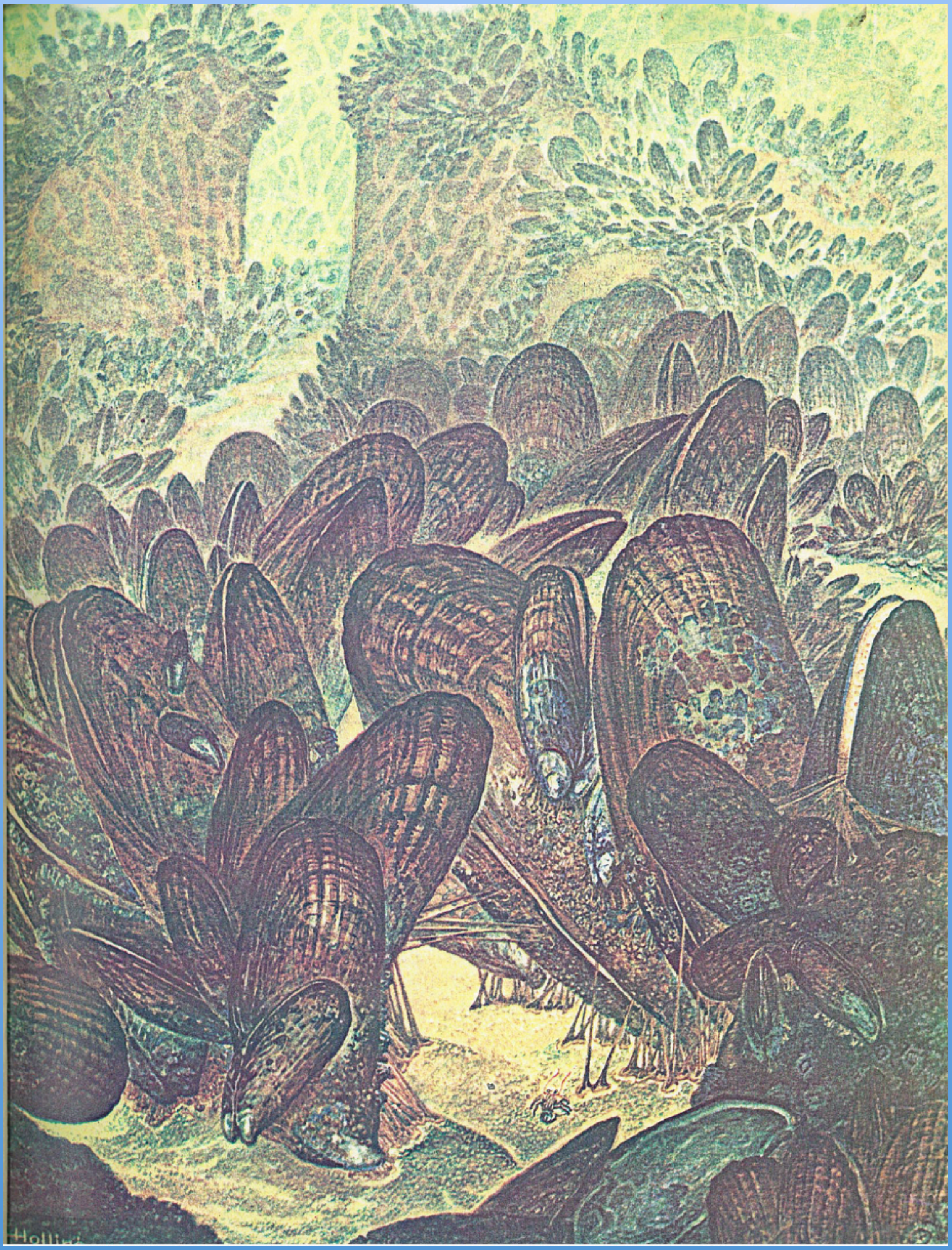
THE *MYTILUS CALIFORNIANUS* COMMUNITY: STUDIES ON THE COMPOSITION, STRUCTURE, ORGANIZATION AND DYNAMICS OF A MUSSEL BED

THOMAS HANUS SUCHANEK



THE *MYTILUS CALIFORNIANUS* COMMUNITY: STUDIES ON THE COMPOSITION, STRUCTURE, ORGANIZATION, AND DYNAMICS OF A MUSSEL BED

by

THOMAS HANUS SUCHANEK, JR.

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CHAPTER 1

GENERAL INTRODUCTION

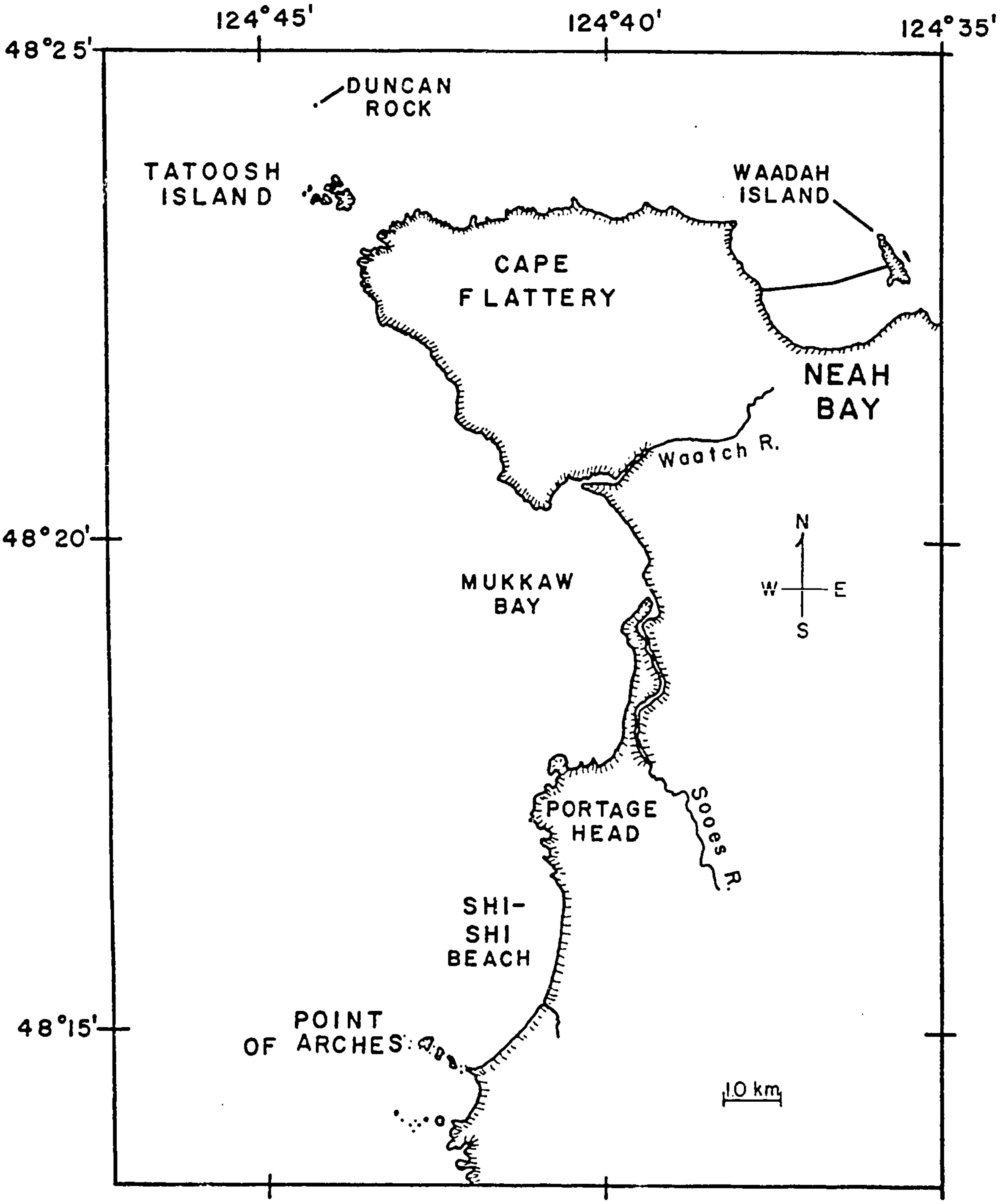
Authors as early as Verrill (1874) and Mobius (1877) recognized the role that intra- and inter-specific interactions play in defining, shaping, and limiting the extent of communities. They were well aware that those relationships must be set in the physical environment, but are determined ultimately by biological forces. For example, Verrill (1874, p. 472) states that "Shells of oysters provide suitable attachment for various shells, bryozoans, ascidians, hydroids, sponges, etc., which could not otherwise maintain their existence on muddy bottoms, while other kinds of animals such as crabs, annelids, etc., find shelter between the shells or in their interstices." It is surprising that the complexity and dynamic nature of bed-forming species such as oysters and mussels have long been recognized, yet these attributes in the *Mytilus californianus* community, the most conspicuous biotic feature of the rocky intertidal zone on exposed shores of Western North America, to date have not been documented.

Complex assemblages with many interacting components are difficult to study, let alone define. Fager (1963), for instance, provided an excellent and sensitive review of both the analytical and definitional problems associated with the concept of "community." Mills (1969) further provided a thorough historical background and discussed various operational definitions of the concept. Finally, some authors (Novikoff, 1945; Feibleman, 1954; Dunbar, 1960; Odum, 1977) have argued that large assemblages of interacting populations are characterized by "emergent properties" of hierarchical organization such that the ecosystem as a whole is a synergistic sum of its component interactions. Without necessarily subscribing to these latter views, I believe that community level studies sensitive to the varied roles of resident species are capable of generating new insights into the complexity, operation, and evolution of natural processes.

In this study, I have analysed the composition, structure, organization, and dynamics of the *Mytilus californianus* community in which "community" is defined *as a recurrent, multi-trophic level assemblage of interacting populations from a particular delineated region*. That is, I have studied the organization of the mussel bed itself, the myriad of species (representing nearly all trophic levels) found directly on mussel shells, and those found in the interstices between and under them. This assemblage represents an extremely well delineated community bounded by the physical limits of the actual mussels, which, in the intertidal, are in turn restricted by physical and biological factors to a well definable zone. Although subtidal beds of *M. californianus* do occur (Paine, 1976b), for the most part I have restricted my study to those in the intertidal.

Because of the necessity for limited destructive sampling, I have chosen rocky intertidal study sites on the exposed outer coast of Washington State (Fig. 1) where well developed continuous mussel beds occur which would not be seriously harmed by such sampling. Both moderately remote sites chosen for this study (Tatoosh Island and Shi-Shi) are also relatively undisturbed by human interference,

Fig. 1. Map of Cape Flattery region of Washington showing the location of study sites Tatoosh Island and Shi-Shi.


124°45'
124°40'
124°35'
48°25'
48°20'
48°15'
DUNCAN ROCK
TATOOSH ISLAND
WAADAH ISLAND
CAPE FLATTERY
NEAH BAY
Waatch R.
N
W
E
S
MUKKAW BAY
PORTAGE HEAD
Sooes R.
SHI-SHI BEACH
POINT OF ARCHES
1.0 km

thereby facilitating the use of various experimental devices which remained undisturbed for long periods of time (i.e., years). Tatoosh Island ($48^{\circ}24'$N:$124^{\circ}44'$W) is an extremely exposed island (ca. 34 hectares) 0.7 km off Cape Flattery on the Washington coast. Fig. 2 shows the location of collecting sites and of experimental manipulations on Tatoosh Island. The intertidal surface topography there is primarily characterized by a gentle sloping shelf with moderately continuous mussel beds surrounding nearly the entire island (Fig. 3). In contrast, Shi-Shi ($48^{\circ}17'$N:$124^{\circ}41'$W) is a mainland site (Fig. 4) with moderate exposure approximately 13 km S.E. of Tatoosh which has only one gentle sloping platform with a continuous cover of mussels (at Shi-Shi Bench). The other mussel beds at Shi-Shi are located on the crowns of small (1-10 meter diameter) hillocks spaced 1-10 meters apart (Fig. 5). The continuous mussel beds characteristic of Tatoosh Island and Shi-Shi Bench were ideal for repeated destructive sampling for the analysis of associated organisms, whereas the small, isolated beds on hillocks (especially common at Wreck Cove) were much more suited for replicated experimental manipulations.

The rocky intertidal communities on the exposed coast of Washington have had a history rich in biological investigations. As early as the summer of 1911, G.B. Rigg visited Tatoosh Island in an Indian dug-out canoe primarily to study the kelps Nereocystis and Macrocystis. In the 1930's, Rigg & Miller (1949) made a comprehensive survey of the intertidal zonation of fauna and flora on Waddah Island and other small islands in the vicinity of Neah Bay (Fig. 1). Detailed analyses on the structure and dynamics of these intertidal

Fig. 2. Map of Tatoosh Island, Washington showing location of collecting and experimental manipulation sites. (Diagram modified from Sebens, 1977)

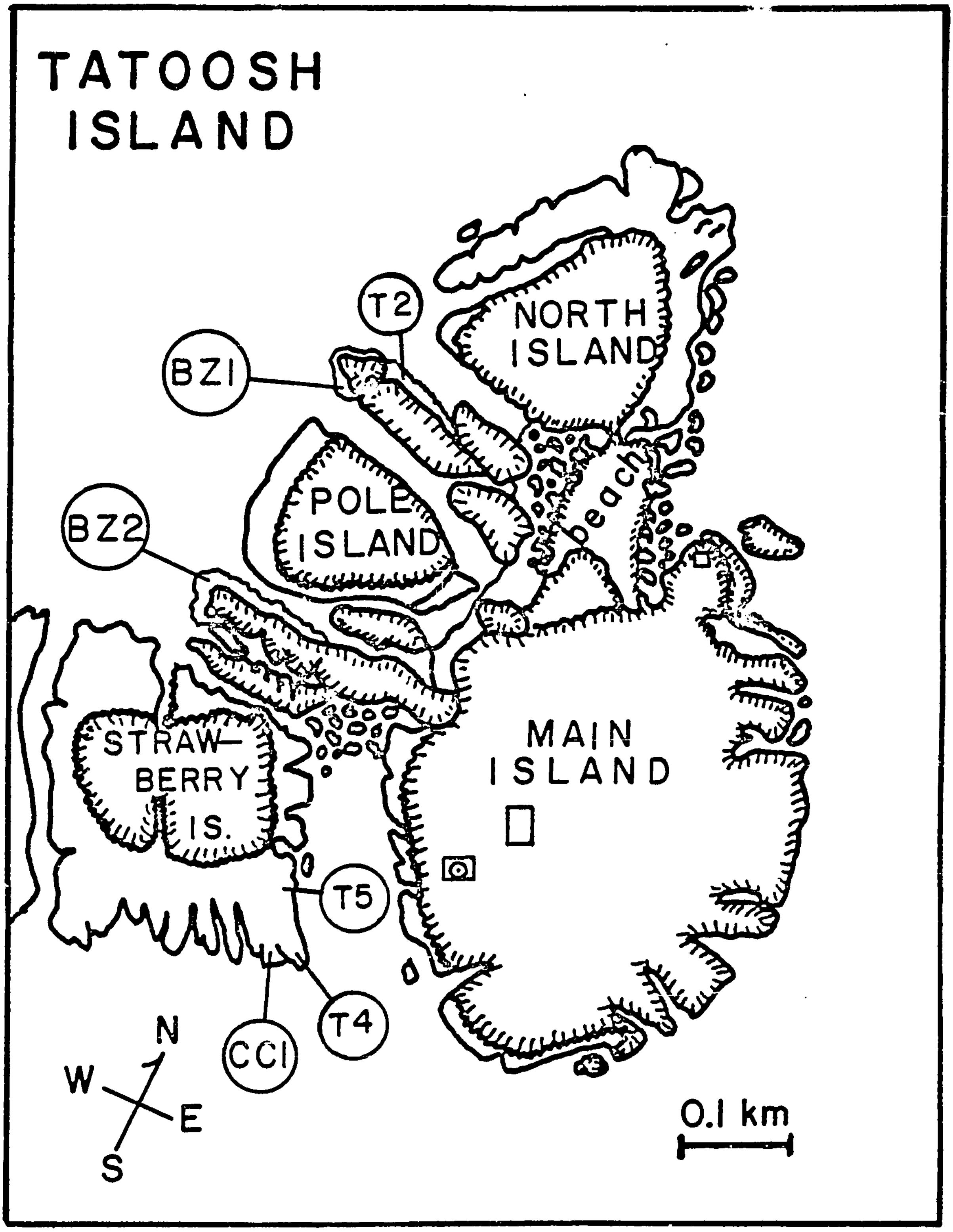

TATOOSH ISLAND
NORTH ISLAND
T2
BZ1
POLE ISLAND
beach
BZ2
MAIN ISLAND
STRAW-BERRY IS.
T5
T4
CC1
N
W
E
S
0.1 km

Fig. 3. Photograph of typical intertidal surface topography at Tatoosh Island, Washington. Note the gentle sloping nature of the intertidal platform and the bucket with meter stick for scale.

Fig. 4. Map of Shi-Shi, Washington showing locations of collecting and experimental manipulation sites.

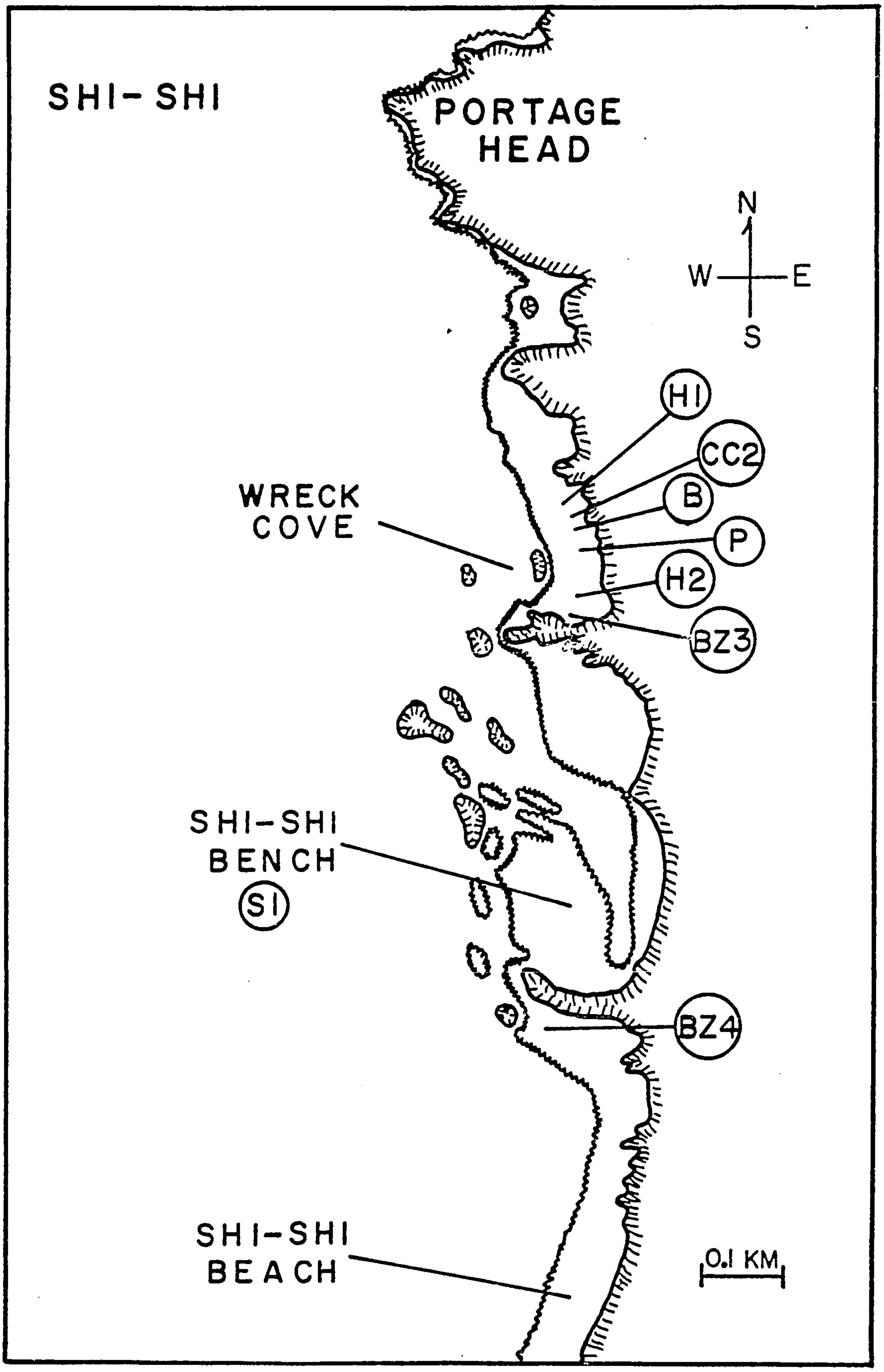

SHI-SHI
PORTAGE HEAD
N
W
E
S
H1
CC2
B
P
H2
BZ3
WRECK COVE
SHI-SHI BENCH
S1
BZ4
SHI-SHI BEACH
0.1 KM

Fig. 5. Photograph of typical surface topography at Shi-Shi, Washington. Note the rounded hillocks (1-10 meters wide) which characterize the intertidal.

communities began with Paine (1966). Through experimental manipulations, he has shown how Pisaster ochraceus, a predatory starfish, limits the lower distribution of M. californianus in the intertidal and has elucidated some of the higher order effects on the composition of the other primary space occupiers (Paine, 1974, 1976a). In addition, he has shown the importance of grazing activities by urchins (Stronglyocentrotus) in structuring dominant plant assemblages (Paine & Vadas, 1969) and has analysed the bioenergetics of another common herbivore, the black turban snail Tegula fenebralis (Paine, 1971a). Other significant work has been performed in this region by Dayton (1971, 1973a, 1973b, 1975) who thoroughly analysed the details of the provision of and subsequent competition for space (the limiting resource) by a hierarchy of plant and animal species.

With the grounding of a 190-meter (662 foot) unmanned troop-ship, the General M.C. Meigs, in January 1972 at "Wreck Cove", Shi-Shi, the intertidal communities in that region were subjected to some persistent oil contamination by small quantities of Navy Special Fuel Oil. Through an analysis of petroleum hydrocarbon uptake patterns in mussels and by observations of plant and animal populations, Clark & Finley (1973) and Clark et al. (1973, 1975, 1978) determined that in this particular instance, the effects of the oil contamination were ameliorated by August 1974. At no time did there appear to be a significant decline in the mussel populations, although other species were affected.

Study sites at Tatoosh Island and Shi-Shi were visited for sample collection or monitoring of study areas and/or experiments over a five year period starting in 1973. The schedule of visits to each of the study sites is given in Appendix I.

Chapter 2 discusses the ecology of *Mytilus edulis* and its interaction with the *Mytilus californianus* community at exposed intertidal sites.

Chapter 3 addresses the question of how the differences in life history strategies between *M. edulis* and *M. californianus* contribute to their different ecological status within the intertidal zone, where *M. californianus* is a long-term competitive dominant and *M. edulis* is a classic fugitive species.

Chapter 4 describes the development of the physical matrix of mussels, defines the biological composition of the assemblage of diverse associated organisms (over 300 species), and provides observational and experimental evidence for the influence of structural heterogeneity on the development of such a diverse, interacting community.

Chapter 5 gives evidence of the close inter-dependence which has developed between the mussels and the associates, a relationship which appears to be necessary for the continued survival and success of the entire community.

Chapter 6 summarizes the major findings and conclusions of this study.

This research has focused on the complex of biological and physical interactions that potentially make the mussel community diverse. I have examined both static attributes as bed limits, depth, and size composition and the dynamic events of bed establishment, recovery, spatial expansion and protection, especially as they are influenced by the complex resident biota. Protracted observation is essential to hypothesis formation, and I have tried to be sensitive to the resident species' natural history. Wherever possible, however, hypotheses have been tested by controlled manipulation. Thus, I have delineated, through observation and experimentation the roles of some of the more influential associated community members and have shown how essential these associates are to the health and well being of the mussel bed complex. The approach, therefore, has been directed towards community ecology with an emphasis on population interactions and natural history of the component species in order to gain a synthetic understanding of the dynamics of the _Mytilus californianus_ community.

CHAPTER 2

THE ECOLOGY OF MYTILUS EDULIS L. IN EXPOSED ROCKY INTERTIDAL COMMUNITIES[1]

INTRODUCTION

In the past, considerable attention has been paid to Mytilus edulis not only in terms of its biology and ecology (Field, 1922; Seed, 1969a, b, 1976), but also relative to its economic value (MacLean, 1972; Mason, 1972, 1976) and its possible use as a pollution indicator organism (Roberts, 1976).

M. edulis has a circumpolar distribution in both boreal and temperate waters of the northern and southern hemisphere (Soot-Ryen, 1955), and Seed (1969a, b) gives an excellent discussion of its occurrence on the exposed rocky shores of Britain. Its range along the western coast of North America has been described as extending from the Arctic Ocean to Cabo San Lucas, Baja California, Mexico (Soot-Ryen, 1955). Although Harger (1970a, b, 1972b) mentions its occurrence on the moderately exposed shores of southern California, it has generally been considered a protected water species on this coast, either occurring on pilings or gravel in protected bays (hence the name 'bay mussel'), or in the extreme case at the semi-exposed mouth

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[1] This chapter has been published in the Journal of Experimental Marine Biology and Ecology, 1978, 31:105-120. Minor changes from the published version have been made in the present version. They are as follows: 1) The average lower limit of the M. californianus zone, as stated in the published version was +5.6 ft (+1.7m) above MLLW. This was an error and has been corrected in the present version to +4.3 ft (+1.3m); 2) Table and figure numbers have been altered to match the format of the dissertation; 3) Table III in the present version has been expanded to include sizes of M. californianus.

of these bays. In this latter case, it has been considered a temporary, inferior competitor to its congener *M. californianus*, the possible result of having finer, weaker byssal threads which cannot survive the heavy surf conditions (Ricketts, Calvin, & Hedgpeth, 1968). Harger (1972b) has examined interspecific competition between these two *Mytilus* species and has shown that the byssal thread attachment is weaker in *M. edulis*. He uses this to explain his observations that some small *M. edulis* may occur in semi- or moderately exposed regions but under extreme exposure, such as found on the Monterey Peninsula (Monterey County, California), *M. edulis* is entirely absent (Harger, 1972b). *M. edulis* also occurs along the west coast of South America. I have noted its occurrence from Mehuin, Chile (39°23'S:73°14'W) south to Canal Beagle, Tierra del Fuego, Argentina (54°50'S:68°12'W) although Soot-Ryen (1955) describes its distribution from Valparaiso, Chile (approx. 33°00'S:71°35'W) to the Strait of Magellan (approx. 53°37'S:70°55'W).

