands.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58:141-55.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. 110:351-369.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130:730-57.

Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, _Acanthina_ punctulata. Oecologia 17:293-316.

Michael, P. F. 1975. Blood glucose concentration and regulation in _Cryptochiton stelleri_ (Mollusca: Polyplacophora). Veliger 18 (Suppl.):117-21.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal Invertebrates of California. Stanford University Press, Stanford, CA. 690 pp.

Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58:1020-32.

Nicotri, M. E. 1980. Factors involved in herbivore food

preference. J. Exp. Mar. Biol. Ecol. 42:13-26.

Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by the echinoid _Diadema antillarum_ Philippi: formation of halos around West Indian patch reefs. Science 182:715-17.

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.

Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the _Mytilus-Pisaster_ interaction. Ecology 57:858-873.

Paine, R. T. 1969. The _Pisaster-Tegula_ interaction: prey patches, predator food preference and intertidal community structure. Ecology 50:950-961.

Paine, R. T., and R. L. Vadas. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Mar. Biol. 4:79-86.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, _Strongylocentrotus_ spp., on benthic algal populations. Limnol. Oceanogr. 14:710-719.

Palmer, J. B., and P. W. Frank. 1974. Estimates of growth of _Cryptochiton_ _stelleri_ (Middendorff, 1846). Veliger 16:301-4.

Palmer, R. A. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia 62:162-172.

Palumbi, S. R. 1984. Measuring intertidal wave forces. J. Exp. Mar. Biol. Ecol. 81:171-79.

Petersen, J. A., and K. Johansen. 1973. Gas exchange in the giant sea cradle _Cryptochiton_ _stelleri_ (Middendorff). J. Exp. Mar. Biol. Ecol. 12:27-43.

Peterson, C.H., and B.P. Bradley. 1978. Estimating the diet of sluggish predator from field observations. J. Fish. Res. Bd. Can. 35:136-40.

Ricketts, E. F., and J. Calvin. 1968. Between Pacific Tides. Revised by J. W. Hedgpeth. Fourth Edition. Stanford University Press, Stanford, California, USA.

Robbins, K. B. 1975. Active absorption of D-glucose and D-galactose by intestinal tissue of the chiton _Cryptochiton_ _stelleri_ (Middendorff, 1846). Veliger 18 (Suppl.):122-27.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-403.

Shepherd, S. A. 1973. Studies on southern Australian abalone (genus <u>Haliotis</u>) I. Ecology of five sympatric species. Aust. J. Mar. Freshwat. Res. 24:217-57.

Southwood, T. R. E. 1978. Ecological methods with particular reference to insect populations. John Wiley and Sons, New York,

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375- 86.

Steinberg, P. D. 1985. Feeding preferences of <u>Tegula</u> <u>funebralis</u> and chemical defenses of marine brown algae. Ecol. Monogr. 55:333-49.

Stenek, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Mar. Biol. 68:299-318.

Stimpson, J. 1970. Territorial behavior of the owl limpet, <u>Lottia</u> <u>gigantea</u>. Ecology 51:114-118.

Stimpson, J. 1973. The role of the territory in the ecology of the intertidal limpet <u>Lottia</u> <u>gigantea</u> (Gray). Ecology 54:1020-1030.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index the forage ratio and a proposed linear index of food selection. Tran. Am. Fish. Soc. 108:344-52.

Talmadge, R. T. 1975. A note on Oceanebra lurida (Middendorff). Veliger 17:414.

Tucker, J. S., and A. C. Giese. 1962. Reproductive cycle of Cryptochiton stelleri (Middendorff). J. Exper. Zool. 150:33-43.

Underwood, A. J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16:111-210.

Underwood, A. J. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia 46:201-13.

Underwood, A. J., and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48:221-33.

Vadas, R. L. 1977. Preferential feeding: An optimization strategy in sea urchins. Ecol. Monogr. 46:337-71.

Watanabe, J. M. 1984. Food preference, food quality and diets of three herbivorous gastropods (Trochidae: Tegula) in a temperate kelp forest habitat. Oecologia 62:47-52.

Webster, S. K. 1968. An investigation of the commensals of Cryptochiton stelleri (Middendorff, 1846) in the Monterey Peninsula area, California. Veliger 11:121-25.