In the relevant literature on the extremely exposed coast of Washington, Rigg & Miller (1949), Paine (1966, 1974), and Dayton (1971) do not mention *M. edulis* as a significant species and Kozloff (1973) states that it is not often observed on the exposed outer coast.

In short, *M. edulis* has been classically considered a rather protected water species in the Western Hemisphere whose contribution to the community is relatively insignificant on exposed coastlines. The purpose of this paper is to present new evidence which demonstrates a much broader distribution and a greater contribution to exposed rocky coast communities.

PRESENT DISTRIBUTION OF M. EDULIS

HIGH-INTERTIDAL BAND:

On the exposed outer coast of Washington, M. edulis L. usually occupies a continuous distinct band in the upper intertidal; the lower part of this band tends to integrate slightly with the upper limits of the broader M. californianus Conrad zone. A few M. californianus individuals may be found at or near the upper margin of the M. edulis zone, but these are often associated with some physical discontinuity in the rock surface which affords them greater protection from desiccation. Fig. 6 shows a diagrammatic representation of a rocky intertidal from Tatoosh Island (48°24'N: 124°44'W) showing the position of the M. edulis zone relative to that of M. californianus. In this upper zone M. edulis occurs either on rock, Balanus spp., or commonly in tufts of the red alga Endocladia muricata from +10.6 ft (3.2 m) above M.L.L.W.[2] down to the upper limit of the Mytilus californianus zone at +9.6 ft (+2.9 m) above M.L.L.W. This results in an average zone of 1.0 ft (0.3 m) in vertical height. Scattered individuals of M. edulis are also found in tide pools as high as +12.0 ft (+3.7 m).

At Cattle Point, San Juan Island, Washington, a more protected region, M. edulis co-occurs with M. californianus in a scattered distribution. Here it generally ranges from +5.0 to +6.0 ft (+1.5 to

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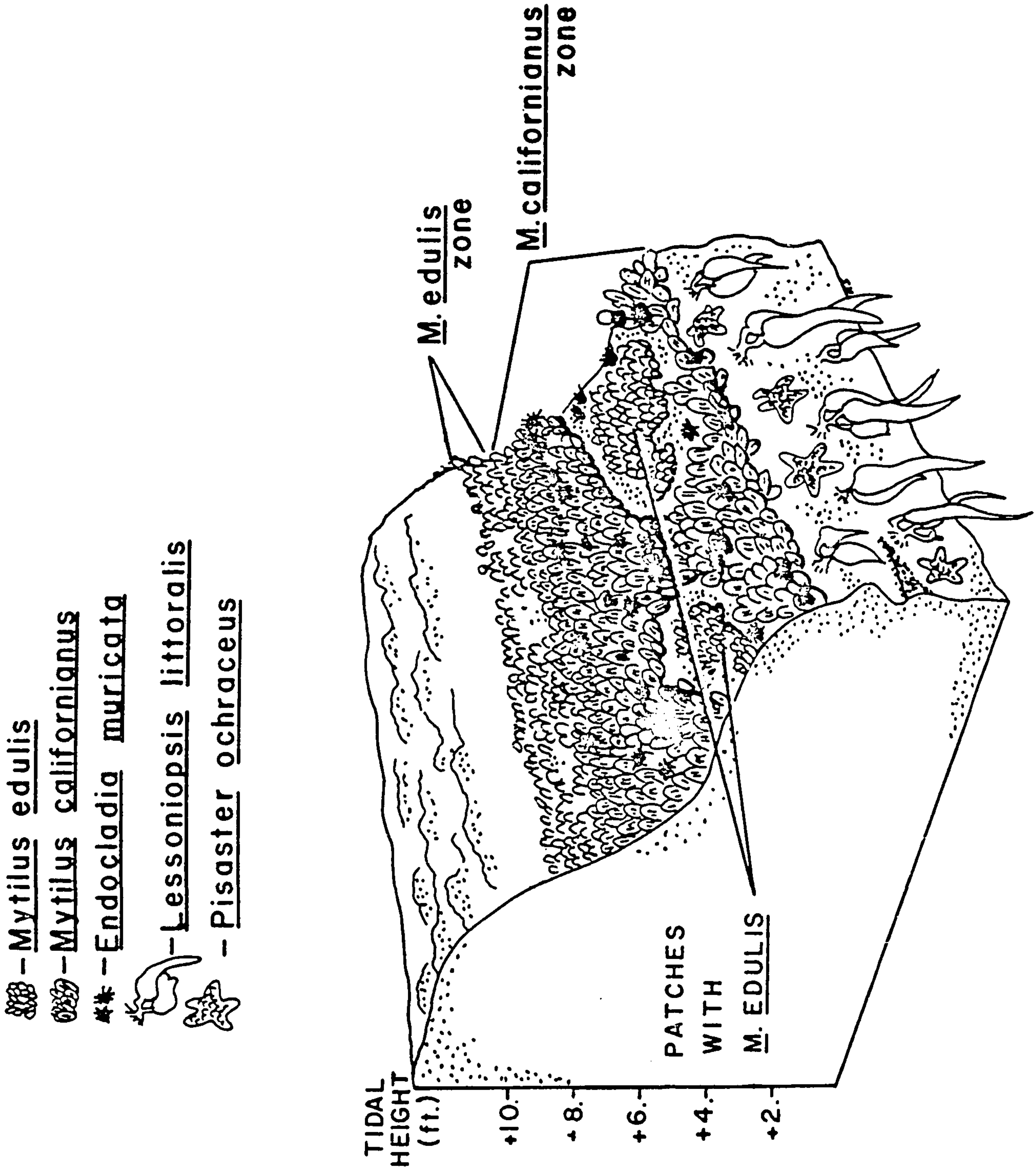
[2] Measurements were taken with a Craftsman 3-C surveyor's transit and no less than eight independent sightings were taken for the interface of each zone. Absolute tidal heights were estimated from the lower-low water levels on each sample date, using the NOAA Tide Tables (Anonymous, 1972-1976). Tidal heights are given in feet to correspond to these Tables. M.L.L.W. (mean low low water) is defined as zero tidal datum.

Fig. 6. Diagrammatic representation of a rocky intertidal from Tatoosh Island, Washington.


– Mytilus edulis
– Mytilus californianus
– Endocladia muricata
– Lessoniopsis littoralis
– Pisaster ochraceus
M. edulis zone
M. californianus zone
TIDAL HEIGHT (ft.)
+10
+8
+6
+4
+2
PATCHES WITH M. EDULIS

1.8 m) tidal height, but it is also found in high, often sun-heated, tide pools up to +8.0 ft (+2.4 m) never occupied by *M. californianus* (pers. obs.).

IN PATCHES WITHIN *M. CALIFORNIANUS* BEDS:

On Tatoosh Island, the *M. californianus* zone extends downward from +9.6 ft (+2.9 m) to a lower limit of +4.3 ft (+1.3 m) resulting in a zone 5.3 ft (1.6 m) in vertical height. By the action of logs, waves, and *Pisaster*, the continuous (often multilayered) carpet of *Mytilus californianus* is disrupted (Paine, 1966, 1974; Dayton, 1971) and various sized patches of open space are formed in this matrix (Levin & Paine, 1974). Although I have only rarely found *M. edulis* in the matrix of the *M. californianus* bed, it does occur quite frequently in this zone. There are two mechanisms that favor this. First, it settles quickly and abundantly in patches within the *M. californianus* zone, either attaching itself directly to rock, in crevices between the plates of *Balanus* spp., on any filamentous substrata within these patches such as *Endocladia muricata* (Postels & Ruprect) J. Agardh, *Gigartina papillata* (C. Agardh) J. Agardh, *Microcladia* sp., or on coralline algae such as *Corallina vancouveriensis* Yendo, *Bossiella plumosa* (Manza) Silva, or *Serraticardia macmillani* (Yendo) Silva. Secondly, it may settle on any substratum which has been recently disturbed, i.e., which has been cleared of its dominant species. In these patches, it tends to grow to reproductive size quickly, often occupying up to 75 to 80% of the available primary or secondary space[3] and in the sense of Pianka (1970) tends to exhibit r-strategist characteristics.

HIGH TO MID-INTERTIDAL IN ENDOCLADIA TUFTS:

As Mytilus californianus becomes older and more eroded, its valves may become encrusted with sponges, ectoprocts, barnacles, and algae. One of the more common epibionts is Endocladia muricata which, in turn, affords an excellent substratum for the settlement of many intertidal species including M. edulis (Bayne, 1964; Glynn, 1965). In such a filamentous substratum, M. edulis is protected from desiccation and predation mostly from shore birds (pers. obs.), two muricid gastropods, Thais canaliculata and T. emarginata (Paris, 1960), and two sea stars, Pisaster ochraceus and Leptasterias hexactis (Menge, 1972a, b; Menge & Menge, 1974). Table I gives the abundance of Mytilus edulis in Endocladia tufts at different tidal heights at Tatoosh Island in 1975. M. edulis seems to recruit better or survive better at lower tidal heights. The reason may be a matter of an increased time of immersion, allowing a greater time for recruitment at lower tidal heights but this has not been tested experimentally.

LOWER INTERTIDAL AND SUBTIDAL:

Below the level of dense M. californianus beds, predation by the sea star Pisaster is more intense and Mytilus edulis is found in any

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[3] Primary space is defined here as the rock substratum. Secondary space is defined as the map area as viewed from above.

Table I. Average number of *M. edulis* per *Endocladia* tuft of 5 cm. diam. (±S.E.): *Endocladia* tufts in 10 random 0.10 m^2 quadrats in parentheses and underlined.

	tidal height (ft)	29.iii.75	10.vi.75	13.vii.75	8.viii.75
High	+10.5	0.00(0) (60)	no data	0.00(0) (89)	0.02(0.16) (41)
Mid	+ 8.0	2.57(5.81) (49)	1.81(3.41) (37)	2.00(3.55) (44)	1.51(3.00) (41)
Low	+ 6.0	4.60(7.46) (30)	4.11(5.06) (27)	7.58(10.66) (43)	5.27(4.67) (11)

space or crevice which will provide it with a refuge. Algal substrata which meet this requirement range from the aforementioned coralline and filamentous algae which occur in patches in the *M. californianus* matrix, to large kelp species which often have convoluted and/or multiple holdfasts or stipes such as *Lessoniopsis littoralis* (Tilden) Reinke and *Pterygophora californica* Ruprect. *Mytilus edulis* is consistently found hidden within the holdfasts or stipe regions to the limit of the kelp's subtidal range (-10 m). Other sufficiently protective substrata include the intricately branched hydroid *Aglaophenia* spp., and the 'hairy' ectoproct *Flustrella corniculata* Smith. Here, the abundance of *Mytilus edulis* is proportional to the size, intricacy, and clumped nature of these substrata. Generally, the greater the amount of minute crevice space the larger the number of *M. edulis* (Table II).

Table II. Occurrence of *M. edulis* on various substrata.

Substratum type	Size (height) of substratum (cm)	Average no. of *M. edulis* per unit substratum	Size range of *M. edulis* (mm)
Coralline algae			
Serraticardia macmillani	3-5	3	2-6
Corallina vancouveriensis	4-5	10	1-8
Filamentous red algae			
Microcladia borealis	4-5	15	1-9
Endocladia muricata	4-5	(see Table I)	1-15
Brown algae			
Lessoniopsis littoralis (on stipe and holdfast)	130-165	105	1-25
Pterygophora californica (in holdfast)	30-50	25	1-21
Ectoprocts			
Flustrella corniculata	10-12	42	1-9
Hydroids			
Aglaophenia spp.	5-6	4	1-4
Abietinaria spp.	3-4	10	1-11

SIZE

Because *M. edulis* ccours over such a broad tidal range, different individuals within a population are exposed to completely different environmental factors, both physical and biological. The single most important factor in determining potential size in *M. edulis* is the abundance of food, which is ultimately controlled by the total immersion time, which in turn is a direct function of intertidal height.

The work of Field (1922) and Baird (1966) on *M. edulis*, and Harger (1970a) on both *M. edulis* and *M. californianus* have shown conclusively that mussels grown at successively higher tidal heights have decreased growth rates and attain smaller ultimate sizes than those lower in the intertidal zone. The average size of the 10 largest *M. edulis* and *M. californianus* from several tidal heights at Tatoosh Island are given in Table III. In the intertidal they show the same size trend with tidal height as does *M. californianus*, with the size inversely proportional to tidal height (Coe & Fox, 1942); subtidal individuals tend to be considerably smaller, probably due to predation by *Pisaster ochraceus* Brandt or other predators. As soon as the mussels get too large to fit into their crevice refuges, they must crawl out and are subsequently eaten. Where there is a lack of predation and a constant, rich rood supply (such as is the case under the U.S.C.G. floating dock at Bodega Bay, Calif.) *M. edulis* may often reach a maximum length of approx. 140 mm (J. Standing, pers. comm.).

Table III. Average size (±S.E.) of 10 largest *M. edulis* and *M. californianus* at different tidal heights; sample area, 1 m^2.

	Tidal height (ft)	*M. edulis* Size (mm)	*M. californianus* Size (mm)
High	+ 10.5	19.50 (3.69) (in *M. edulis* zone)	-
Mid	+ 9.5	-	65.40 (3.30)
	+ 8.5	28.28 (2.78) (in patches in *M. californianus* zone)	-
Low	+ 7.5	-	103.60 (9.50)
	+ 6.5	40.37 (10.26) (in patches in *M. californianus* zone)	-
	+ 4.5	-	171.80 (20.50)
Low intertidal to subtidal	+ 4.5 to - 30.0	21.30 (2.91) (on holdfasts and stipes of kelp)	-

FACTORS CONTROLLING THE DISTRIBUTION OF M. EDULIS ON THE WASHINGTON COAST

SPAWNING AND SETTLEMENT CHARACTERISTICS:

Much of the distribution of M. edulis, before the effects of competition and predation are taken into account, may be explained by its settlement characteristics. It has long been known that M. edulis settles profusely on both biological and artificial filamentous substrata (reviewed by Bayne, 1964; Seed, 1969a, 1976). In British waters. M. edulis settles first on filamentous substrata and when the plantigrades attain a size large enough to compete successfully with adults, they move secondarily into established mussel beds (Bayne, 1964): information on this is lacking for the American coasts.

Previous work in California (Graham & Gay, 1945; Reish, 1964) has indicated a late winter to early spring settlement for M. edulis. On the Washington coast, settlement generally occurs in late winter either sparsely on filamentous substrata or other intricately arranged material which afford some protection from predation, or massively on newly available rocky substrata.

A winter settlement period may be advantageous to M. edulis for several reasons. First, because of severe storms, the season of greatest patch formation in the M. californianus bed matrix is during the winter (R.T. Paine, pers. comm.), and this would enable M. edulis quickly to occupy this newly available primary space after a relatively short larval life. Secondly, winter is a time of lower distribution and decreased feeding activity for many of the predators of M. edulis such as *Pisaster* (Mauzey, 1966; Paine, 1969b) and *Thais* spp. (Emlen, 1966; Feare, 1970) and settlement during this period would allow maximum time for growth to reproductive size before the onslaught of heavy predation during the summer months. Paine (pers. comm.) has already noted these phenomena for many other patch-occupying species and here I simply add *Mytilus edulis* to the list.

A possible cue which *M. edulis* may use to initiate spawning (and, therefore, subsequent settlement) is the extremely rough physical pounding experienced by wave action during a severe winter storm. This is also supported by data on the artificial induction of spawning in the laboratory. Successful methods of inducing spawning often involve rough physical treatment of the entire mussel, scraping of the shell, or pulling of the byssal threads (Field, 1922; Bouxin, 1956; Loosanoff & Davis, 1963; Wilson & Hodgkin, 1967; Hrs-Brenko & Calabrese, 1969; Ahmed & Sparks, 1970; Seed, 1976). *M. edulis* seems, therefore, to spawn at a time which is best for maximizing settlement opportunities and/or maximizing growth before being preyed upon.

This pattern of winter spawning and settlement appears to be in sharp contrast to that of *M. californianus* which maintains a relatively high, constant gonad size throughout the year without any major period when it 'spawns out' completely as does *M. edulis*. In addition, preliminary observations indicate that *M. californianus* larvae usually settle continuously on byssal threads of their own species in adult beds to give a relatively continuous size-frequency distribution for small individuals beginning often at 1-2 mm. In contrast, *M. edulis* show a continual progression in size of specific age classes with time (see Chapter 4).

PHYSIOLOGICAL STRESS:

The growth rates at higher tidal heights and the upper limit of M. edulis are controlled to a large degree by limits of physiological tolerance (Baird & Drinnan, 1957; Baird, 1966), especially to temperature and desiccation.

At Tatoosh Island there is a wide range of exposures to different intensities of sunlight and wave action. Strawberry Island is a part of Tatoosh Island separated at high tide (Paine and Leigh, in prep.) and there, at a site with southerly exposure, the upper limit of M. edulis is +10.6 ft (+3.2 m). During extremely hot days in the summer, individuals at the upper edge die and hundreds of thousands of mussels are found gaping, still with their viscera intact. This easily accessible food resource is utilized by the glaucous-winged gulls (Laurus glaucescens Naumann) nesting on the island, and subsequently fed to nestlings. This massive summer mortality occurred in the three consecutive summers, 1974-1976. Fig. 7 shows the relative mortality of Mytilus edulis measured along a line down from the upper edge of the mussel bed immediately after a series of hot days in 1975.

At a somewhat more protected location nearby (in a wide channel with a westerly exposure) this control of the upper limit of M. edulis, by summer mortality is supported by five years of measurements by R.T. Paine (pers. comm.) (Fig. 8). In general, there is a distinct

Fig. 7. Percentage dead Mytilus edulis measured along a line down from the upper edge of the mussel bed showing the effect of desiccation (10.vi.75). Numbers on graph refer to total number of mussels surveyed at each point.

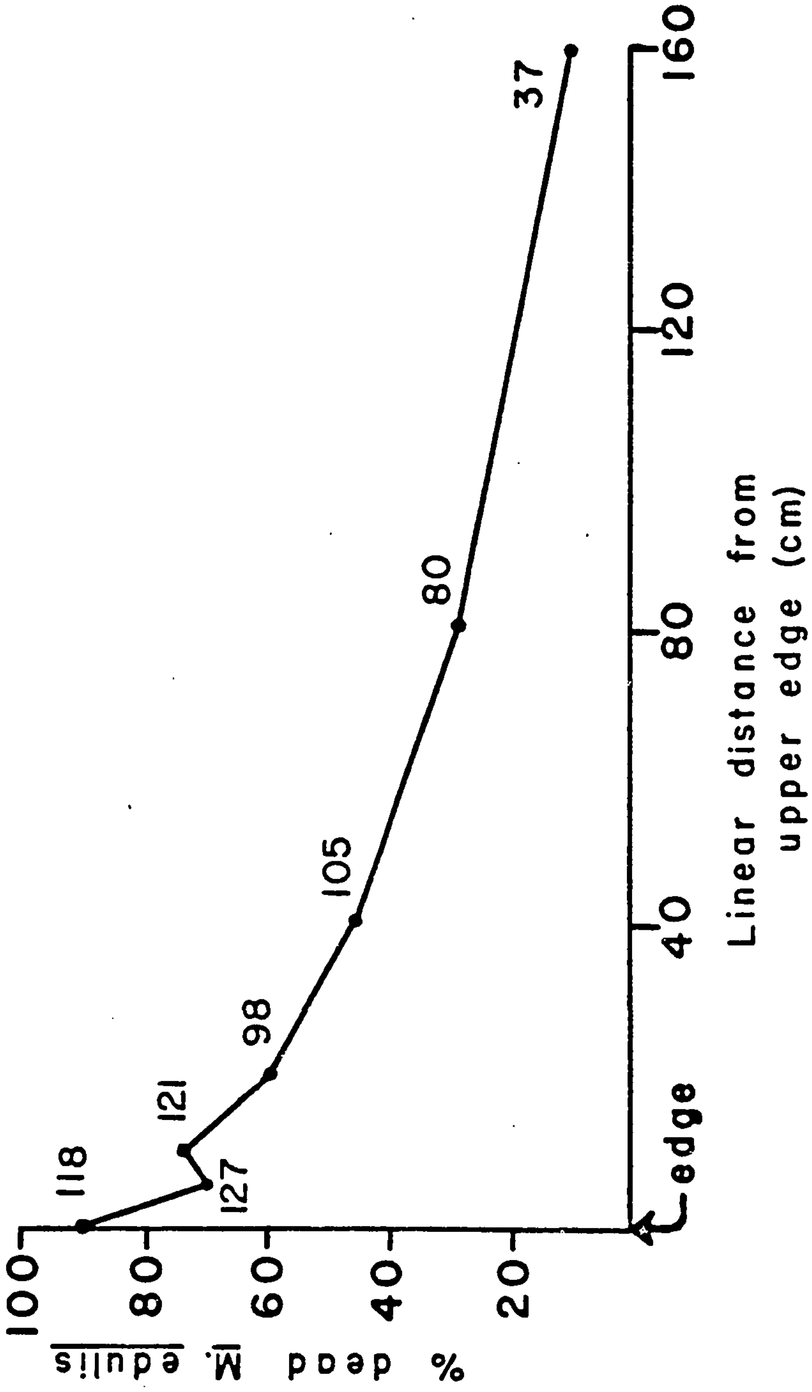
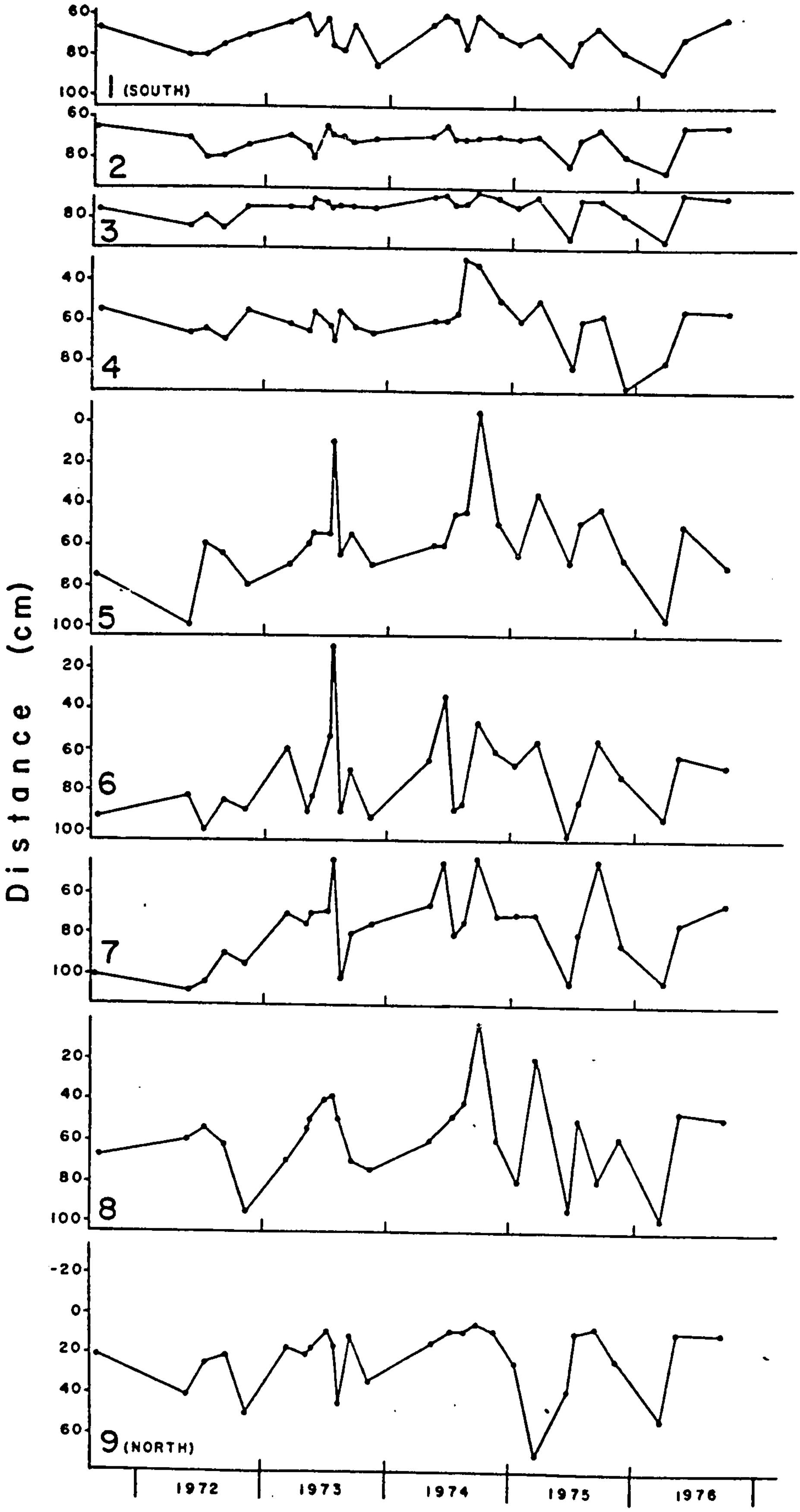

% dead M. edulis
100
80
60
40
20
edge
40
80
120
160
Linear distance from upper edge (cm)
118
127
121
98
105
80
37

Fig. 8. Absolute distances from permanent markers (Nos. 1-9), approx. 3 m apart, along a rocky shore at Tatoosh Island, Washington to the upper edge of the *Mytilus edulis* bed to show seasonal fluctuation in the upper edge of the bed: A rise in the graph indicates a rise in the position of the upper edge of the bed. The channel runs in a north-south direction with marker No. 1 at the southern end.


Distance (cm)
1 (SOUTH)
2
3
4
5
6
7
8
9 (NORTH)
60
80
100
40
0
20
-20
1972
1973
1974
1975
1976

decline in the position of the upper edge at some variable time during each summer, with a subsequent increase during late winter or early spring months. Since it may take one to several months for the dead shells to be washed away because most are bound securely into a matrix by the byssal threads of both live and recently dead mussels, there may be a lag before the decline of the upper edge of the _M. edulis_ populations becomes evident. Fig. 8 also shows that the northerly populations fluctuate more widely than those at the southern end of the channel. This is due to a more gentle slope at the northern as compared with the southern end, resulting in a greater linear distance for the same absolute tidal height difference. Had the distances been standardized to absolute tidal heights, the variability would probably be the same for all nine locations. The linear distance is used so that fluctuations in the upper limits of these _M. edulis_ populations may be directly compared with those of the upper limits of the _M. californianus_ populations of Paine (1974, his Table 1) which were measured from the same markers.

COMPETITION AND PREDATION:

A majority of the intertidal zone from +4.3 to +9.6 ft (+1.3 to +2.9 m) on the exposed rocky coast of Washington is occupied by _M. californianus_. In this zone, where _M. californianus_ is dominant, _M. edulis_ is generally excluded, but when _M. californianus_ is removed by physical or biological factors and patches are formed, _M. edulis_ has an opportunity to colonize this available primary space. This only occurs if the diameter of the patch is greater than ∿40 cm;

otherwise, the grazing action of limpets, chitons, and an opisthobranch (Onchidella borealis Dall) associated with the Mytilus californianus matrix will remove all settling plantigrades and/or filamentous algae on which M. edulis larvae may settle. 20 cm is the approximate limit of movement of such grazers from each edge of a M. californianus bed which results in a distinct 'browse zone' in large patches (see Figs. 6 and 9). After the formation of a large patch (i.e., >40 cm diameter) M. edulis colonizes and grows quickly and may soon occupy as much as 75-80% of the interior of the patch within six months to one year depending on the season of patch formation.

After colonization and domination of the primary and/or secondary space by M. edulis, predation may occur by the sea stars Pisaster ochraceus or Leptasterias hexactis, by sea birds and shorebirds such as scoters, wandering tattlers, surf birds and oyster catchers, or by predatory gastropods such as Thais spp. Thais canaliculata and T. emarginata migrate into the area, feeding and laying egg capsules at the site of this rich, easily accessible food resource. The two Thais species selectively prey upon M. edulis which has a thinner, weaker shell than M. californianus (Harger, 1972b) even though many individuals of the latter species may be present, having rolled in from other areas (Paine, 1974). Table IV shows the percentage of empty shells of each species of Mytilus found drilled in two large natural patches at Tatoosh Island. Once this selective predation has eliminated M. edulis from large patches, it is then slowly re-colonized by M. californianus by three alternative methods: 1) adult M.

Fig. 9. Natural patch in Mytilus californianus bed showing a distinct browse zone (approx. 20 cm) and macroalgae (Alaria) growing in the central area of the patch: M. edulis (not evident in the Fig.) have also settled and occupy primary and secondary space under the cover of macroalgae.

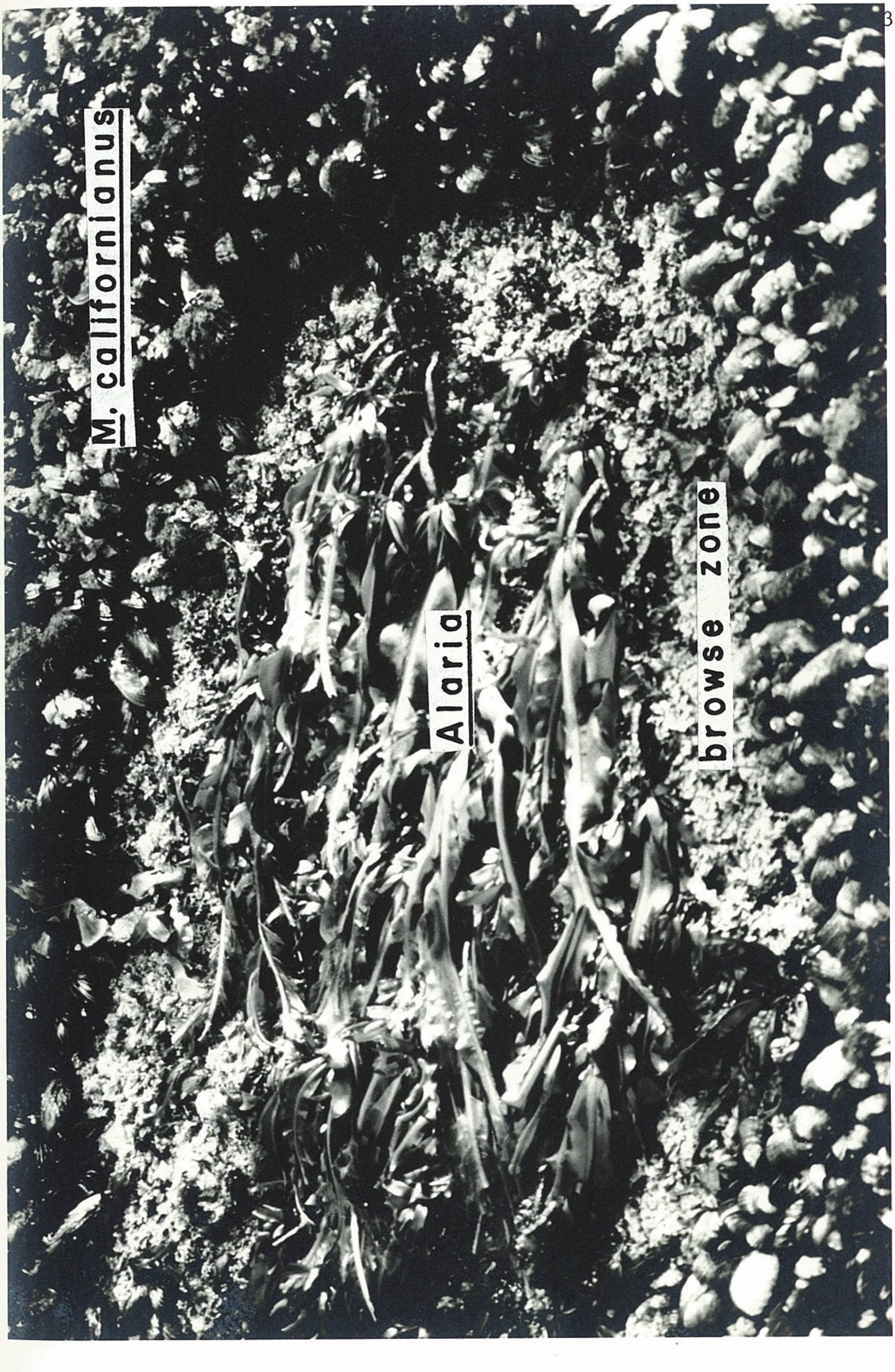

M. californianus
Alaria
browse zone

Table IV. Average no. animals per 0.10 m^2 from two natural patches in the mid-intertidal zone of Tatoosh Island.

	Mytilus edulis			*Mytilus californianus*		
	Average no. live	Average no. empty shells	% drilled	Average no. live	Average no. empty shells	% drilled
T/4NP I						
26.xi. 74	223	16	81	7	0	-
28.ii. 75	151	10	90	0	0	-
10.vi. 75	173	3	100	7	0	-
13.vii. 75	137	8	63	9	0	-
8.viii.75	186	0	-	24	0	-
4.ix. 75	43	0	-	20	0	-
9.viii.76	no data	2	90	no data	1	0
T/4NP II						
10.vi. 75	727	25	64	2	0	-
13.vii. 75	677	24	100	2	0	-
8.viii.75	798	13	82	24	1	0
4.ix. 75	770	29	100	9	1	100
9.viii.76	no data	6	84	no data	0	-

californianus may roll in from other areas and re-attach themselves; 2) juveniles may colonize by settling on the byssal threads of their own adults already in the patch; and 3) juveniles may occassionally settle on filamentous algae (e.g., *Endocladia*) in patches.

At Torch Bay, a very exposed rocky coast in Alaska (58°20'N: 136°48'W), *M. edulis* is the major occupier of space in the upper intertidal and its upper limit is again almost certainly determined by physiological tolerance limits. In contrast, however, to the Washington coast, *M. californianus* is unable to occupy any major primary space and does not, therefore, compete with *M. edulis*. Here, *M. californianus* appears to be controlled by freezing rather than by heat or desiccation stress. Its distribution is restricted to tide pools and subtidal regions (pers. obs.). On 21 March 1974, J.F. Quinn (pers. comm.) observed the death of all *M. californianus* (39 animals) whose shells were exposed more than 2 cm out of water at the brim of a tide pool; all viscera were intact and frozen, and yet there appeared to be no mortality among hundreds of other individuals which were completely submerged.

In this Alaskan habitat, the lower limit of *M. edulis* seems to be determined mainly by heavy predation from a variety of sources, the most significant of which are *Evasterias troschelii* Stimpson, *Pycnopodia helianthoides* Brandt, *Pisaster ochraceus* and four species of *Thais*, *T. canaliculata* Duclos, *T. emarginata* Deshayes, *T. lamellosa* Gmelin, and *T. lima* Gmelin. In September, 1976, I observed a clear lower limit of live *Mytilus edulis*, below which only dead shells were found along with high numbers of *Thais* spp. The average percentage of drilled shells in this lower region ranged from 60.5% at more protected sites to 94.5% at more exposed sites in Torch Bay. Such a predator-controlled lower limit, is comparable with that described by Paine (1974) for Pisaster preying on Mytilus californianus in Washington.

DISCUSSION

M. edulis, a species not previously noted on the very exposed west coast of North America, is clearly an important component of the intertidal community. These data are particularly relevant to the field guide and taxonomic keys of Kozloff (1973, 1974, respectively) which are used by lay as well as scientific persons and to the work of Paine (1966, 1974), Harger (1968, 1970c, 1972a), and Dayton (1971). Paine describes the upper limit of M. californianus, and states that its upper extent is represented by a few small, thick shelled, weathered individuals; these are almost certainly largely M. edulis and his small (≤1.50 cm) M. californianus (Paine, 1974, his Table IV) are almost certainly a mixture of the two Mytilus species. It is often impossible to distinguish conclusively small (≤1.0 cm) Mytilus spp. on the basis of shell morphology. Furthermore, the mussels which he describes as existing above the top of the band as scattered small individuals occupying "safe sites" are again almost certainly primarily M. edulis.

In general, M. edulis is quite tolerant of a wide range of environmental conditions (Seed, 1969b). On the Washington coast it has a broader distribution than does M. californianus and is able to survive slightly more extreme environmental stresses. Although I have not found any populations of M. edulis below 10 m it most likely has the potential to occupy regions as deep as M. californianus (30 m depth; Paine, 1976b). It survives higher in the intertidal zone than M. californianus, occupying sites with higher temperature and desiccation stresses on the exposed outer coast of Washington as well as the more protected coasts of the San Juan Archipelago. Harger (1968, 1970a, b, c, 1972a, b, c) has given a detailed account of competition between *M. edulis* and *M. californianus*, mostly in protected bays and often in mixed clumps. Two important phenomena which determine the outcome of competition in protected bays as described by Harger, namely, the crawling behavior of *M. edulis* and the crushing ability of *M. californianus*, appear not to be as important on the exposed coast of Washington. At Tatoosh Island, where the zones of the two *Mytilus* species overlap in the high intertidal, *M. edulis* does not show the typical crawling behavior, possibly because of severe wave action, nor does it appear to be crushed by its congener which, at that tidal height, is about the same size.

As noted earlier, on the exposed Washington coast where *M. edulis* has invaded patches in the *M. californianus* zone, it grows quickly but is selectively removed by both *Thais emarginata* and *T. canaliculata*. In California, Harger (1972b) observed that *T. emarginata* selectively preys on *Mytilus edulis* over *M. californianus* in the field, and A.R. Palmer (pers. comm.) has further evidence from laboratory experiments of this preference by *Thais canaliculata*. He found that the percentage predation on *Mytilus edulis* and *M. californianus* offered separately to caged *Thais canaliculata* was 71% and 13%, respectively. Harger (1972b) considered that this preference is not based simply on shell thickness. Perhaps the mechanism for selection is based on the net difference in energy obtained per unit feeding time from preying on *Mytilus edulis* rather than *M. californianus*.

This could be the result of either increased energy or time expended on drilling a thicker shell or lower calorific value obtained from metabolizing *M. californianus* tissue, or both. The energy that *M. edulis* puts into rapid growth and gonad development may be channelled away from protective mechanisms such as producing a thick shell or a predator-deterring chemical. In laboratory experiments, A.R. Palmer (unpubl.) has shown that over one month the average percentage change in weight of *Thais canaliculata* fed *Mytilus edulis* was +17.3±14.62 g (n=23) whereas those fed on *M. californianus* was -2.00±4.59 g (n=20), indicating a significantly lower growth rate on *M. californianus*.

If this selective predation on *M. edulis* by *Thais* spp. or other predators did not occur in the *Mytilus californianus* zone, it is uncertain what the result of interference competition (Miller, 1969) would be when the two *Mytilus* populations physically contacted each other in the mid- to low-intertidal; it is possible that *M. edulis* (with a thinner and usually smaller shell) may be crushed by its congener as Harger (1972b) has shown in mixed clumps of the two species.

In the low-intertidal and subtidal *M. edulis* is again preyed on heavily, mainly by sea stars or fish rather than by gastropods or shore birds; the lower limit of *M. edulis* populations is, therefore, determined primarily by two factors, competition from *M. californianus* and predation by gastropods, fish, and sea stars.

CHAPTER 3

THE ROLE OF DISTURBANCE IN THE EVOLUTION OF DIVERGENT LIFE HISTORY STRATEGIES IN THE INTERTIDAL MUSSELS *MYTILUS EDULIS* AND *MYTILUS CALIFORNIANUS*

INTRODUCTION

Since the seminal works of Fisher (1930) and Cole (1954) on reproductive strategies, numerous authors have attempted to define and analyse various adaptive characteristics of populations which seem to maximize fitness through natural selection (Williams, 1966a, b; Hairston *et al*., 1970; Tinkle *et al*., 1970; Gadgil & Bossert, 1970; Wilbur *et al*., 1974; Hirshfield & Tinkle, 1975; reviews by Giesel, 1976; Stearns, 1976, 1977). The features which have received the most attention are fecundity, longevity, age at first reproduction, size, growth rates, mode of reproduction, and niche status (or ecological role). Various approaches have been used to form generalized predictions and simplify the theory of life history strategies. Some authors have concentrated on only one or a few specific aspects of the aforementioned life history parameters (Tinkle, 1969; Murdoch, 1966; Ricklefs, 1977; Snell & King, 1977; Ballinger, 1977), while others have tried a more synthetic approach. Williams (1966a, b), Gadgil & Bossert (1970), and Schaffer (1974) emphasized the theory of a schedule of energy allocation into major categories of maintenance, growth, and reproduction (originally introduced by Cole, 1954), whereas Wilbur *et al*. (1974) considered environmental predictability, niche position, and availability of resources of major importance in specifying differences between various adaptive strategies.

Some have focused on a comparison of the same or closely related species (of the same genera) living in different hatitats (Alm, 1959; Tilley, 1973; McNaughton, 1975). Others have compared unrelated species (of different genera) living in the same habitats (Randolph, 1973). But none of these carefully considers species which are closely related, are living in the same habitats, and are still competing for a common requisite, thereby identifying the mechanism for effective ecological divergence.

The most inclusive attempt to specify life history strategies was forwarded by MacArthur & Wilson (1967). This body of theory (which centers on the concept of "r" and "K" selection) has been further developed, tested, and finally determined to be of questionable empirical value in describing and predicting differences in life history phenomena (Pianka, 1970, 1972, 1974; King & Anderson, 1971; Roughgarden, 1971; Menge, 1974; McNaughton, 1975; Nichols _et al_., 1976). Although the concept most likely has outgrown its usefulness, the relative positioning of various species along an r-K continuum is still a valuable tool when applied on a comparative basis only (Gadgil & Solbring, 1972).

Another relatively new, but rapidly expanding, literature is developing on the influence of disturbance on the structuring of ecosystems. Various types of disturbance processes have been identified by Harper (1977).[1] Sources of these disturbances include predation (Paine, 1966, 1971, 1974b, 1976a; Paine & Vadas, 1969; Dayton & Hessler, 1972; Dayton, 1975), climatic disasters (Dayton et al., 1970; Loya, 1972), climatic catastrophes (Heinselman, 1973; Henry & Swan, 1974), spatially unpredictable stochastic events such as tree falls (Richards, 1952; Richards & Williamson, 1975), and temporally predictable disasters such as patch formation by wave-driven logs or wave action alone in the rocky intertidal (Dayton, 1971; Levin & Paine, 1974). Recently, analyses of controlled and uncontrolled (i.e., as a result of human intervention) artificial catastrophes have been performed to elucidate mechanisms and effects of disturbance on community organization (Edmondson, 1970; Allen & Forman, 1976; Loya, 1976; Brugam, 1978).

It is becoming increasingly evident that disturbance processes, both stochastic and predictable, may be some of the most influential factors in structuring populations and ecological systems. This chapter demonstrates how disturbance of a resource can influence the reproductive strategies of species competing for that resource. Specifically, it is a comparison of the strategies used by two sympatric, congeneric, intertidal mussels competing for space on the exposed outer coast of Washington State. I will demonstrate how the competitively inferior species has diverged in life history and

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[1] Harper defines disasters as those disturbances which recur frequently enough for there to be reasonable expectation of occurrence within the life cycles of successive generations. Hence organisms may become adapted to such disasters by normal mechanisms of natural selection. A catastrophe, on the other hand, is distinguished by occurring sufficiently rarely that few of its selective consequences are relevant to the fitness of succeeding generations.

reproductive strategies by using disturbance as a cue in order to utilize successfully a limited resource, space. In so doing, my aim is to join two areas of current research which heretofore have remained relatively discreet, the study of life history strategies and the study of how disturbance affects population and community dynamics.

GENERAL ECOLOGY OF THE MYTILUS SPECIES

Mytilus edulis is a relatively small (≤ 10 cm in Washington State), competitively inferior species which occupies a broader global and intertidal range than does its congener. It is almost cosmopolitan in distribution, being abundant in the Northern, Southern, Eastern, and Western Hemispheres (Soot-Ryen, 1955; Seed, 1976). In Washington, it occupies a high intertidal band from 9.6 ft (2.9 m) to 10.6 ft (3.2 m), settles in patches of open space formed in the matrix of M. californianus beds in the mid-intertidal, and in the lower intertidal and subtidal regions colonizes protective refugia such as kelp holdfasts, hydroid and ectoproct colonies and coralline algae (Chapter 2). It has also been found as deep as 10-20 fathoms (18.3-36.6 m) (Soot-Ryen, 1955).

Mytilus californianus is a larger, competitively dominant bivalve restricted to the west coast of North America. Although its range extends from the Aleutian Islands south to Isla Socorro, Mexico (Soot-Ryen, 1955), it only occupies significant areas of intertidal space from British Columbia south. This is where the most intense competition for space with M. edulis occurs. On the Washington coast (in the middle of its range), it occupies a zone from 4.3 ft (1.3 m) to 9.6 ft (2.9 m) above MLLW (Chapter 2), although it can be found as deep as -100 ft (-30 m) (Paine, 1976b).

Harger (1967, 1968, 1970a, b, c, 1972a, b, c) has discussed competitive co-existence between these two Mytilus species along the California coast. His studies showed that they compete for a common resource, solid primary attachment sites on pilings or rocky shores. He demonstrated that behavioral and physiological differences between the two species allow them to apportion the solid intertidal substrata such that, on a global scale, coexistence is accomplished. In those habitats where *M. edulis* is favored by the environmental conditions (i.e., in bays), *M. californianus* would be covered with silt and subsequently smothered. In more exposed environments, Harger felt that the rapid crawling behavior of *M. edulis*, which promotes its survival in bays, leads to its demise because it is washed away from the substrata more easily by waves. However, I have shown (Chapter 2) that both species are quite capable of occupying areas of even the most severe wave action. Although Harger states that competitive elimination of one species by the other is rare in the zone of overlap, he also claims that the smaller, weaker shell of *M. edulis* is crushed by the most substantial shell of its congener.

In Washington, where *M. edulis* occurs in the *M. californianus* zone (usually only in patches of cleared space), it is subject to intense predation by the carnivorous gastropods *Thais canaliculata* and *T. emarginata*, inevitably eliminating it from these temporal refugia (Chapter 2). The definitive experiment, i.e., to remove the source of predation and observe interference competition (sensu Miller, 1969), has not yet been performed.

STUDY AREA AND METHODS

Most of the field work for this study was performed on the exposed outer coast of Washington State either at Shi-Shi ($48^{o}17'$N: $124^{o}41'$W) or at Tatoosh Island ($48^{o}24'$N:$124^{o}44'$W). Other field observations and comparative samples were taken from Torch Bay, Alaska ($58^{o}20'$N:$136^{o}48'$W), an exposed locality, and upper Glacier Bay, Alaska ($58^{o}47'$N:$136^{o}29'$W), a more protected site.

For the determination of reproductive effort in *M. californianus*, samples for gonad analysis were collected from high (9.0 ft, 2.7 m) and low (4.5 ft, 1.4 m) intertidal sites at Tatoosh Island from 1974-1976 at approximately bimonthly intervals. 50-100 intact mussels (representing the entire size range at each site) were collected at each time period and frozen at -20^{o}C until samples were analysed. Length (from umbone to posterior end) was measured to the nearest mm. Gonad and associated mantle tissue (with stored gametic products) was excised and blotted dry; wet weight was measured to the nearest 0.001 g.

Because of the nature of the field work involved, a number of inherent problems arise in the analysis of factors influencing different life history strategies between these mussels. Qualitative and quantitative data on spawning from natural field populations of mussels is nearly impossible to obtain. Therefore, inference from gonad levels was used as the most reasonable indicator of gametic output. Larvae were equally as difficult to follow in terms of their dispersal, early mortality rates, and settlement sites. Data on growth rates, age at potential first reproduction, and mode of reproduction, on the other hand, were directly obtainable from field observations. Life span must again be inferred from growth ring analyses (a poor indicator in this environment) or other means. The life span of low intertidal individuals of *M. edulis* can be observed directly since it is so short (on the order of a few years), but high intertidal individuals could not be aged. Elsewhere, this species may live at least 20 years (Seed, 1969b). Data for the life span estimates of *M. californianus* were obtained from information on recovery rates of small and large regions of mussel beds disrupted during winter storms and from extrapolated growth rate data.

RESULTS

An analysis of the major factors influencing life history strategies is given for the two mussels Mytilus edulis and Mytilus californianus. The following parameters are considered.

1) Size
2) Growth rate
3) Age at first reproduction
4) Life span
5) Mode of reproduction
6) Niche status

Results have been compiled from both existing literature and from new data and field observations presented here.

SIZE:

The size of intertidal mussels depends on many factors, most important of which is intertidal height (Baird & Drinnan, 1957; Baird, 1966). With unlimited food supply, M. edulis may attain a length of 140 mm or more, but on the exposed Washington coast it usually only reaches 40-50 mm even in the lower intertidal (Chapter 2). Although subtidally M. californianus may reach 250 mm (Paine, 1976b), intertidally it is smaller and only attains approx. 200 mm in length.

Shell thickness and durability may also give M. californianus a competitive and/or anti-predatory edge over M. edulis. To test this difference, thirty individuals of each species were collected from the same location at Tatoosh Island. The body tissue was excised and the shells dried in an oven for two hours at 105°C to remove excess water. Shells were then weighed to the nearest 0.001 g. Fig. 10 shows that shells of *M. californianus* are on the average significantly heavier than those of comparable sized *M. edulis*. Analysis of co-variance yields a significant difference at $p < .05$. Harger (1967) reported similar results from California and also showed that *M. edulis* shells tend to be more brittle when the mussels are alive and disintegrate more quickly after death than those of *M. californianus* (Harger, 1972b). These major differences in thickness, strength and durability of the shell may be due to an additional inner prismatic layer of calcite present in the shell of *M. californianus* but not in that of *M. edulis* (Dodd, 1964). This overall superiority of *M. californianus* in terms of size (Table III; Figs. 10 & 11) and strength may be an important factor in its dominance over *M. edulis*, especially if it can crush its congener. However, it may play another important role as an anti-predatory mechanism against drilling gastropods of the genus *Thais*. The preference of *Thais* spp. for *M. edulis* over *M. californianus* has been documented earlier (Harger, 1972b; see also Chapter 2) and will be discussed further under the section Niche Status.

GROWTH RATES:

Growth rates for these two mytilids are dependent both on tidal height and on the amount of available food (Coe & Fox, 1942; Rao, 1953, 1954; Dehnel, 1956), but differ substantially between the two species. While under continual submersion, *M. edulis* has the potential to

Fig. 10. Shell weight versus length for *M. edulis* and *M. californianus* from the high intertidal at Tatoosh Island, Washington.

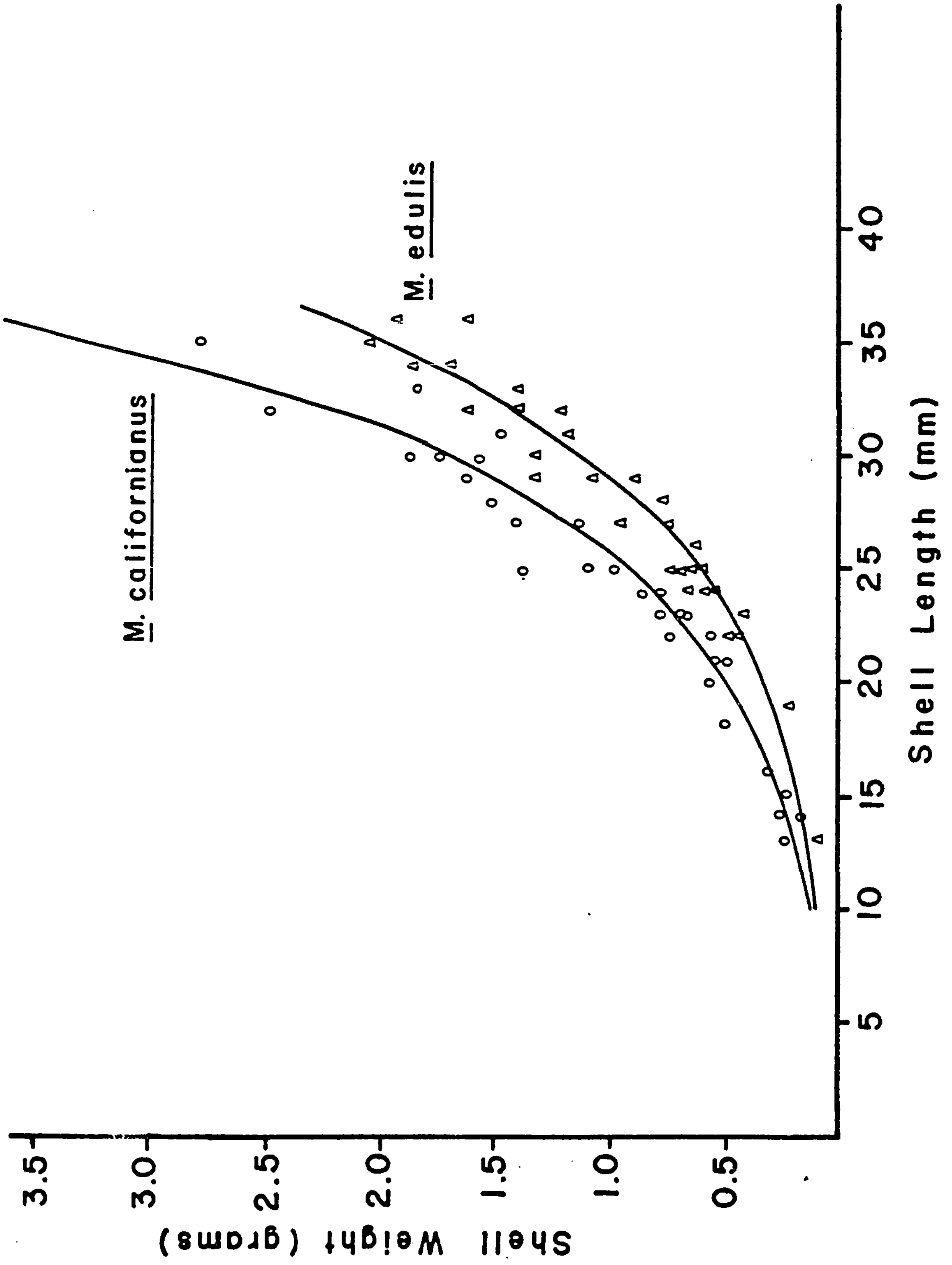
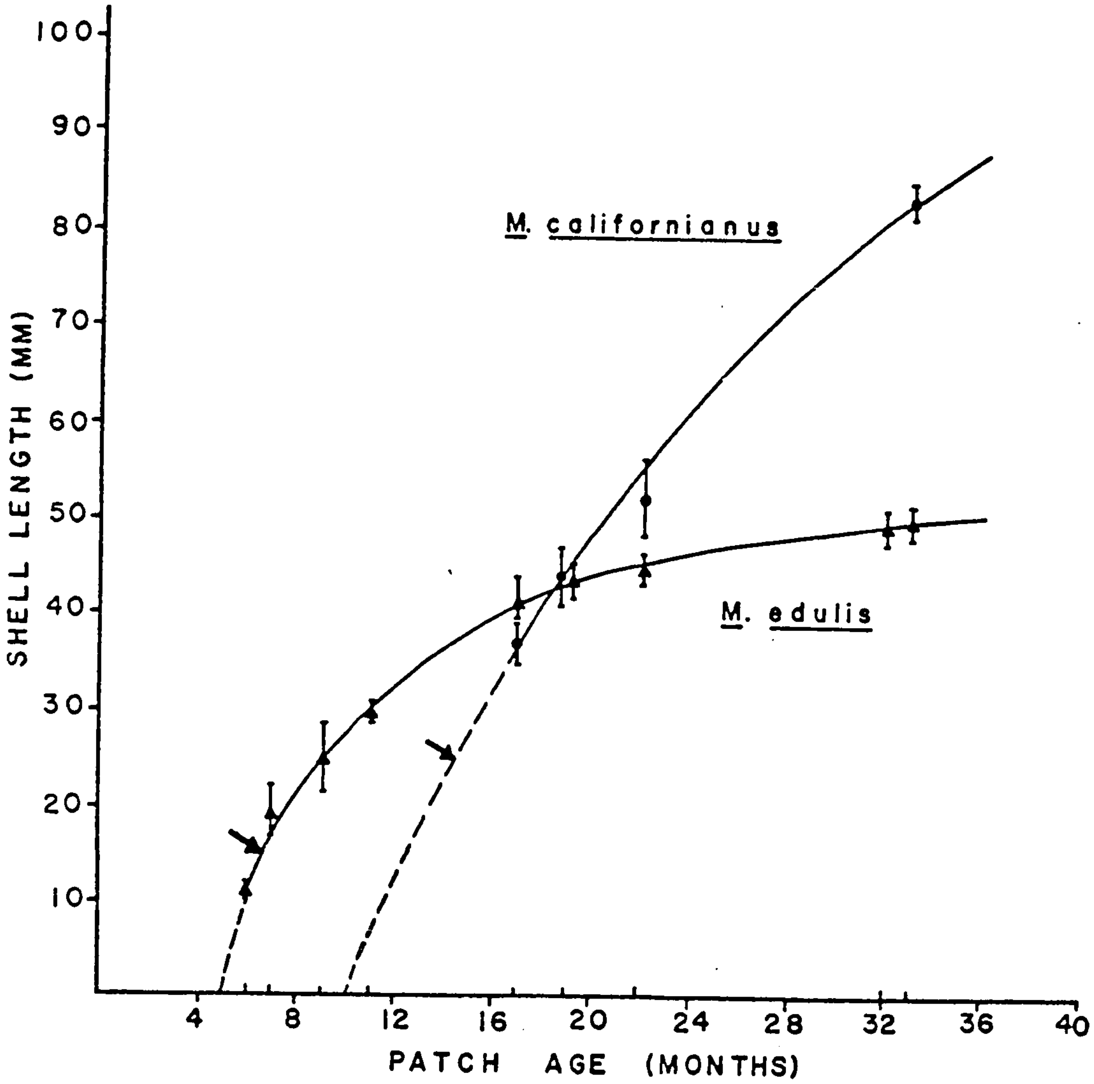

M. californianus
M. edulis
Shell Weight (grams)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Shell Length (mm)
5
10
15
20
25
30
35
40

Fig. 11. Growth rates of *M. edulis* and *M. californianus* in a patch from the mid intertidal on Strawberry Island (Tatoosh), Washington. Dashed lines to the abscissa indicate estimated times of settlement and initial growth in the patch (which was opened naturally in November, 1975 by storm action). Arrows indicate the first potential reproductive maturation time for each species (i.e., first visible storage of gametic products in the mantle tissue).


SHELL LENGTH (MM)
100
90
80
70
60
50
40
30
20
10
PATCH AGE (MONTHS)
4
8
12
16
20
24
28
32
36
40
M. californianus
M. edulis

exceed 80 mm within 9 months (an average growth rate of 9 mm/mo.; Reish, 1964). In the low intertidal at Tatoosh Island, its growth rate is initially rapid (ranging from 8-12 mm/mo.), but then decreases as the length asymptotically approaches 55-60 mm (Fig. 11), agreeing with rates published by Graham & Gay (1945) and Stubbings (1954). At 40 mm, it is surpassed in growth rate and age-specific size by its congener. These findings are consistent with the projected growth curves of Harger (1970a).

The relative growth rates of the two *Mytilus* species in Fig. 11 were taken from an area in the mid-intertidal (+6.0 ft, 1.8 m above MLLW) at Tatoosh Island which was naturally denuded during a storm in November 1975. The dashed lines projected to the abscissa represent estimated times of settlement for both species. No *M. californianus* were identified *in situ* on 10/21/76, for if they were present, they were virtually indistinguishable from *M. edulis* at that size (4-5 mm).

M. californianus usually settles later (in cleared intertidal patches) and grows continuously but more slowly (maximum growth rate 2-5 mm/mo., Coe & Fox, 1942; Dehnel, 1956) than does *M. edulis*, but becomes much larger than its congener within 1-2 years, depending on tidal height. The rate of growth for *M. californianus* in Fig. 11 is initially ca. 5.0 mm/mo., and at the end of 33 months, had declined to ca. 2.0 mm/mo. These figures are consistent with Coe & Fox (1942) who kept *M. californianus* in subtidal cages, but are considerably greater than those of Paine (1976a), who obtained a rate of ca. 1.0 mm/mo. for *M. californianus* at Mukkaw Bay, Washington (at a tidal height of 4.5-5.6 ft, 1.4-1.7 m).

AGE AT FIRST REPRODUCTION:

Fig. 11 also indicates the reproductive maturation times for the two mussel species (indicated by the arrows). For M. edulis, earliest gonad development and gamete storage into the mantle tissue occurs at about 15-20 mm length, which may occur within 1-2 months following settlement. M. californianus lags behind in settlement, growth rate, and reproductive maturity. It may be reproductive at 25-30 mm (but usually isn't until 35-40 mm); this usually takes 4-8 months to develop. Maturation size depends on rate of growth (Seed, 1969a) and therefore may differ with tidal height so that lower populations, with a more rapid growth rate, would be potentially reproductive sooner than higher ones for both species.

LIFE SPAN:

The potential life span of these two species is unknown and absolute aging is often difficult. Even the standard growth-line analysis historically used on bivalve species, which measures differences in the relative proportions of organic material (conchiolin) and calcium carbonate (aragonite or calcite), may not reflect yearly marks and may yield spurious results (Barker, 1970; Craig & Hallam, 1963; Pannella & MacClintock, 1968; Clark, 1974; Lutz, 1976). In calm, predictable environments, growth lines and inner shell lines may be an adequate measure of age, but in harsh, unpredictable environments, "check-lines" may be laid down in response to a wide variety of extrinsic factors including storms, salinity changes, hot-spells, cold-snaps, sexual reproduction, or plankton blooms (Orton, 1926; Dodd, 1963, 1974; Craig & Hallam, 1963; Barker, 1970) or may be abraded beyond recognition (Seed, 1973).

The most important aspects of an organism's life history strategy is its success at contributing gametes and resulting offspring to the gene pool of subsequent generations. Although age at first reproduction is more important, an organism's *actual life span* will reflect the relative potential contribution it can make to future populations, assuming it can continue to reproduce.

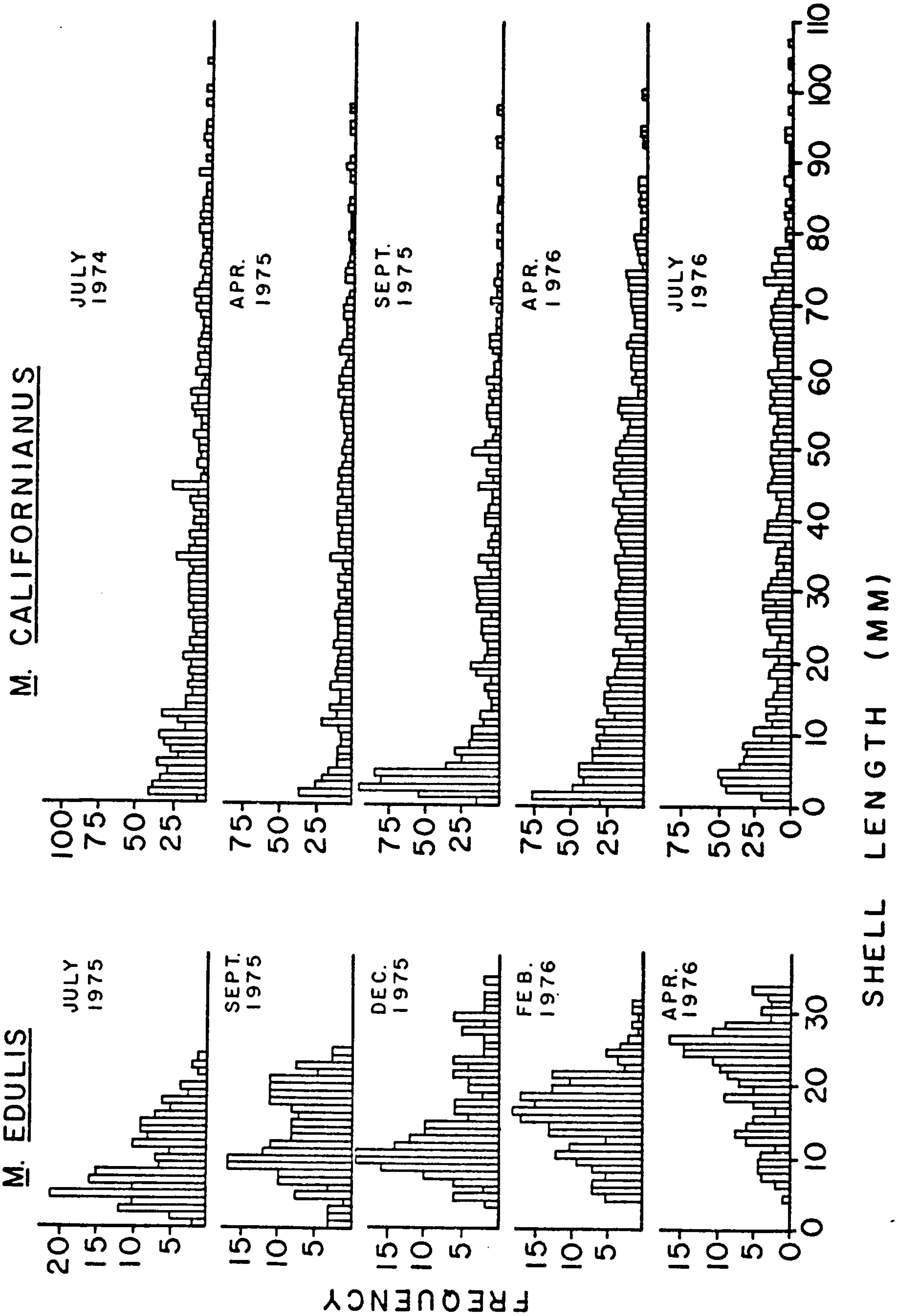
Although precise aging is difficult, some good estimates of actual life span have been made on *M. edulis* based on disturbance rings (which were shown to be laid down on a mostly annual basis). On the east coast of Britain, where there is no other major competitor for intertidal space, Seed (1969b, 1973, 1976) has estimated that *M. edulis* may attain an age of 18-24 years or more. Near the northern extent of *M. edulis*' range, in upper Glacier Bay, Alaska (where *M. californianus* is not a major competitor for space (see Chapter 2)), lengths of *M. edulis* shells in the mid-intertidal reach 100 mm and ring numbers indicate that their age is at least 11 years (pers. obs.). And towards the southern extent of its range, where again *M. californianus* does not compete for space (on the exposed outer coast of southern Chile), intertidally *M. edulis* reaches 100 mm, indicating substantial age. However, in Washington, where *M. edulis* in the mid to low intertidal is more ephemeral and must often wait for gaps in the *M. californianus* cover to colonize, it tends to be a more short-lived species, and may only survive for 1-5 years as a result of predation and competition. Individuals of *M. edulis* in the high intertidal band are undoubtedly older but so far it has been impossible to age these. In any event, high individuals are smaller, mature later, and invest a lower percentage of body tissue into gametes than those lower on the shore, so their reproductive contribution is considerably reduced (see next section: Mode of Reproduction).

The actual life span of *M. californianus* is considerably longer than that of *M. edulis*. *M. californianus* outcompetes its congener in the long run, usually persisting up to 7-20 years minimum (data based on recover rates for disturbed mussel beds and extrapolated growth rate data), very possibly reaching 50-100 years of age in some regions.

MODE OF REPRODUCTION:

Fig. 12 shows a comparison of size-frequency distributions over time for both species. It is clear that for *M. edulis* there is a single size-class growing progressively larger with time, strongly implying a single massive settlement and, very likely, a single massive spawning from which it was derived. *M. californianus* populations instead usually show a continual, rather even size-frequency distribution further implying a slow, but continual, recruitment of individuals over time. These data support other accounts of size-frequency distributions of the two mussel species (for *M. edulis*, Craig & Hallam, 1963; Seed, 1973: for *M. californianus*, Ackermann, 1971), but differ from that of Paine (1976a) who found a bimodal size distribution for the latter species. He suggested that this could be caused by the limited period of establishment of the original matrix

Fig. 12. Changes in size-frequency histograms for *M. edulis* and *M. californianus* over time. Samples were collected destructively for each species, each within a 10 m^2 area. Note different scales on ordinate axes.

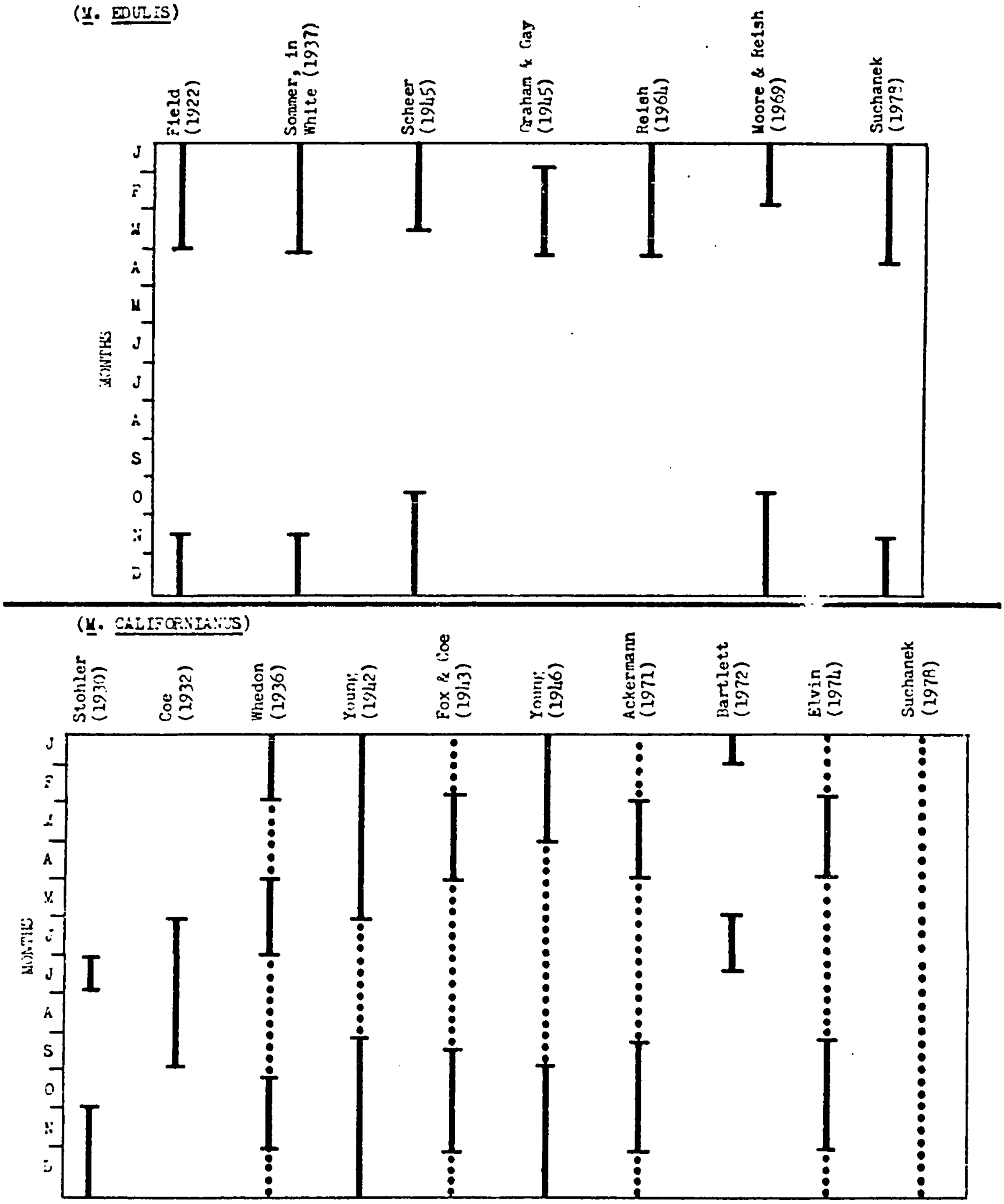

M. EDULIS
JULY 1975
SEPT. 1975
DEC. 1975
FEB. 1976
APR. 1976
20
15
10
5
0
10
20
30
M. CALIFORNIANUS
JULY 1974
APR. 1975
SEPT. 1975
APR. 1976
JULY 1976
100
75
50
25
0
10
20
30
40
50
60
70
80
90
100
110
FREQUENCY
SHELL LENGTH (MM)

mussels and the predatory activities of Leptasterias hexactis acting within the confines of the matrix.

To support further the distinction between spawning characteristics, a review of the literature from West Coast North America dealing directly with gonad development, spawning periods, plankton records, or settlement dates is given in Fig. 13. Planktonic existence for veliger larvae was assumed to be 2-4 weeks (Bayne, 1964; Seed, 1969a, 1976) and the original data for Fig. 13 was adjusted accordingly. That is, for those authors reporting settlement times only, I subtracted 3 weeks from their dates to yield an estimate for spawning dates. From these data it is clear that on the west coast of North America, where M. edulis depends on seasonally available settling sites, it spawns primarily in the winter months. This allows larvae to settle into newly created patches of cleared space in the M. californianus zone in later winter and early spring (Chapter 2). Since Washington represents the middle of M. californianus' range, in 2-4 weeks M. edulis larvae produced here or elsewhere along this coast would land in a location similar in disturbance features to the conditions which characterize Washington.

Since there is a new outflow of surface waters (i.e., above 64 meters depth) from Puget Sound out through the Strait of Juan de Fuca (Barnes & Ebbesmeyer, 1978), it is unlikely that coastally produced larvae would land in the inner waters of Puget Sound. Even the exchange of inner (Puget Sound) waters with coastal (Cape Flattery) waters takes on the order of one to two months duration (reaching the maximum period of larval life for M. edulis). Therefore, even if some

Fig. 13. Review of literature on spawning dates for *M. edulis* and *M. californianus*. Solid lines indicate major spawns. Dotted lines for *M. californianus* indicates sporadic or low level continuous spawning.


(M. EDULIS)
Field (1922)
Sommer, in White (1937)
Scheer (1945)
Graham & Gay (1945)
Reish (1964)
Moore & Reish (1969)
Suchanek (1978)
MONTHS
J F M A M J J A S O N D
(M. CALIFORNIANUS)
Stohler (1930)
Coe (1932)
Whedon (1936)
Young (1942)
Fox & Coe (1943)
Young (1946)
Ackermann (1971)
Bartlett (1972)
Elvin (1974)
Suchanek (1978)
MONTHS
J F M A M J J A S O N D

larvae from the inner Sound region were to travel in this water mass, dispersion would be so great that they would make up an extremely minute contribution to the settling larvae on the coast in any one season (C.A. Barnes, pers. comm.). However, genetically they could mix by a stepping stone method of colonization and further larval dispersal in subsequent years.

In other parts of the world, M. edulis may spawn at any of a variety of times throughout the year (see Seed, 1976 for a comprehensive list). In any one region, investigators have found consistent spawning periods over many years, but these periods differ from region to region, probably influenced more by local selection pressures such as disturbance of the physical environment or predation. Unfortunately, no analysis of spawning dates has been done in the Alaskan habitat, where M. californianus poses no threat to the settling larvae of M. edulis.

M. californianus has the potential to spawn throughout the year. Although localized populations may undergo partial epidemic spawning, especially in the spring and fall, they often will continue to "dribble" gametes the entire year, assured of consistently available settling sites for larvae onto the byssal threads of adults of their own species (Chapter 2).

In order to estimate quantitatively the reproductive status of the population at various times during the yearly cycle, a formula for a GONAD INDEX (G.I.) as a weight of gonad/length ratio has been calculated as follows:

$$\text{GONAD INDEX} = \frac{\text{Gonad Weight (g)}}{\text{Length (mm)}^3} \times 10^6$$

Because the weight of mussel tissue (both somatic and gonadal) increases as a cubic function of the length (Fig. 14), the ratio of gonad weight/length^3 represents an estimate of the proportion of tissue which is invested into reproduction. This ratio is then multiplied by 10^6 to make the resulting values more manageable. The average Gonad Index for the sample in Fig. 14 is 4.99 and is described by the fitted exponential curve of gonad weight, with the formula $y = 0.05e^{0.05x}$ (coefficient of determination, $r^2 = 0.89$).

As seen from the labeled examples in the figure, generally those values above the curve have a larger G.I. than the average, while those below are smaller. Therefore, each sample could be represented by an entire family of exponential curves of representative gonad weight versus size, depending on the relative state of development of the gonadal tissue. Final G.I. values for each sample date consist of an average for all sizes. A check on the accuracy of this Gonad Index as an estimator of the proportion of body tissue invested into reproduction was done on the data in Fig. 14. The comparison is presented graphically in Fig. 15 and shows a close relationship between the calculated G.I. and the real percentage of gonad with a correlation coefficient of $r = 0.86$. Some caution is in order when using only gonad and mantle weights as an indicator of gamete production, for carbohydrate storage products such as glycogen have been shown to constitute, or be transformed from, considerable portions of this tissue during periods of low food availability in *M. edulis*

Fig. 14. Relationship between total weight and gonad weight versus shell length for *M. californianus*. The numbers on the Gonad Weight curve represent calculated *Gonad Index* values using the formula derived in the text.

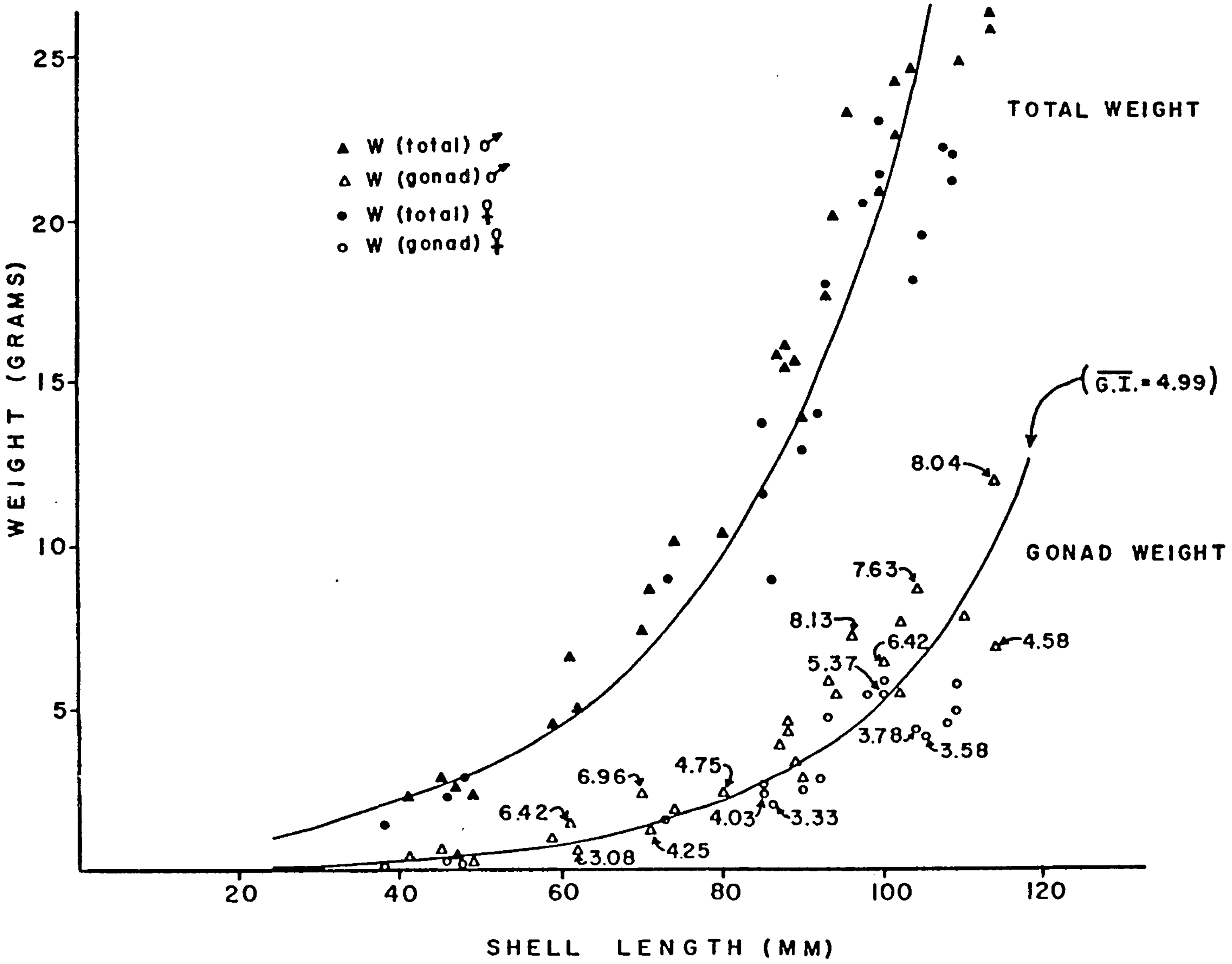
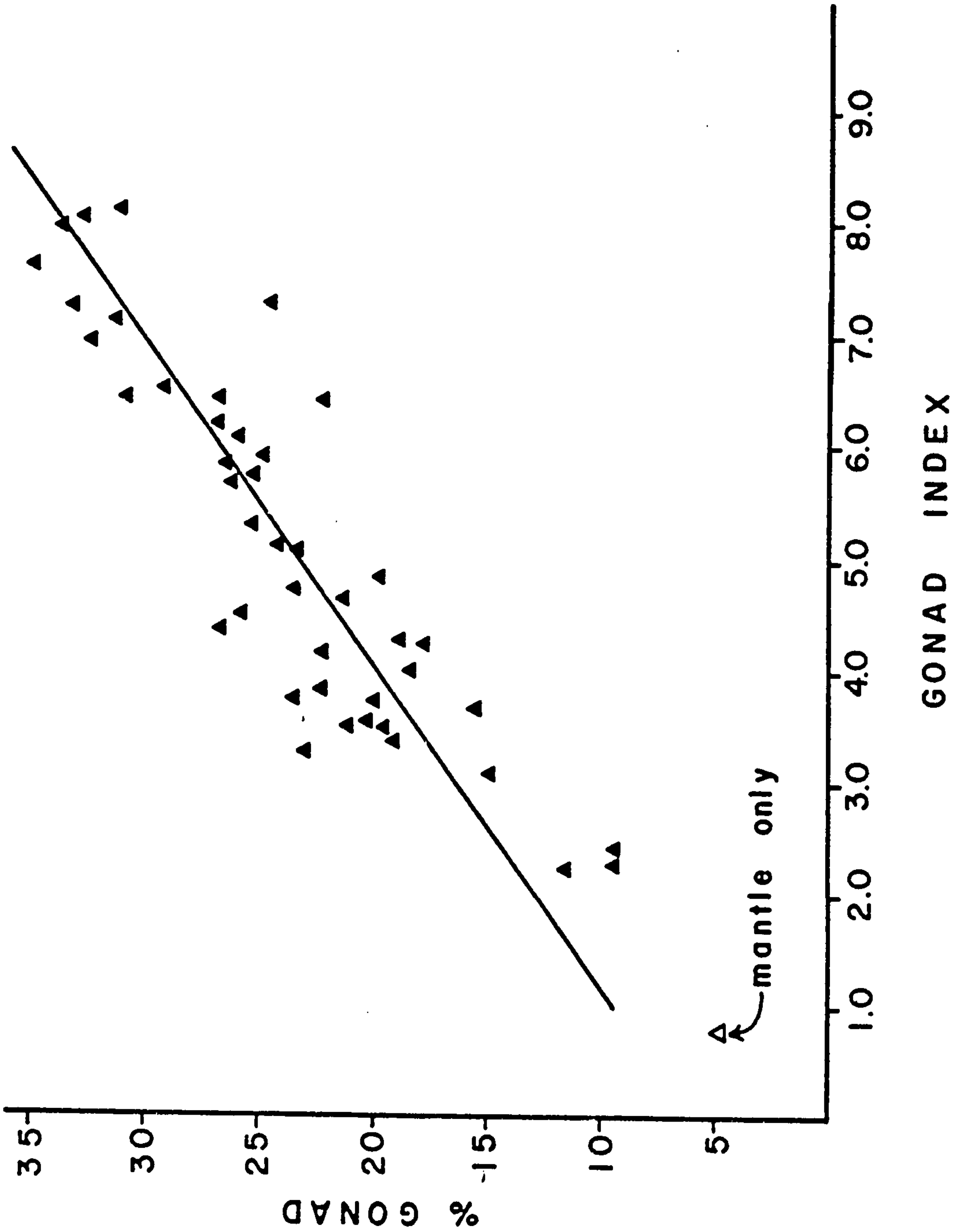

▲ W (total) ♂
△ W (gonad) ♂
● W (total) ♀
○ W (gonad) ♀
TOTAL WEIGHT
GONAD WEIGHT
($\overline{G.I.}$ = 4.99)
8.04
7.63
8.13
6.42
5.37
4.58
3.78
3.58
6.96
4.75
6.42
4.03
3.33
4.25
3.08
WEIGHT (GRAMS)
25
20
15
10
5
SHELL LENGTH (MM)
20
40
60
80
100
120

Fig. 15. Comparison of actual gonad tissue (as a percentage of total body weight) with the calculated Gonad Index derived in the text. r = 0.86.

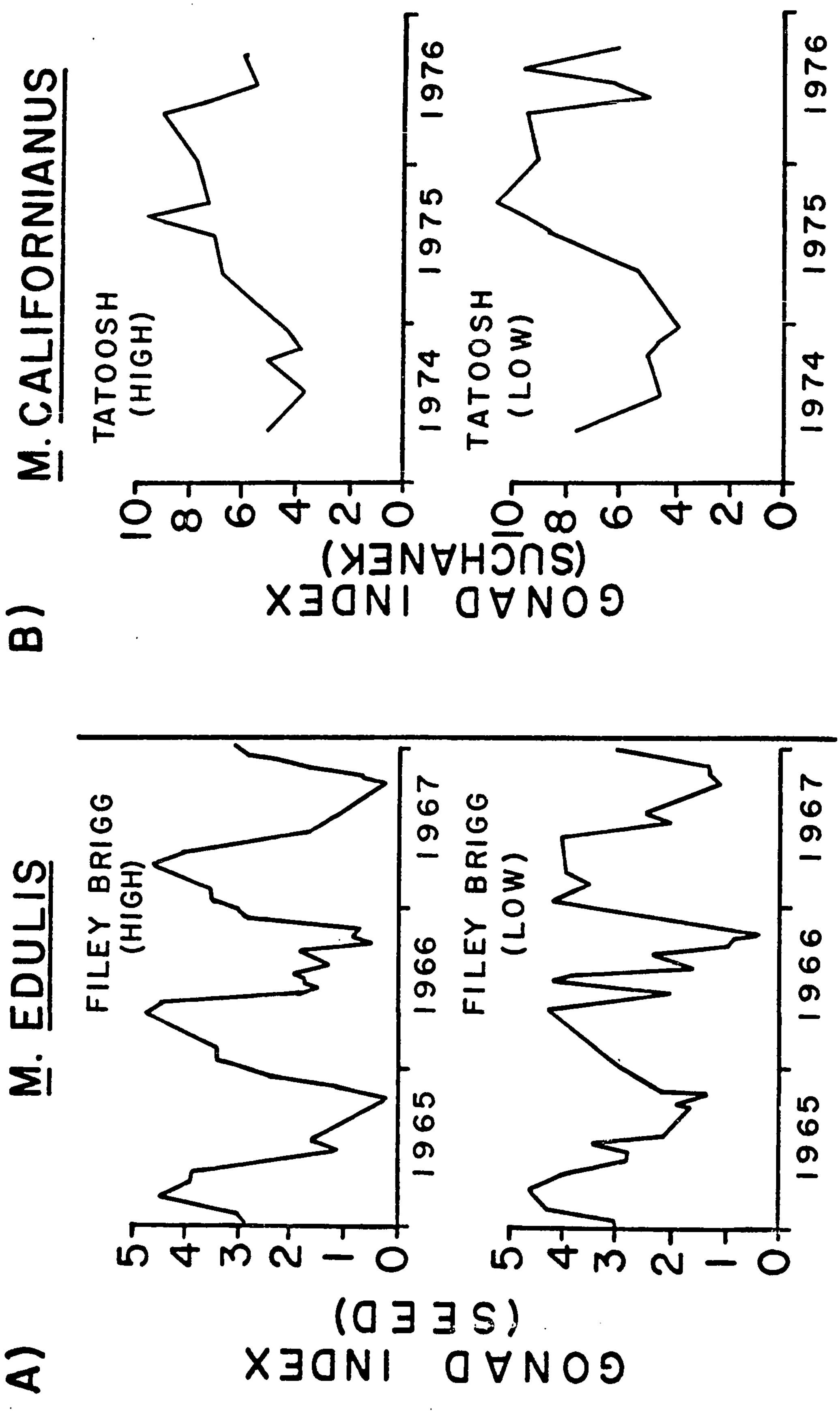

% GONAD
35
30
25
20
15
10
5
GONAD INDEX
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
mantle only

(Gabbot & Bayne, 1973; Thompson *et al*., 1974; Gabbott, 1976). However, Elvin (1974) has shown these reserves to be minimal in *M. californianus*, mainly because it lives in such a productive environment. I would therefore expect the same to be true for *M. edulis* on the Washington coast.

M. edulis shows a clearly cyclical development of gonadal tissue until a "ripe" gonad is obtained, at which point full or nearly complete spawning occurs. An in-depth analysis of the variation of gonadal tissue in local *M. edulis* was not performed. However, Fig. 16A demonstrates the yearly fluctuations of a different gonad index for *M. edulis* redrawn from Seed, 1975) over a three year period at Filey Brigg, England. It shows the distinct seasonal nature of gonad development and the fact that gametic products of this species will be nearly or completely spent at the end of a spawning season, only to build up and crash again the following season.

In contrast, *M. californianus* is not at all predictable. Fig. 16B shows the yearly cycle of gonad development in *M. californianus* as calculated by the Gonad Index derived above (see Fig. 14). No consistent seasonal trends can be discerned. Ackerman (1971), working in California, and Elvin (1974), on the Oregon coast, similarly found a relative high, constant gonad index but found some noticeable peaks in spring and autumn for this species. This is also consistent with the cumulative data of Fig. 13, i.e., that gonad levels are maintained at a relatively constant level throughout the year and that only partial spawning is likely to occur, possibly several times or continuously throughout the year. From these data and gonad fluctuations

Fig. 16. Comparison of gonad development in *M. edulis* (taken from Seed, 1975 in England) and *M. californianus* from Tatoosh Island, from high and low intertidal sites over three year periods. Note different scales on ordinate.


A)
M. EDULIS
GONAD INDEX (SEED)
FILEY BRIGG (HIGH)
FILEY BRIGG (LOW)
0
1
2
3
4
5
1965
1966
1967
B)
M. CALIFORNIANUS
GONAD INDEX (SUCHANEK)
TATOOSH (HIGH)
TATOOSH (LOW)
0
2
4
6
8
10
1974
1975
1976

it is apparent that the mode of reproduction for M. californianus can be likened to continuous iteroparity. Relatively speaking, M. edulis is at the other end of the spectrum by producing one massive spawn yearly. If it survives the pressures of competition and predation during its first year, it can spawn again a second and third year. M. edulis thus more closely approaches a semelparous reproductive strategy.

Because an organism's fitness depends on its genetic contribution to future generations, the clutch size or absolute number of gametes produced classically has been an important tool for intra- and interspecific comparisons of reproductive investment (Svardson, 1949; Mountford, 1968; Payne, 1974; Price, 1974). While the percentage of body tissue incorporated into gonads and gametes varies throughout the year (predictably for M. edulis and unpredictably for M. californianus, see Fig. 16), the contributions that individuals from the high and low intertidal make to the gene pool are substantially different. Based on estimates for the volume and number of eggs per spawn for M. edulis (Field, 1922), I have calculated the absolute potential contribution to "r" for high and low populations. Since each cubic centimeter of female spawn contains approximately 2.8×10^6 eggs (Field, 1922), an average sized (19.5 ± 3.7 mm) female from the high intertidal M. edulis zone (producing about 0.01 cc of spawn) yields about 2.9×10^4 eggs, whereas each female from patches in the low intertidal (average size = 40.4 ± 1.03 mm, yielding 0.9 cc of spawn) will produce roughly 2.6×10^6 eggs, a 90 fold difference!

This per-individual comparison is striking but not representative of the populations taken in their entirety. Since there are significant differences in the densities of M. edulis between high and low intertidal regions, I have also calculated the comparison on a population-wide basis. High in the M. edulis zone, densities of M. edulis reach 8132 ± 2072/m^2, whereas those in the lower intertidal patches only reach 3872 ± 980/m^2. Again, using these average values, a square meter of high intertidal M. edulis would produce approximately 2.3×10^8 eggs, whereas a square meter of the lower population would produce about 1.0×10^{10} eggs, still a 43 fold difference. Assuming no differences in fertilization probability or larval mortality rates between those derived from high and low populations, this strongly indicates that without these lower temporary refugia, M. edulis would have a difficult time maintaining its population levels.

NICHE STATUS:

M. edulis is well known as a widely tolerant species, capable of withstanding severe heat, cold, and desiccation (Seed, 1976). While in Washington, its upper limit is physiologically controlled by heat and desiccation stress during summer months (Chapter 2), this limit still exceeds that of M. californianus. Its lower limit is set primarily by competitive exclusion by M. californianus except in localized patches where it gains a temporary reprieve. I have found no evidence of M. edulis being crushed by M. californianus (Harger, 1967), but at the same time I have never found it present or settling into the matrix of *M. californianus* beds either. Also, as the proportion of *M. californianus* increases in natural patches, the settlement of *M. edulis* appears to decline dramatically. The evidence for competitive exclusion is apparent but the mechanism is unclear. It is possible that juvenile *M. edulis* have a greater susceptibility to predation with time or that *M. californianus* produces an allelochemical defense against settling *M. edulis*, but neither hypothesis has been tested. In any case, in the range of sympatry, *M. edulis* is clearly a small, competitively inferior, fugitive species which puts maximum effort into reproduction and relatively little into growth and/or defense against predators.

Nearly throughout its range, *M. californianus* is the dominant competitor for intertidal space and puts maximum effort into growth and predator defenses. It avoids predation mainly in two ways. First, by producing an extra inner shell layer (see above), it develops a more robust shell than *M. edulis* and is consequently a less preferred prey item for predatory gastropods (Chapter 2). Second, it attains a considerably larger size than *M. edulis*, especially in the lower intertidal, which enables it to exceed the predatory capabilities of the sea star *Pisaster ochraceus* (Paine, 1976a).

It is clear that in the zone of sympatry *M. edulis* is the inferior competitor. However, when *M. californianus* drops out (for physiological or other reasons), *M. edulis* becomes the dominant space occupier, growing much older, larger, and covering a majority of the intertidal space (e.g., to the north of *M. californianus*' range in

Alaska). In upper Glacier Bay, I have observed M. edulis to cover 15.6 feet (4.8 m) of vertical height including intertidal and subtidal space. In the southern hemisphere, on the exposed shores of Chiloe in southern Chile, and in Inner Puget Sound waters where M. californianus drops out (pers. obs.), similar extensions occur.

M. edulis is generally a poor competitor and I suggest that the features of this replacement phenomenon by a dominant competitor should prevail on other continents as well. In Chile, most large intertidal shellfish are exploited for food, but the less preferred purple mussel, Perumytilus purpuratus (Lamarck, 1819) exists in sympatry with M. edulis. P. purpuratus is a heavily ribbed mytilid with a nearly complementary range to that of M. californianus along the coast of South America (i.e., from 0°-55° south latitude; Marincovich, 1973). P. purpuratus is abundant and forms conspicuous and persistent intertidal beds, relegating M. edulis to inferior habitats such as crevices and under boulders, resulting in extremely diminished populations for this latter species. Another land mass for which this evidence exists is New Zealand. Here, M. edulis is again small, scarce, and insignificant (Stephenson & Stephenson, 1972), and the larger competitive dominant, Perna canaliculus occupies a lower, broader intertidal band (Paine, 1971b; Kennedy, 1976).

DISCUSSION:

When competing for a common requisite, species either diverge in their characteristics and niche parameters or become locally or globally excluded (Darwin, 1859; Harper *et al*., 1961; MacArthur &

Levins, 1964, 1967). The two species discussed here have apportioned bare rock substrata in the rocky intertidal on both a spatial and a temporal basis, and have diverged in their life history and reproductive strategies thereby facilitating coexistence.

Spatially, the intertidal range of _M. edulis_ extends above that of _M. californianus_, whereby _M. edulis_ escapes predation and competition. Individuals in this high intertidal band may have found an effective refuge, but probably contribute little to the gene pool because of their small absolute size and lower production of gametes. On an individual comparison basis, individuals in the lower intertidal have the potential to contribute 90 times as many gametes (on a population basis, this figure is a 43 fold increase) and, accordingly, may be more important to the overall fitness of the population. Thus, _M. edulis_ individuals in the mid to lower intertidal are those which face higher risks but potentially make the greatest contributions to fitness via reproductive investment and output. I suspect that without these lower intertidal, high risk individuals, the local _M. edulis_ populations would be in serious jeopardy.

In the lower zones, _M. edulis_ successfully acquires space by utilizing the temporal predictability of disturbance in this region. Space, the limiting resource, is predictably made available by storms during winter months (Dayton, 1971; Levin & Paine, 1964; Paine & Levin, in prep.). The timing of reproduction in _M. edulis_ along western North America appears to be cued to this predictable disturbance, but differs from that in other parts of the world where there appears to be a regional adjustment. This adjustment is probably driven by a multitude of latitudinal and regional factors which determine the right spawning period. Finally, niche status and life history strategies for M. edulis, nearly a cosmopolite, are often a function of the presence or absence of a superior competitor which usually has the characteristics of being a larger, more robust, longer-lived species. Along Western North America, M. californianus fills this role.

M. californianus is a larger, slower-growing mussel which matures late, invests little energy into reproduction each season and outlives its congener in years by up to 1-2 orders of magnitude. Rather, it channels energy into long-term growth, predator deterring mechanisms, and overall superior competitive abilities. Its reproductive output is slow but continual, since settling sites are always available (i.e., on byssus of its own adults).

Williams (1966a, b) has claimed that a high per-season reproductive effort should characterize small, short-living rather than large long-lived species. M. edulis is consistent with this prediction representing a small, relatively short-lived fugitive which undergoes a precisely timed, massive, seasonal reproductive effort cued to a stimulus which is correlated with the availability of potential settling sites. It has channelled energy away from large size and predator-deterring mechanisms in favor or rapid growth to reproductive size and maximum early dispersal abilities. M. californianus lies at the opposite end of this spectrum.

In summary, an analysis of many parameters of life history and reproductive strategies indicates divergence between these two competing mussels in their range of sympatry. Elsewhere, without competition from *M. californianus* and without disturbance, *M. edulis* covers the full extent of the intertidal zone. It is clear that the zone above *M. californianus* on the Washington outer coast represents a spatial refuge for *M. edulis* but an ineffectual one in terms of fitness. It also appears that *M. californianus* outcompetes its congener in mid- to lower intertidal regions in their range of sympatry. I claim that the evolutionarily predictable renewal of cleared space by annual disturbance processes, which has facilitated a divergence of life history and reproductive strategies between these two species, has permitted their coexistence in the rocky intertidal.

CHAPTER 4

STRUCTURAL HETEROGENEITY AND THE DEVELOPMENT OF A DIVERSE COMMUNITY ASSOCIATED WITH THE INTERTIDAL MUSSEL *MYTILUS CALIFORNIANUS*

INTRODUCTION

Patterns of species richness or diversity have long been studied and recognized as generalizable phenomena. The most striking and consistent pattern which has been observed is the gradient as one approaches tropical latitudes of increasing species richness for a variety of taxonomic groups (Darlington, 1957; Fischer, 1960; Simpson, 1964; Fleming, 1973; Ricklefs, 1977). Reviews by Pianka (1966, 1974) discuss the relatively scant ecological evidence supporting various theories on factors which control species diversity, which include 1) time, 2) spatial heterogeneity, 3) competition, 4) predation, 5) climatic stability, and 6) productivity. Numerous tests of these (or combinations of these) factors have led to further speculations and testing, usually with success in application to a specific system or guild (Root, 1967) of organisms. Yet, it is clear that communities are diverse for a variety of reasons, and that no single factor can account for all diversity trends. Once a community has been identified and defined, it will show a certain amount of variability in diversity. This can be due to a) historical effects, b) differences in the physical structure of the environment, or c) differences in successional status. Stochastic influences are usually evidenced by sampling variance, which is generally lower within a region than between regions.

In this study, I test the influence of structural heterogeneity on species diversity. Investigators as early as Wallace (1890) have hypothesized that structural complexity begets diversity. In the recent past, most have chosen to approach this question by considering either a particular guild of combined taxa (such as carnivorous snails, Kohn & Leviten, 1976), or a single taxon (such as plants - Harner & Harper, 1972; decapod crustaceans - Abele, 1974; lizards - Schoener, 1968; Pianka, 1973; birds - MacArthur, 1964; Ricklefs, 1966; Willson, 1974; Tomoff, 1975; Roth, 1976; and mammals - Fleming, 1973), but no one has considered how the diversity of an entire community (a multiple trophic level assemblage) is influenced by its structural setting.

Those that have attempted the analysis of an entire community often have done so descriptively rather than asking specific process-oriented questions about the factors controlling diversity (Hagerman, 1966; Haage & Jansson, 1970; McCloskey, 1970). Even the process-oriented studies usually have focused on metabolism of the entire community, not concentrating on inter-trophic level interactions or causal factors of diversity within the system (Teal, 1962; Pamatmat, 1968; Nixon _et_ _al_., 1971; Bahr, 1976).

The best documented studies on the effects of structural complexity on species diversity have been those of MacArthur & MacArthur (1961) for birds, Kohn (1967) and Kohn & Leviten (1976) for a marine gastropod _Conus_, Schoener (1968) for _Anolis_ lizards, and Allan (1975) for benthic stream insects. In each case, an increase in the structural complexity of the environment (either physically or biologically derived) yields an increase in the species diversity of the taxa in question. However, these accounts still do not cross taxonomic lines.

In this study, I have observed and described the variation in diversity of the entire assemblage of organisms associated with the intertidal mussel beds of *Mytilus californianus*. I have asked the question: To what extent can variation in the observed diversity be explained by variation in the structural complexity of the physical matrix created by the mussels themselves? I have attempted to resolve the issue by observation and experimental manipulation.

STUDY AREA AND METHODS

SAMPLING SCHEME:

Samples for diversity analysis were obtained from intertidal mussel beds of _Mytilus californianus_. The samples were collected from high, mid, and low intertidal heights, from each of four study areas of varying degrees of wave exposure (see below), on five sampling dates spanning a two year period. The code for sample designations corresponding to study area, collecting site, tidal height, and sample date is given below.

Sample code (example)	=	_T_	_4_	_L_	_5_
Position #	=	1	2	3	4

Position #1 represents the study area. This is a letter code which is either a _T_ (for Tatoosh Island) or an _S_ (for Shi-Shi). See Chapter 1 for detailed map of study areas and collecting locations.

Position #2 represents the collecting site within each study area. This is a number code varying from _1_ - _5_ which corresponds to the following gradient of relative wave exposure.

S1 T2 T5 T4

least exposed ⟶ most exposed

Position #3 represents the tidal height. This is a letter code which is either an _H_ (for high), an _M_ (for mid) or an _L_ (for low) and corresponds to the upper, middle, and lower positions (respectively) along the band of mussels for each collecting site. An estimate of tidal height for each collecting site is given below in Table V. These tidal height estimates are an average of no less than eight measurements taken on different dates from a known fixed point to the tidal datum (= mean-lowest-low-water: MLLW).

Position #4 represents the sampling date. This is a number code corresponding to the following dates:

_3_ = July 1974
_4_ = April 1975
_5_ = September 1975
_6_ = May 1976
_7_ = July 1976

Samples were collected by removal of all mussels, associated organisms and gorp (the organic and inorganic material composed of accumulated sediment, shell debris, and fecal material deposited at the base of the mussel bed) from 0.10 m^2 areas. This material was placed in plastic bags and frozen at $-20^{o}C$ until the associated organisms and gorp were picked and sorted from the mussel matrix. All organisms and gorp (as small as 1.0 mm) were included for diversity analysis. Associated organisms were initially preserved in 10% formalin (buffered with methenamine) and stored permanently in 80% EtOH (with 5% glycerine). Between 1,000 and 21,000 organisms per sample (for all 55 samples) were processed at least once during each of the collecting, sorting, identifying, counting, and preserving

Table V. Tidal heights for diversity samples.

SAMPLE CODE	TIDAL HEIGHT (ft)	TIDAL HEIGHT (m)
S1H	5.1	1.5
S1M	4.6	1.4
S1L	3.1	1.0
T2H	10.9	3.3
T2M	7.4	2.3
T2L	5.5	1.7
T5H	8.2	2.5
T5M	6.8	2.1
T5L	no data	
T4H	10.5	3.2
T4M	8.6	2.6
T4L	4.1	1.3

procedures, resulting in a total of approximately 459,000 organisms processed for the diversity analysis portion of this study.

THE MUSSEL MATRIX

Mytilus californianus beds are a consistent feature of the rocky intertidal zone of the exposed outer coast of Western North America (Rigg & Miller, 1949; Widdowson, 1965; Paine, 1966, 1974; Rickets *et al.*, 1968; Dayton, 1971). Chapter 2 describes the absolute positioning of *M. californianus* and its relative position to *M. edulis* on the Washington coast. In general, on the exposed coast, *M. californianus* beds may exist from approximately 4.3 ft (1.3 m) to 9.6 ft (2.9 m) tidal height in a variety of structural forms. In the higher portion of their intertidal range and in newly established or developing beds in the lower zone, the mussels are found in a monolayered arrangement. That is, a single layer of adult mussels is found attached to the primary substrate (rock). In older beds, and usually in the lower intertidal, a multilayered structure is found. Here also, a continuous layer of adults is attached to the primary substrate, but one to 5 or 6 more layers of mussels are attached to subsequently higher layers, creating a complex and heterogeneous structure, sometimes over 30 cm deep. The consequence of this load being attached by only a single layer of mussels affects the dynamics of the natural development and destruction cycle of the mussel beds and will be considered later.

The structural complexity and heterogeneity of a mussel bed depends on two factors: The size of mussels and the number of mussels within the matrix. As a bed matures both the size and number of mussels comprising it increase. As juveniles continually recruit into the matrix (colonizing the byssal threads of existing adults), they not only replenish those individuals which have been lost (due to predation or other sources of mortality), but also add more complexity to the structure. As they grow in size, they also slowly push other mussels upwards, resulting in a deepening of the matrix. It is assumed here that within any one tidal height and region, a deeper bed indicates an older bed. Therefore, for natural beds, I have used a depth of the mussel matrix (which combines the contributions from both size and abundance of mussels) as a measure of the structural complexity of this assemblage. Beds of comparable structural complexity could then be formed by, say, two layers of very large mussels (150-200 mm in length) or four to five layers of medium-sized mussels (50-100 mm in length). Fig. 17 shows the average depth of mussel beds from each of the sampling localities as a function of tidal height. Because of the high wave exposure conditions at the Tatoosh sites compared to those at Shi-Shi, mussel beds are found much higher in the intertidal at Tatoosh. For instance, even the highest sampling site at Shi-Shi is below some of the lowest sites at Tatoosh Island (Table V). Fig. 18 shows the results of transects across three individual mussel beds on Tatoosh Island from low to high intertidal. The upper zone (i.e., that above approximately 9.5 ft (2.9 m)) consists primarily of _M_. _edulis_.

Although these mussel beds occasionally become physically disrupted and locally destroyed during the normal course of events, the discussion here pertains primarily to those beds in which _M_. _californianus_ is the dominant space occupier, and has developed at

Fig. 17. Average depth of mussel beds from each sampling locality.

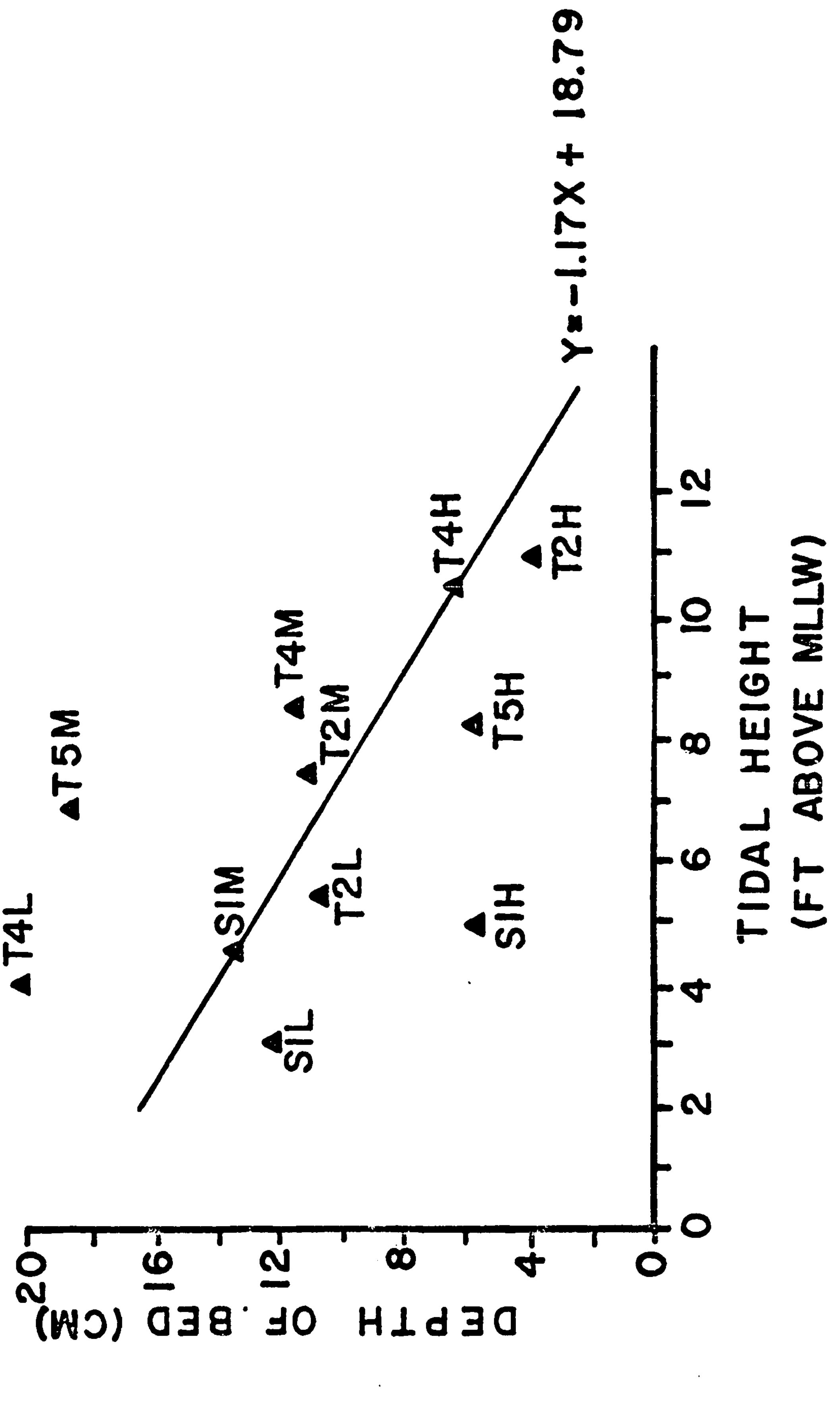
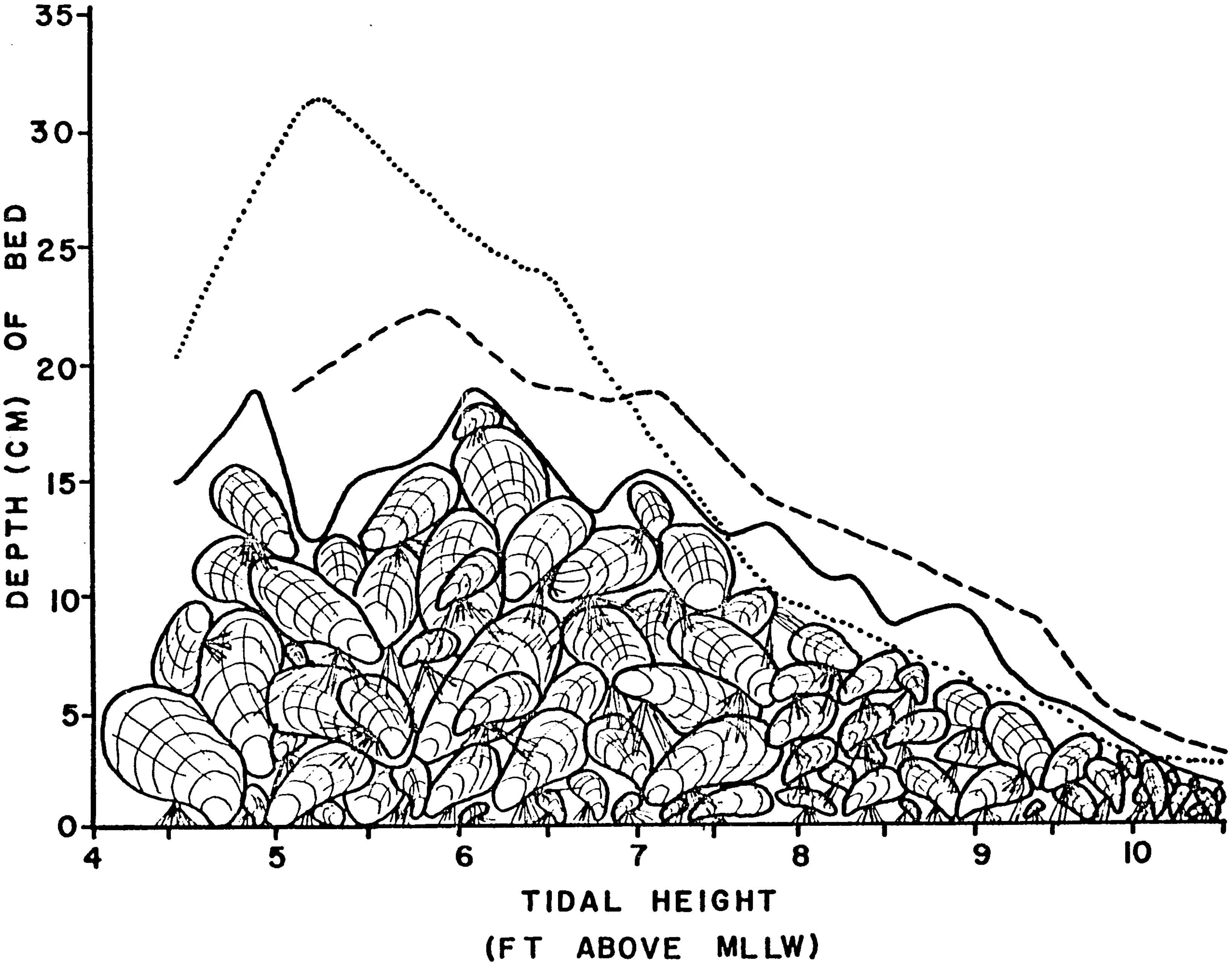

DEPTH OF BED (CM)
0
4
8
12
16
20
TIDAL HEIGHT
(FT ABOVE MLLW)
0
2
4
6
8
10
12
Y=−1.17X + 18.79
T4L
T5M
SIL
SIM
T2L
T2M
T4M
SIH
T5H
T4H
T2H

Fig. 18. Transects through three typical mussel beds to show the variation in depth profile with tidal height.


35
30
25
20
15
10
5
0
DEPTH (CM) OF BED
4
5
6
7
8
9
10
TIDAL HEIGHT
(FT ABOVE MLLW)

the minimum a continuous monolayer coverage (which may take a minimum of three years to develop from a bare rock substratum). Once the mussels have reached the status of a continuous monolayer coverage, I consider this to be an "established" bed. Normally, ca. 80% of the *M. californianus* zone is occupied by established *M. californianus* beds.

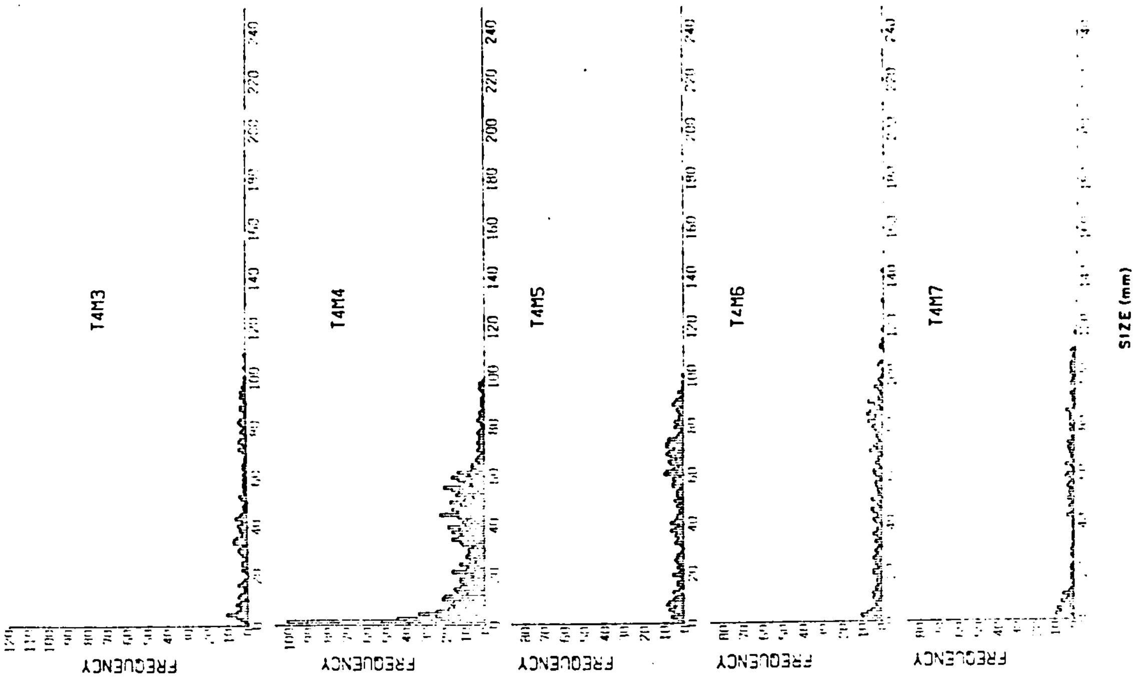
In Chapter 3, I have shown a growth curve for *M. californianus* during the developmental stages of bed formation. Once an established bed is formed, the maximum size of the mussels within that bed continues to increase, but at a progressively slower rate as the bed matures with age. The mussels asymptotically approach a maximum size that is negatively correlated with tidal height. Therefore, the size structure of any bed is dependent upon both tidal height and age of the bed.

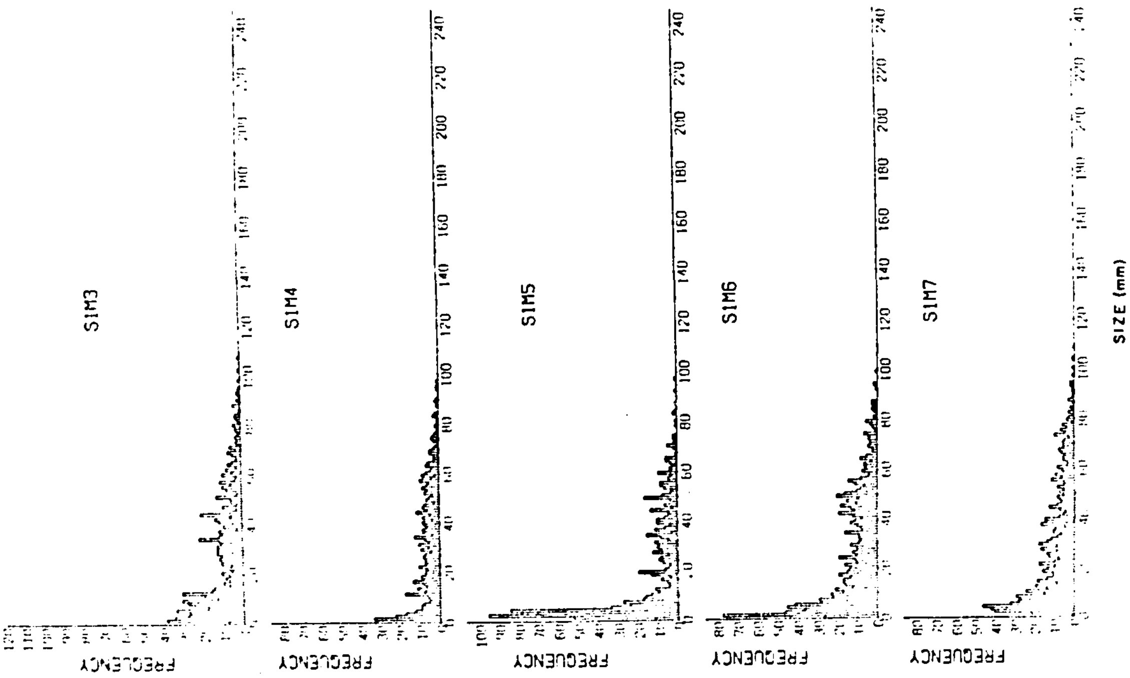
The mussel beds sampled for diversity analyses were chosen with no knowledge or preconceived notion of size structure or age; the only requirement was that they were established beds. Therefore, I have sampled each bed at some unknown point in time relative to its own developmental cycle and have followed the physical and biological components therein for a two year period.

Size-frequency distributions of *M. californianus* appear to be relatively consistent over time (within any particular tidal height) during the two year study period (Fig. 19). The complete set of size-frequency distributions is given in Appendix II.

Although consistent over time, the size-frequency distributions vary between areas and between tidal heights, generally demonstrating a preponderance of juvenile (≤ 10 mm) mussels in the lower intertidal

Fig. 19. Size-frequency distributions for *M. californianus* from the mid-intertidal zone for each sampling date at Shi-Shi (least exposed site) and Tatoosh Island Area 4 (most exposed site). These samples taken destructively from within a 10 m^2 area at each site, show a relatively consistent trend over time.


T4M3
T4M4
T4M5
T4M6
T4M7
FREQUENCY
SIZE (mm)
0 20 40 60 80 100 120 140 160 180 200 220 240

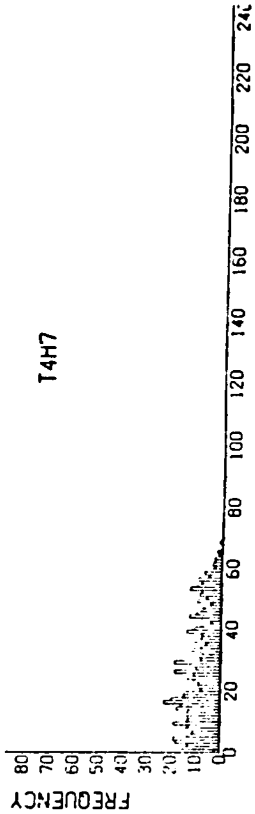

S1M3
S1M4
S1M5
S1M6
S1M7
FREQUENCY
SIZE (mm)
0 20 40 60 80 100 120 140 160 180 200 220 240

beds. This continual rain of settling larvae is evidenced by the abundance of 1-5 mm mussels in the low beds at Shi-Shi and Tatoosh shown in Fig. 20.

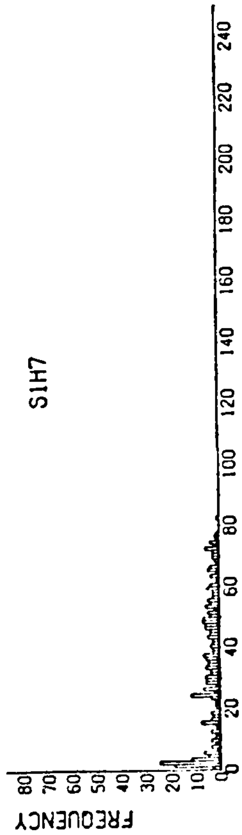
Although the maximum size of low intertidal mussels is always greater than mid-intertidal mussels, which in turn is greater than high intertidal mussels, the data given here are only for those established beds sampled for diversity analyses, which usually (but not always) represents the largest mussels at that particular tidal height. Since the average size of the entire population is a deceptive measure, for it is often more skewed toward smaller sizes in lower intertidal beds with a preponderance of juveniles (see above), I have calculated the mean size and range of the 10 largest individuals at each collecting location to represent the basic structure of the matrix (Fig. 21). During this two year study, the size structure of the mussel beds was consistent and a record of the average mussel size from each sample as well as the average size of the 10 largest individuals over time is given in Appendix III.

As a mussel bed matures, increasing the depth profile and structural complexity, many micro-habitat parameters are altered and this has a direct influence on the success of various species which can specialize on these microhabitats. The major changes are: increased surface area, reduced sunlight (reducing temperature and increasing relative humidity), and reduced wave action (increasing sedimentation). Although I was unable to measure relative humidity, Fig. 22 shows the temperature profile (on a sunny day) for various depths within a mussel bed. Temperatures were measured with an

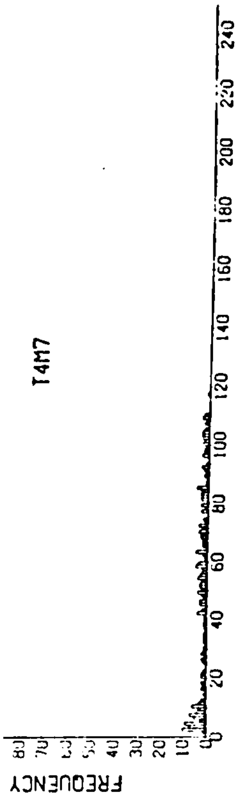
Fig. 20. Comparison of size-frequency distributions between high, mid, and low mussel bed samples from Shi-Shi (least exposed site) and Tatoosh Island (most exposed site).



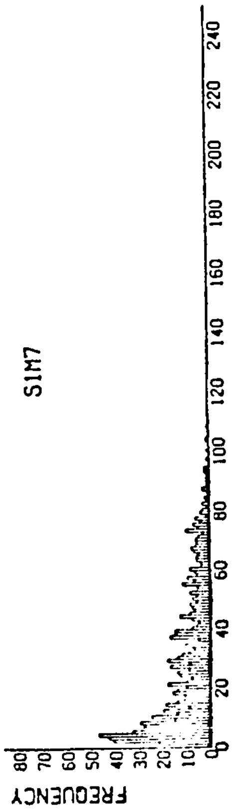
T4H7



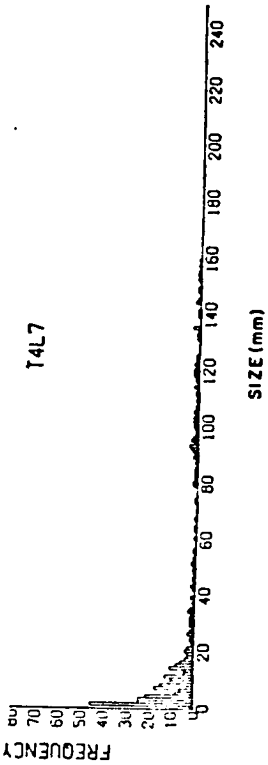
S1H7



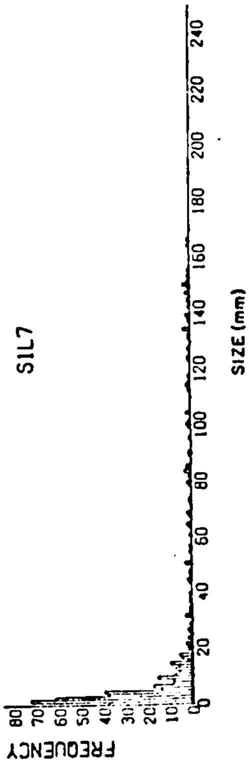
T4M7



S1M7



T4L7



S1L7

Fig. 21. Mean size and range of the 10 largest mussels at each collecting location (averaged for all dates) along the exposure gradient.

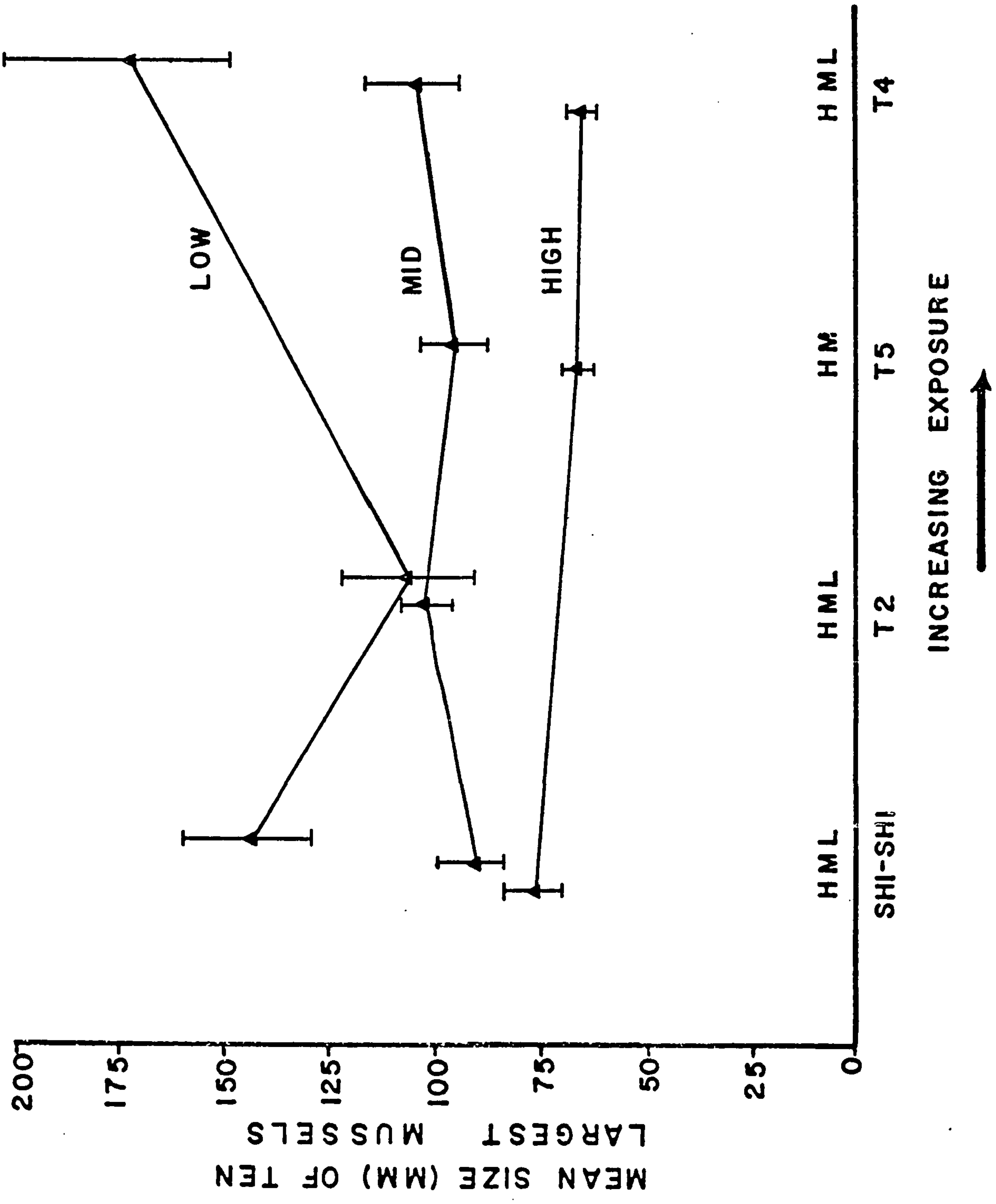
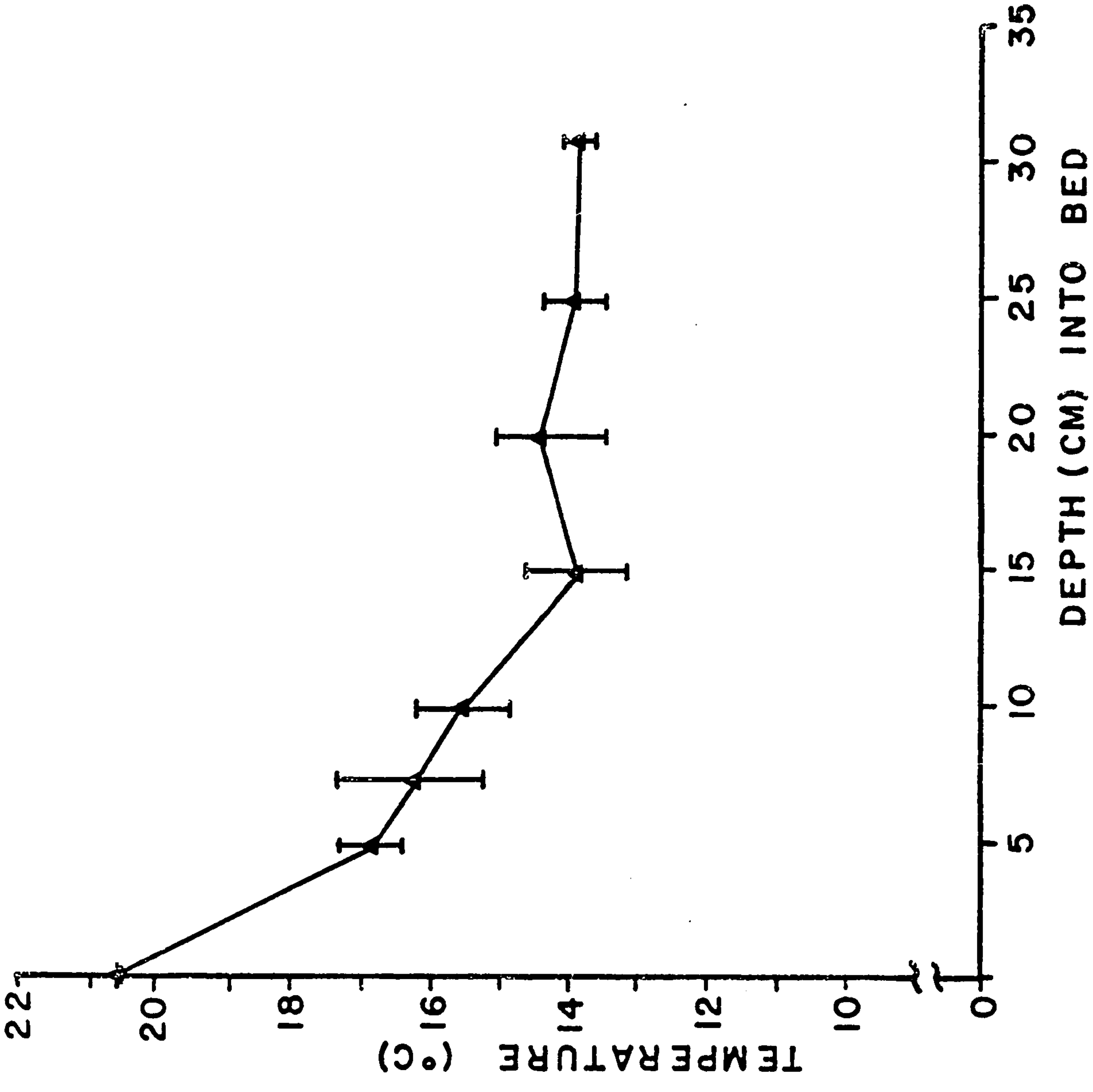
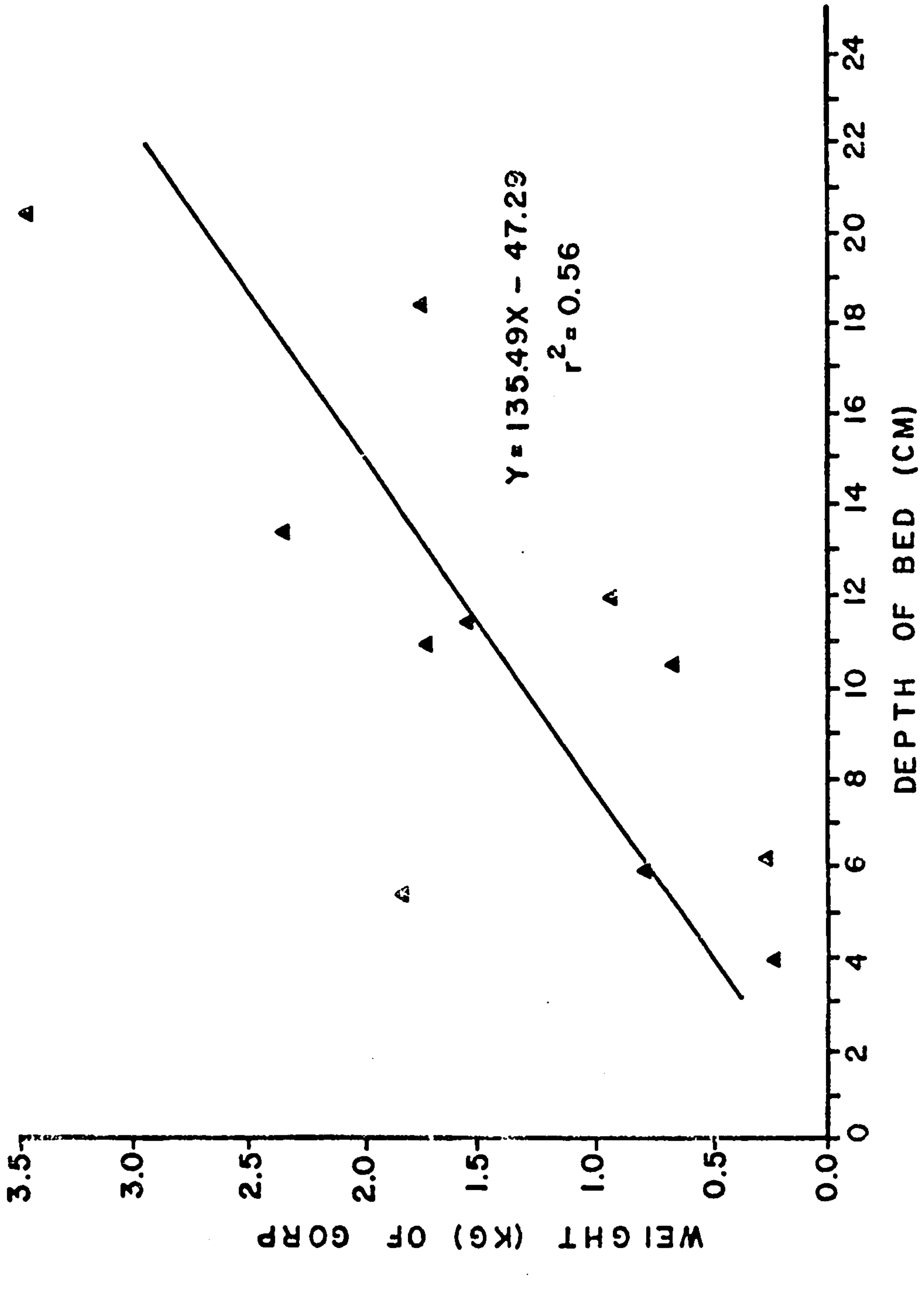

MEAN SIZE (MM) OF TEN LARGEST MUSSELS
0
25
50
75
100
125
150
175
200
LOW
MID
HIGH
H M L
SHI-SHI
H M L
T2
H M
T5
H M L
T4
INCREASING EXPOSURE

Fig. 22. Temperature profile of a *M. californianus* bed from Tatoosh Island on a sunny day.


TEMPERATURE (°C)
22
20
18
16
14
12
10
0
DEPTH (CM) INTO BED
0
5
10
15
20
25
30
35

electronic Y.S.I. Tele-thermister point-source probe. Gorp accumulation is a direct result of the decreased wave action and provides a habitat and often nutrition for many detritivores and filter feeders. It tends to accumulate most heavily in deeper, more mature beds. Fig. 23 gives the average gorp accumulation in samples from each of the study sites as a function of mussel bed depth and shows a coefficient of determination of $r^2 = 0.56$. These values represent dry weights of gorp after maintaining the sediment samples in an oven at approx. 105°C for 24 hrs. to remove excess water.

Fig. 23. Dry weight (kg) of gorp as a function of mussel bed depth.


Y = 135.49X − 47.29
r² = 0.56
WEIGHT (KG) OF GORP
DEPTH OF BED (CM)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
2
4
6
8
10
12
14
16
18
20
22
24

THE ASSOCIATED COMMUNITY

An analysis of the organisms found associated with the mussel matrix yields a surprisingly diverse assemblage. While the richest 0.10 m^2 sample yielded only 136 taxa (local species richness), the global richness (the combined species of associated organisms found at all collecting sites in this survey) reached 303 taxa (87% of which were identified to species). The identified associated organisms included the three divisions of marine algae, 12 phyla of invertebrates, and 3 species of fishes. Groups that were not examined were diatoms (known to be very rich; Nicotri, 1977), blue green algae, bacteria and fungi. With few exceptions, I included all organisms down to 1.0 mm in size. One species of Foraminifera was observed in this assemblage, sometimes reaching a size of over 1-2 mm. But, because most individuals were below the lower critical sampling size, I have chosen not to consider them in the formal count for diversity analysis. Another problem organism was Cliona, the boring sponge. Again, although present, because of the difficult in discerning its bore holes from erosion in M. californianus shells, it was also excluded from the quantitative diversity analysis. Table VI provides a list of the identified taxa.

For the purpose of computing measures of diversity, unknown species, questionable species, or lumped species were conservatively considered as a single species. For encrusting species, the continuing problem of "what to consider as an individual" was resolved in the following manner. An individual was considered to be any

Table VI. List of taxa encountered in the _M_. _californianus_ bed community.

ALGAE:
- CHLOROPHYTA
  - *Cladophora* spp.
  - Ulvoids
  - *Urospora* sp.
- PHAEOPHYTA
  - *Alaria marginata* Postels & Ruprecht, 1840
  - *Analipus japonica* (Harvey) Wynne, 1971
  - *Fucus distichus* Linnaeus, 1767
  - *Haedophyllum sessile* (C. Agardh) Setchell,
  - *Laminaria* spp.
  - *Pelvetiopsis limitata* (Setchell) Gardner, 1910
  - *Ralfsia pacifica* Hollenberg, 1944
- RHODOPHYTA
  - *Callophyllus* spp.
  - corallines
  - *Endocladia muricata* (Postels & Ruprecht) J.G. Agardh, 1847
  - *Gigartina* sp. A
  - *Gigartina* sp. B
  - *Halosaccion glandiforme* (Gmelin) Ruprecht, 1851
  - *Hildenbrandia* sp.
  - *Iridaea cornucopiae* Postels & Ruprecht, 1840
  - *Iridaea* sp.
  - *Microcladia borealis* Ruprecht, 1851
  - *Petrocelis* spp.
  - *Polysiphonia* spp.
  - *Porphyra* sp. A
  - *Porphyra* sp. B
  - *Schizymenia* spp.

PROTOZOA:
- *Eponides columbiensis* (Cushman, 1925)

PORIFERA:
- DEMOSPONGIAE
  - *Cliona celata* Grant, 1826
  - *Halichondria panicea* Pallas, 1766
  - *Haliclona permollis* (Bowerbank, 1866)

CNIDARIA:
- HYDROZOA
  - Hydroida
    - *Abietinaria abietina* (Linnaeus, 1758)
    - *Abietinaria amphora* Nutting, 1904
    - *Abietinaria anguina* (Trask, 1857)
    - *Aglaophenia* sp.
    - *Campanularia* sp.
    - *Clytia hesperia* (Torrey, 1904)
    - *Garveia groenlandica* Levinson, 1893
    - *Sertularella fusiformis* (Hincks, 1861)
  - Hydrocorallina
    - *Stylantheca porphyra* Fisher, 1931
- ANTHOZOA
  - Actinaria
    - *Anthopleura elegantissima* (Brandt, 1835)
    - *Anthopleura xanthogrammica* (Brandt, 1835)
    - *Diadumene* sp.

PLATYHELMINTHES:
- TURBELLARIA
  - Polycladida
    - *Notoplana* sp. (?*inquieta* (Heath & McGregor, 1912))

NEMERTEA:
- Enopla
  - Hoplonemertea
    - *Amphiporus* sp. (?*formidabilis* Griffin, 1898)
    - *Emplectonema gracile* (Johnston, 1837)
    - *Paranemertes peregrina* Coe, 1901

NEMATODA:
- Unidentified sp. A
- Unidentified sp. B

- MOLLUSCA:
  - POLYPLACOPHORA
    - Neoloricata
      - *Cyanoplax dentiens* (Gould, 1846)
      - *Katharina tunicata* (Wood, 1815)
      - *Mopalia ciliata* (Sowerby, 1840)
      - *Mopalia muscosa* (Gould, 1846)
  - GASTROPODA
    - PROSOBRANCHIA
      - Archaeogastropoda
        - *Acmaea mitra* Rathke, 1833
        - *Calliostoma ligatum* (Gould, 1849)
        - *Collisella digitalis* (Rathke, 1833)
        - *Collisella pelta* (Rathke, 1833)
        - *Collisella strigatella* (Carpenter, 1864)
        - *Diodora aspera* (Rathke, 1833)
        - *Homalopoma lacunatum* (Carpenter, 1864)
        - *Homalopoma luridum* (Dall, 1885)
        - *Lirularia lirulata* (Carpenter, 1864)
        - *Lirularia succincta* (Carpenter, 1864)
        - *Littorina scutulata* Gould, 1849
        - *Littorina sitkana* Phillipi, 1845
        - *Notoacmea scutum* (Rathke, 1833)
        - *Tegula funebralis* (A. Adams, 1855)
      - Mesogastropoda
        - *Alvinia carpenteri* (Weinkauff, 1885)
        - *Alvinia compacta* (Carpenter, 1864)
        - *Alvinia dinora* (Bartsch, 1917)
        - *Balcis* sp.
        - *Barleeia sanjuanensis* Bartsch, 1920
        - *Bittium eschrichtii* (Middendorff, 1849)
        - *Cerithiopsis stejnegeri* Dall, 1884
        - *Crepidula adunca* Sowerby, 1825
        - *Crepidula convexa* Say, 1822
        - *Crepidula fornicata* Linnaeus, 1758
        - *Crepidula plana* Say, 1822
        - *Crepipatella lingulata* (Gould, 1846)
        - *Lacuna vincta* (Montagu, 1803)
        - *Opalia chacei* Strong, 1937
        - *Trichotropis cancellata* Hinds, 1843
        - *Velutina velutina* (Müller, 1776)
      - Neogastropoda
        - *Alia* (=*Mitrella*) *carinata* (Hinds, 1844)
        - *Amphissa columbiana* Dall, 1916
        - *Ceratostoma foliatum* (Gmelin, 1791)
        - *Granulina margaritula* (Carpenter, 1857)
        - *Mitrella tuberosa* (Carpenter, 1864)
        - *Nassarius mendicus* (Gould, 1850)
        - *Ocenebra lurida* (Middendorff, 1848)
        - *Searlesia dira* (Reeve, 1846)
        - *Thais canaliculata* (Duclos, 1832)
        - *Thais emarginata* (Deshayes, 1839)
    - OPISTHOBRANCHIA
      - Pyramidellida
        - *Odostomia* (*Evalea*) *deliciosa* Dall & Bartsch, 1907
      - Onchidiacea
        - *Onchidella borealis* Dall, 1871
    - PULMONATA
      - Basommatophora
        - *Siphonaria thersites* Carpenter, 1864
  - BIVALVIA
    - PTERIOMORPHA
      - Mytiloida
        - *Adula californiensis* (Philippi, 1847)
        - *Modiolus* sp.
        - *Musculus taylori* (Dall, 1897) (?=*M. pygmaeus* Glynn, 1964)
        - *Mytilus californianus* Conrad, 1837
        - *Mytilus edulis* Linnaeus, 1748
      - Pterioida
        - *Chlamys* sp.
        - *Pododesmus cepio* (Gray, 1850)

MOLLUSCA: (cont.)
BIVALVIA (cont.)
HETERODONTA
Veneroida
Kellia laperousii (Deshayes, 1839)
Lasaea rubida (Montagu, 1804)
Lasaea subviridis Dall, 1899
Macoma inquinata (Deshayes, 1855)
Mysella tumida (Carpenter, 1864)
Petricola carditoides (Conrad, 1837)
Protothaca staminea (Conrad, 1837)
Saxidomus giganteus (Deshayes, 1839)
Myoida
Hiatella arctica (Linnaeus, 1767)
Mya arenaria Linnaeus, 1758
ANOMALODESMATA
Pholadomyoida
Entodesma saxicola (Baird, 1863)

ANNELIDA:
OLIGOCHAETA
Unidentified sp. A
POLYCHAETA
Orbiniida
Orbiniidae
Naineris dendritica (Kinberg, 1867)
Spionida
Spionidae
Polydora (=*Boccardia*) *proboscidea* Hartman, 1940
Cirratulidae
Cirratulus cirratus (Müller, 1776)
Tharyx multifilis Moore, 1909
Opheliida
Opheliidae
Armandia brevis (Moore, 1906)
Travisia sp.
Phyllodocida
Phyllodocidae
Eulalia levicornuta Moore, 1909
Eulalia viridis (Linnaeus, 1767)
Polynoidae
Arctonoe vittata (Grube, 1855)
Eunoe senta (Moore, 1902)
Halosydna brevisetosa Kinberg, 1855
Harmothoe extenuata Grube, 1840
Harmothoe lunulata (delle Chiaje, 1841)
Harmothoe multisetosa Moore, 1902
Hesperone (?*adventor* (Skogsberg, 1928))
Lepidasthenia longicirrata Berkeley, 1923
Lepidonotus squamatus (Linnaeus, 1767)
Polyeunoa tuta (Grube, 1855)
Sigalionidae
Pholoe minuta (Fabricius, 1780)
Chrysopetalidae
Paleanotus bellis (Johnson, 1897)
Paleanotus (=*Chrysopetalum*) *occidentale* Johnson, 1897
Hesionidae
Micropodarke dubia (Hessle, 1925)
Syllidae
Syllis adamantea adamantea (Treadwell, 1914)
(=*Typosyllis adamanteus* (Treadwell, 1914))
Syllis alternata Moore, 1908
Syllis armillaris (Müller, 1771)
Syllis elongata (Johnson, 1901)
Syllis gracilis Grube, 1840
Syllis harti Berkeley & Berkeley, 1938
Syllis heterochaeta Moore, 1909
Syllis pulchra Berkeley & Berkeley, 1938
Syllis stewarti Berkeley & Berkeley, 1942
Syllis variegata Grube, 1860
Syllis spp.
Nereidae
Cheilonereis cyclurus (Harrington, 1897)
Nereis limnicola Johnson, 1903
Nereis vexillosa Grube, 1851
Nereis sp. A
Nereis sp. B
Sphaerodoridae
Unidentified sp.

ANNELIDA: (cont.)
- POLYCHAETA (cont.)
  - Eunicida
    - Lumbrineridae
      - *Lumbrineris zonata* (Johnson, 1901)
    - Arabellidae
      - *Arabella iricolor* (Montagu, 1804)
      - *Arabella semimaculata* (Moore, 1911)
  - Terebellida
    - Sabellariidae
      - *Idanthyrsus armatus* Kinberg, 1867
      - *Sabellaria cementarium* Moore, 1906
    - Pectinariidae
      - *Pectinaria californiensis* Hartman, 1941
      - *Pectinaria* (=*Cistenides*) *granulata* (Linnaeus, 1767)
      - *Pectinaria* (=*Amphictene*) *moorei* Annenkova, 1929
    - Ampharetidae
      - Unidentified sp. A
    - Terebellidae
      - *Eupolymnia* (?*heterobranchia* (Johnson, 1901))
      - *Laphania boecki* Malmgren, 1866
      - *Streblosoma bairdi* (Malmgren, 1866)
  - Sabellida
    - Sabellidae
      - *Demonax* (=*Sabella*) *medius* (Bush, 1904)
      - *Distylia rugosa* Moore, 1904
      - *Eudistylia polymorpha* (Johnson, 1901)
      - *Eudistylia vancouveri* (Kinberg, 1867)
      - *Laonome kroyeri* Malmgren, 1866
      - *Myxicola infundibulum* (Renier, 1804)
      - *Potamilla* (=*Pseudopotamilla*) *intermedia* Moore, 1905
      - *Potamilla* (=*Pseudopotamilla*) *myriops* Marenzeller, 1884
      - *Potamilla neglecta* (Sars, 1851)
      - *Schizobranchia insignis* Bush, 1904
    - Serpulidae
      - *Serpula vermicularis* Linnaeus, 1767
      - Unidentified sp. A
    - Spirorbidae
      - Unidentified sp. A
      - Unidentified sp. B

SIPUNCULIDA:
- *Phascolosoma agassizii* Keferstein, 1867

ARTHROPODA:
- PYCNOGONIDA
  - *Achelia latifrons* (Cole, 1904)
  - *Nymphopsis spinosissima* (Hall, 1912)
  - *Phoxichilidium femoratum* (Rathke, 1799)
  - *Pycnogonum stearnsi* Ives, 1892
- ARACHNIDA
  - Pseudoscorpionida
    - *Halobisium occidentale* Beier, 1931
    - Unidentified sp. A
  - Acari
    - Unidentified sp. A
    - Unidentified sp. B
    - Unidentified sp. C
    - Unidentified sp. D
    - Unidentified sp. E
    - Unidentified sp. F
    - Unidentified sp. G
    - Unidentified sp. H
    - Unidentified sp. I
    - Unidentified sp. J
- CRUSTACEA
  - CIRRIPEDIA
    - Thoracica
      - *Balanus cariosus* (Pallas, 1788)
      - *Balanus crenatus* Bruguière, 1789
      - *Balanus glandula* Darwin, 1854
      - *Balanus nubilus* Darwin, 1854
      - *Chthamalus dalli* Pilsbry, 1916
      - *Pollicipes* (=*Mitella*) *polymerus* Sowerby, 1833

- ARTHROPODA: (cont.)
  - CRUSTACEA (cont.)
    - MALACOSTRACA
      - Tanaidacea
        - *Anatanais normani* (Richardson, 1905)
        - *Leptochelia dubia* (Krøyer, 1842)
        - *Pancolus californiensis* Richardson, 1905
        - *Synapseudes intumescens* Menzies, 1949
      - Isopoda
        - *Cirolana harfordi* Lockington, 1877
        - *Dynamenella dilitata* (Richardson, 1899)
        - *Dynamenella sheareri* Hatch, 1947
        - *Edotea sublittoralis* Menzies & Barnard, 1959
        - *Exosphaeroma amplicauda* (Stimpson, 1857)
        - *Exosphaeroma octoncum* Richardson, 1897
        - *Exosphaeroma rhomburum* Richardson, 1899
        - *Gnorimosphaeroma oregonensis* (Dana, 1854-1855)
        - *Ianiropsis analoga* Menzies, 1952
        - *Ianiropsis* (=*Janiropsis*) *kincaidi* Richardson, 1904
        - *Idotea* (=*Pentidotea*) *schmitti* Menzies, 1951
        - *Idotea wosnesenskii* (Brandt, 1851)
        - *Jaeropsis dubia* Menzies, 1951
        - *Jaeropsis* (?*lobata* Richardson, 1899)
        - *Munna chromatocephala* Menzies, 1952
        - *Synidotea bicuspida* (Owen, 1839)
      - Amphipoda
        - *Ampithoe simulans* Alderman, 1936
        - *Aoroides columbiae* Walker, 1898
        - *Caprella angusta* Mayer, 1903
        - *Caprella greenleyi* McCain, 1969
        - *Corophium brevis* Shoemaker, 1949
        - *Deutella* (?*californica* (Mayer, 1890))
        - *Hyale anceps* (Barnard, 1969)
        - *Hyale frequens* (Stout, 1913)
        - *Hyale grandicornis californica* Barnard, 1969
        - *Hyale plumulosa* (Stimpson, 1857)
        - *Ischyrocerus anguipes* Krøyer, 1838
        - *Ischyrocerus serratus* Gurjanova, 1938
        - *Jassa falcata* (Montagu, 1808)
        - *Melita californica* Alderman, 1936
        - *Melita desdichada* Barnard, 1962
        - *Metopa cistella* Barnard, 1969
        - *Najna* sp. (?=*consiliorum* Barnard, 1962)
        - *Oligochinus lighti* Barnard, 1969
        - *Orchestia* sp.
        - *Orchomene* sp. A
        - *Orchomene* sp. B
        - *Parallorchestes ochotensis* (Brandt, 1851)
        - *Paramoera* cf. *mohri* Barnard, 1952
        - *Paramoera* (undescribed species of Armstrong *et al*., 1976)
        - *Paraphoxus* cf. *obtusidens* (Alderman, 1936)
        - *Parapleustes den* Barnard, 1969
        - *Parapleustes nautilus* Barnard, 1969
        - *Parapleustes pugettensis* (Dana, 1853)
        - *Photis* sp.
        - *Pontogeneia intermedia* Gurjanova, 1938
        - *Stenothoides burbanki* Barnard, 1969
      - Decapoda
        - *Cancer branneri* Rathbun, 1898
        - *Fabia subquadrata* Dana, 1851
        - *Hemigrapsus nudus* (Dana, 1851)
        - *Oedignathus inermis* (Stimpson, 1860)
        - *Pachycheles rudis* Stimpson, 1859
        - *Pagurus* spp.
        - *Petrolisthes cinctipes* (Randall, 1839)
        - *Petrolisthes eriomeris* Stimpson, 1871
        - *Pugettia gracilis* Dana, 1851
        - *Pugettia richii* Dana, 1851
  - INSECTA
    - PTERYGOTA
      - Diptera
        - *Coelopa* sp.
        - *Oedoparena glauca* (Coquillett, 1900)
        - *Paraclunio alaskensis* (Coquillett, 1900)
        - *Paraphrosylus nigripennis* (VanDuzee, 1924)
        - Unidentified sp. A
        - Unidentified sp. B
        - Unidentified sp. C

ARTHROPODA: (cont.)
INSECTA (cont.)
PTERYGOTA (cont.)
Coleoptera
Diaulota densissima Casey, 1893
Liparocephalus brevipennis Maklin, 1853
Unidentified sp. A

BRYOZOA:
GYMNOLAEMATA
Ctenostomata
Alcyonidium polyoum (Hassall, 1841)
Flustrella corniculata (Smitt, 1871)
Cyclostomata
Crisia occidentalis Trask, 1857
Crisia pugeti Robertson, 1910
Tubulipora pacifica Robertson, 1910
Cheilostomata
Bugula pugeti Robertson, 1905
Callopora horrida (Hincks, 1880)
Cellaria mandibulata Hincks, 1882
Dendrobeania curvirostrata (Robertson, 1905)
Dendrobeania (?*laxa* (Robertson, 1905))
Hippodiplosia insculpta (Hincks, 1882)
Hippothoa hyalina (Linnaeus, 1758)
Microporella californica (Busk, 1856)
Microporella (?*marsupiata* (Busk, 1860))
Schizoporella linearis inarmata (Hincks, 1884)
Smittina retifrons (Osborn, 1952)
Tricellaria ternata (Solander, 1786)

ECHINODERMATA:
ASTEROIDEA

Spinulosida
Henricia leviuscula (Stimpson, 1857)
Forcipulatida
Leptasterias hexactis (Stimpson, 1862)
Pisaster ochraceus (Brandt, 1835)
ECHINOIDEA
Strongylocentrotus droebachiensis (O.F. Müller, 1776)
Strongylocentrotus franciscanus (A. Agassiz, 1863)
Strongylocentrotus purpuratus (Stimpson, 1857)
HOLOTHUROIDEA
Cucumaria pseudocurata Deichmann, 1938
Cucumaria miniata (Brandt, 1835)
Eupentacta quinquesemita (Selenka, 1867)
OPHIUROIDEA
Ophiopholis aculeata (Linnaeus, 1767)

CHORDATA:
UROCHORDATA
ASCIDIACEA
Pyura haustor (Stimpson, 1864)
VERTEBRATA
OSTEICHTHYES
Clinocottus embryum (Jordan & Starks, 1895)
Phytichthys chirus (Jordan & Gilbert, 1880)
Xiphister atropurpureus (Kittlitz, 1858)

successful propagule within the community. If this propagule subsequently grew into a colony with many zooids, this was considered only growth and the entire colony was counted as a single individual. Therefore, algal tufts and crusts, and colonies of sponges, bryozoans, hydrocorals, and hydroids, although occupying substantial space, were conservatively counted as single individuals. If these "single" counts had been weighted for their areal coverage, it would have increased the equitability component of diversity, and therefore the absolute diversity values.

Two measures are used to compare species diversity between sampling sites. 1) Species richness (total number of species = S) is given as the simplest, and intuitively, most useful measure of community diversity. 2) The Shannon-Weaver information theory index, H' (shown below), is also calculated because it is a weighted measure which takes into account the relative abundance of individuals of each species in an "indefinitely large" community (Peet, 1974; Pielou, 1975); that is, removing samples caused no perceptible change in the total community. This is certainly the case for the mussel bed community along the Washington coast. The Shannon-Weaver index is represented by the formula

$$H' = -\sum_{1}^{S} p_i \log_{10} p_i$$

where S = the number of species

p_i = the proportion of individuals represented by the i^{th} species

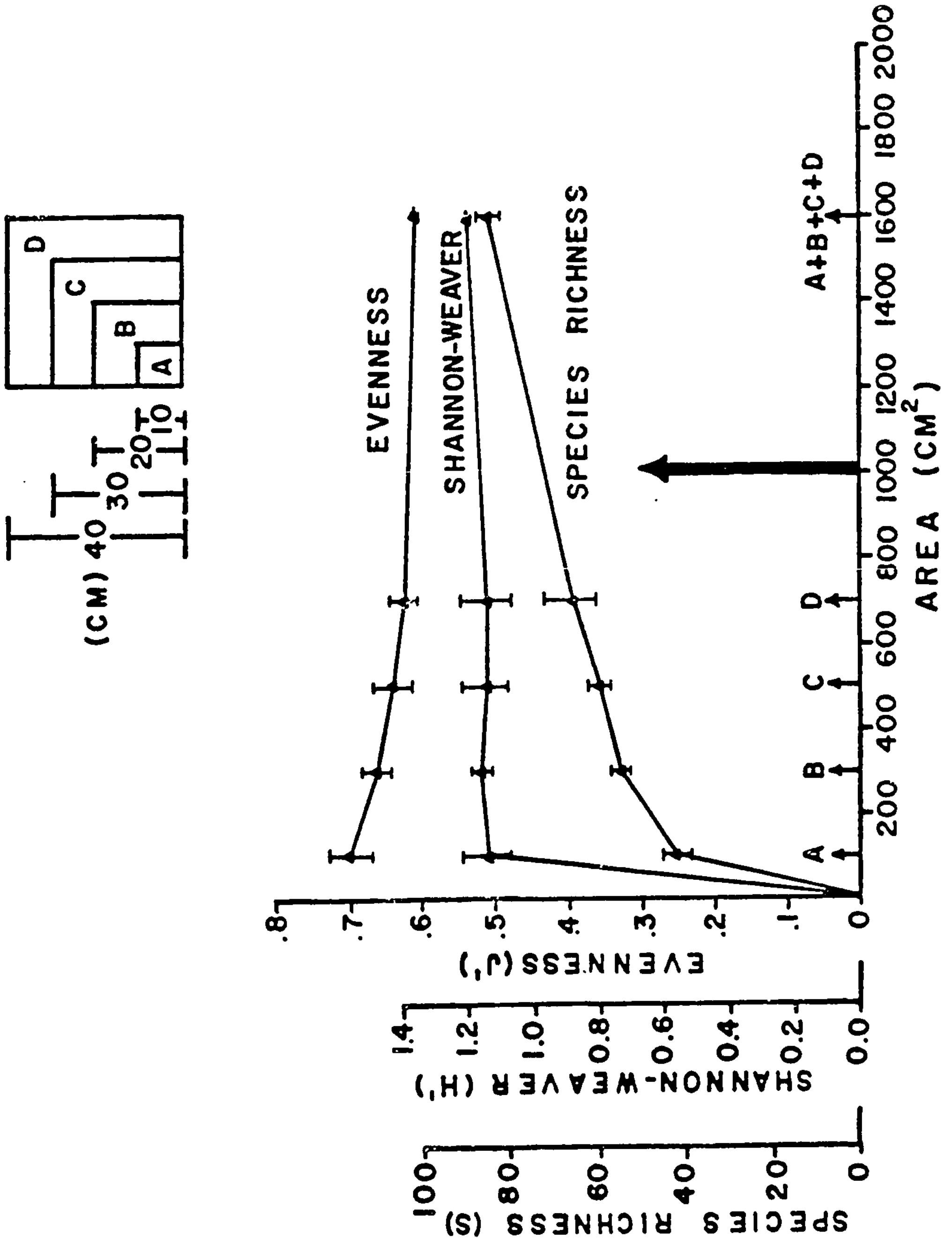
The evenness (equitability) component of the information theory diversity index was also calculated. This yields a measure of how evenly the number of individuals are distributed among the species in a collection. The evenness index (J') used here is one derived by Pielou (1966).

$$J' = \frac{H'}{\log_{10} S}$$

(terms defined above)

In order to determine the adequate sample size for diversity analyses, a replicated series of samples of progressively larger areas were collected and analyzed for species richness, the Shannon-Weaver Index, and Pielou's evenness index. Fig. 24 demonstrates the nested sampling scheme used and shows that the species-area curves for both species richness and Shannon-Weaver Index rise quickly with increasing area and plateau fairly rapidly. I conclude that the sample area used throughout this survey for all diversity samples (indicated by the arrow at 1000 cm^2 = 0.10 m^2) allows a reasonable representation of the entire community at each site. Each sample is near local species saturation and therefore provides an adequate basis by which to compare diversity between sites. As more and more rare species are added with increasing sample size, the evenness index declines and levels out to a moderately stable value, again indicating reasonable homogeneity between samples taken at the 0.10 m^2 area size.

Fig. 24. Relationship between increasing sample size and the species richness, Shannon-Weaver, and evenness values. Insert shows the nested sampling scheme used to calculate these values. The sample size used for diversity analysis in this survey is indicated by the heavy arrow at 1000 cm^2.


(CM) 40
30
20
10
A
B
C
D
EVENNESS
SHANNON-WEAVER
SPECIES RICHNESS
A
B
C
D
A+B+C+D
200
400
600
800
1000
1200
1400
1600
1800
2000
AREA (CM^2)
.8
.7
.6
.5
.4
.3
.2
.1
0
EVENNESS (J')
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
SHANNON-WEAVER (H')
100
80
60
40
20
0
SPECIES RICHNESS (S)

Results of diversity analyses for species richness (S), the Shannon-Weaver Index (H'), and the evenness index (J') for all sampling sites over time are given in Figs. 25, 26 and 27 (respectively). No samples were taken at site T5L because the mussel beds were scattered and non-contiguous. Sample T4H4 was destroyed in transit and therefore no data are available for it. Each data point on each curve represents a complete analysis of all associated organisms from that collecting site excluding the mussel matrix itself.

The abundance of associated organisms as well as that of mussels (*M. californianus*) is shown in Fig. 28. Although neither show any distinct trends over time during the two year study period, the abundance of associates clearly differs between tidal heights, and with the exception of site T5, universally shows increasing abundance with decreasing tidal height. The abundance values for both *M. californianus* and associates in each sample are listed in Appendix IV.

Statistical analysis of samples using the Friedman's Rank Sums Test demonstrates that, for most collecting sites, the greatest diversity of associates (both in terms of species richness and the Shannon-Weaver Index) is found in low, exposed intertidal mussel beds, and that diversity decreases as one proceeds both to progressively higher intertidal mussel beds and to areas of reduced wave intensity. Only sites T5 and T4 (the most exposed sites) showed this same trend for the evenness index. In addition, an analysis over time (using the same statistical test) demonstrates a significant increase in species richness (but not the Shannon-Weaver Index or the evenness index) for most sites with time (Table VII). Even though the duration of the

Fig. 25. Species richness (S) trends over time for all study sites.

▲ - HIGH INTERTIDAL STUDY SITES

● - MID INTERTIDAL STUDY SITES

■ - LOW INTERTIDAL STUDY SITES

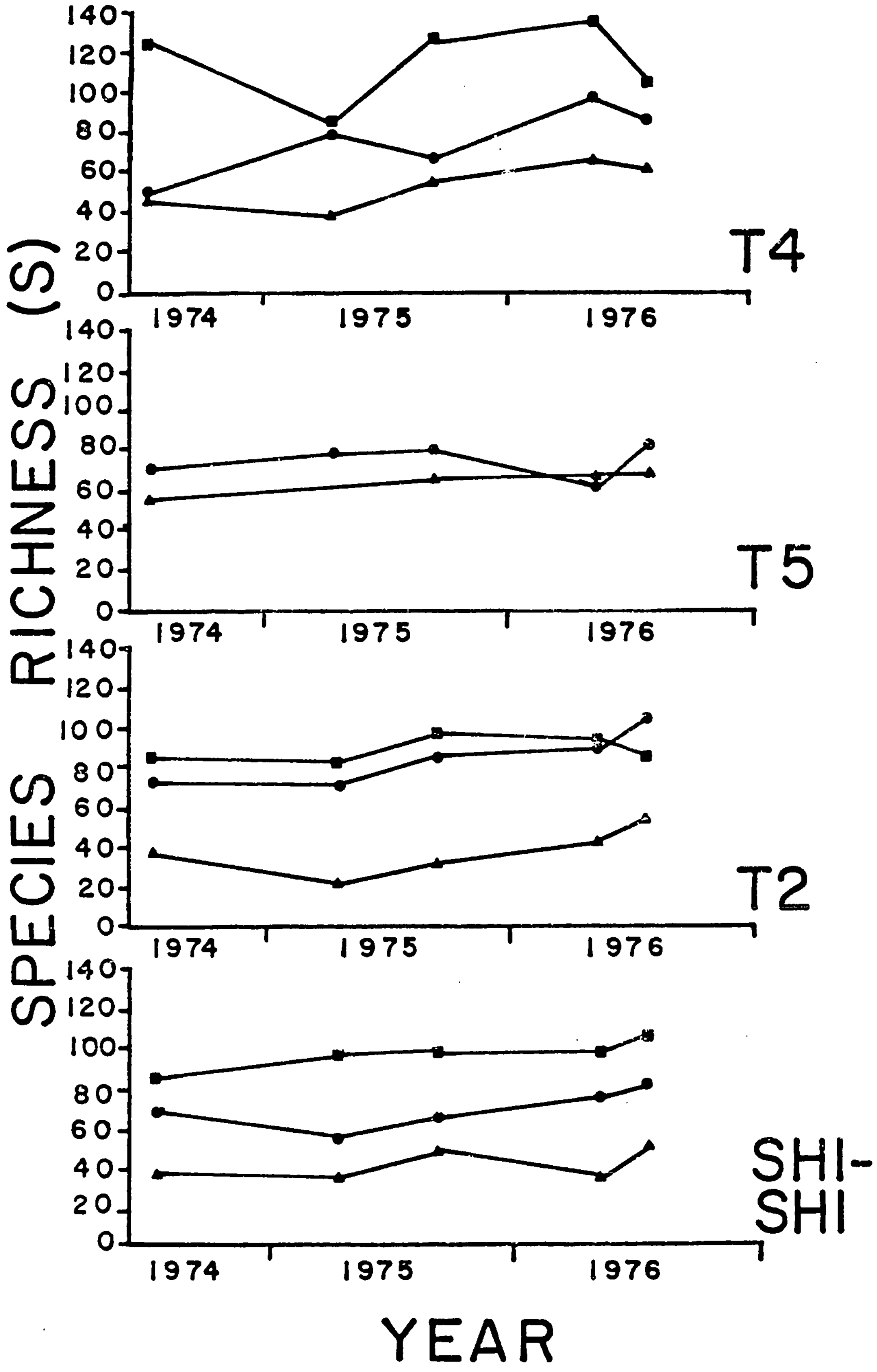

SPECIES RICHNESS (S)
140
120
100
80
60
40
20
0
1974
1975
1976
T4
T5
T2
SHI-
SHI
YEAR

Fig. 26. Shannon-Weaver (H') trends over time for all study sites.

▲ - HIGH INTERTIDAL STUDY SITES

● - MID INTERTIDAL STUDY SITES

■ - LOW INTERTIDAL STUDY SITES

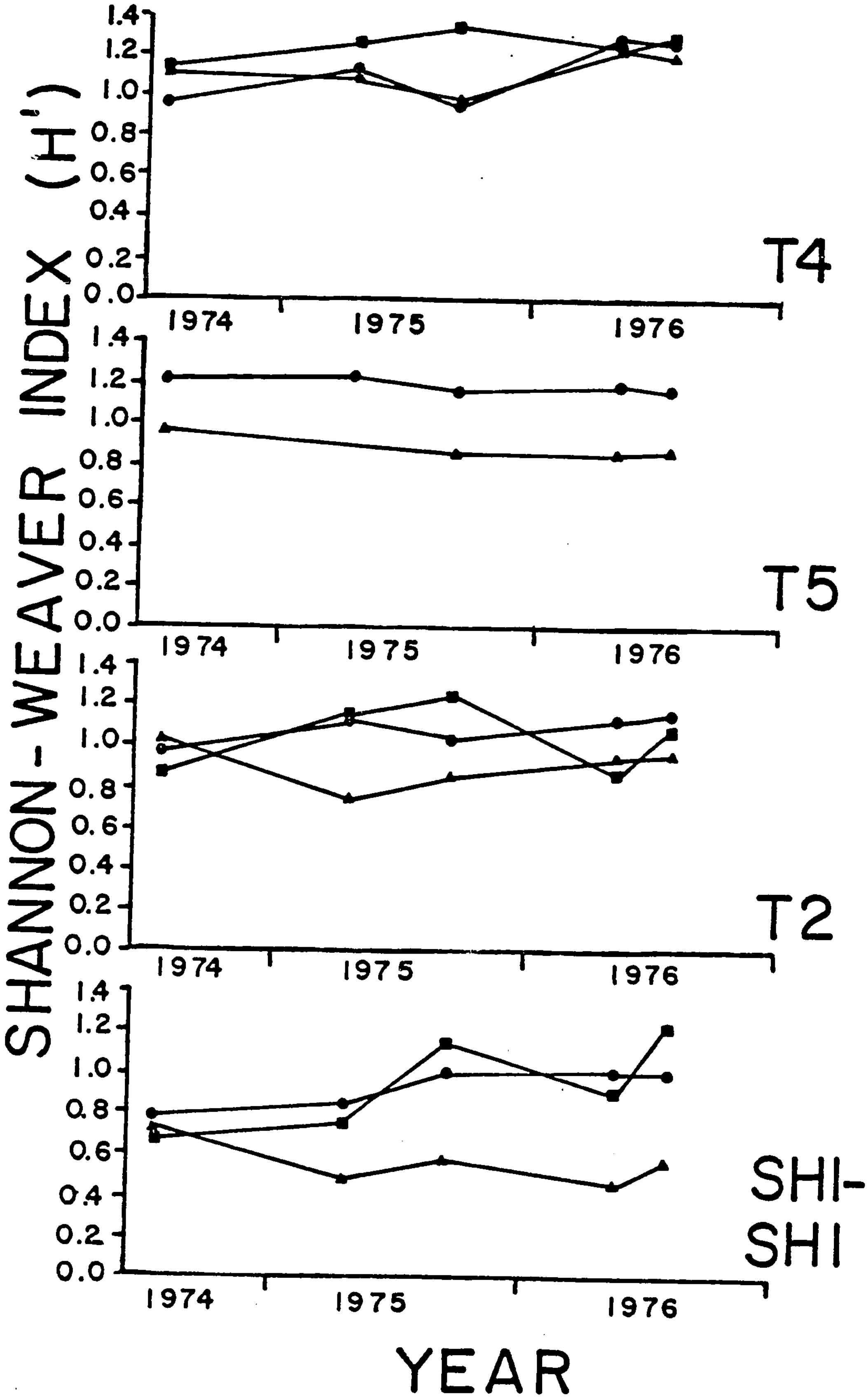

SHANNON - WEAVER INDEX (H')
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
T4
T5
T2
SHI-
SHI
1974
1975
1976
YEAR

Fig. 27. Evenness (J') trends over time for all study sites.

▲ - HIGH INTERTIDAL STUDY SITES

● - MID INTERTIDAL STUDY SITES

■ - LOW INTERTIDAL STUDY SITES

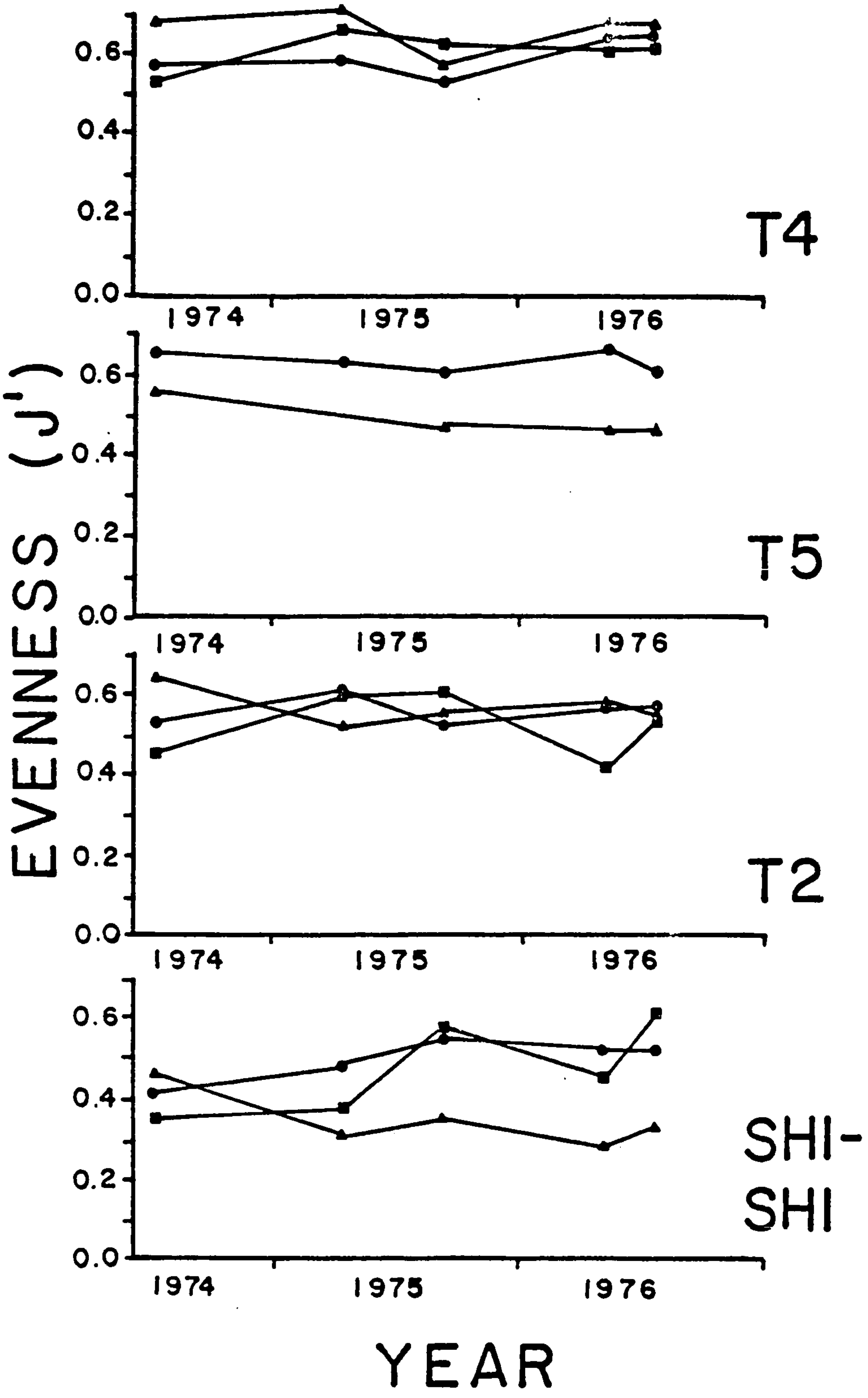

EVENNESS (J')
0.0
0.2
0.4
0.6
1974
1975
1976
T4
T5
T2
SHI-
SHI
YEAR

Fig. 28. Abundance of associated organisms and _M. californianus_ (averaged for all dates).

Bars indicate ± standard error.

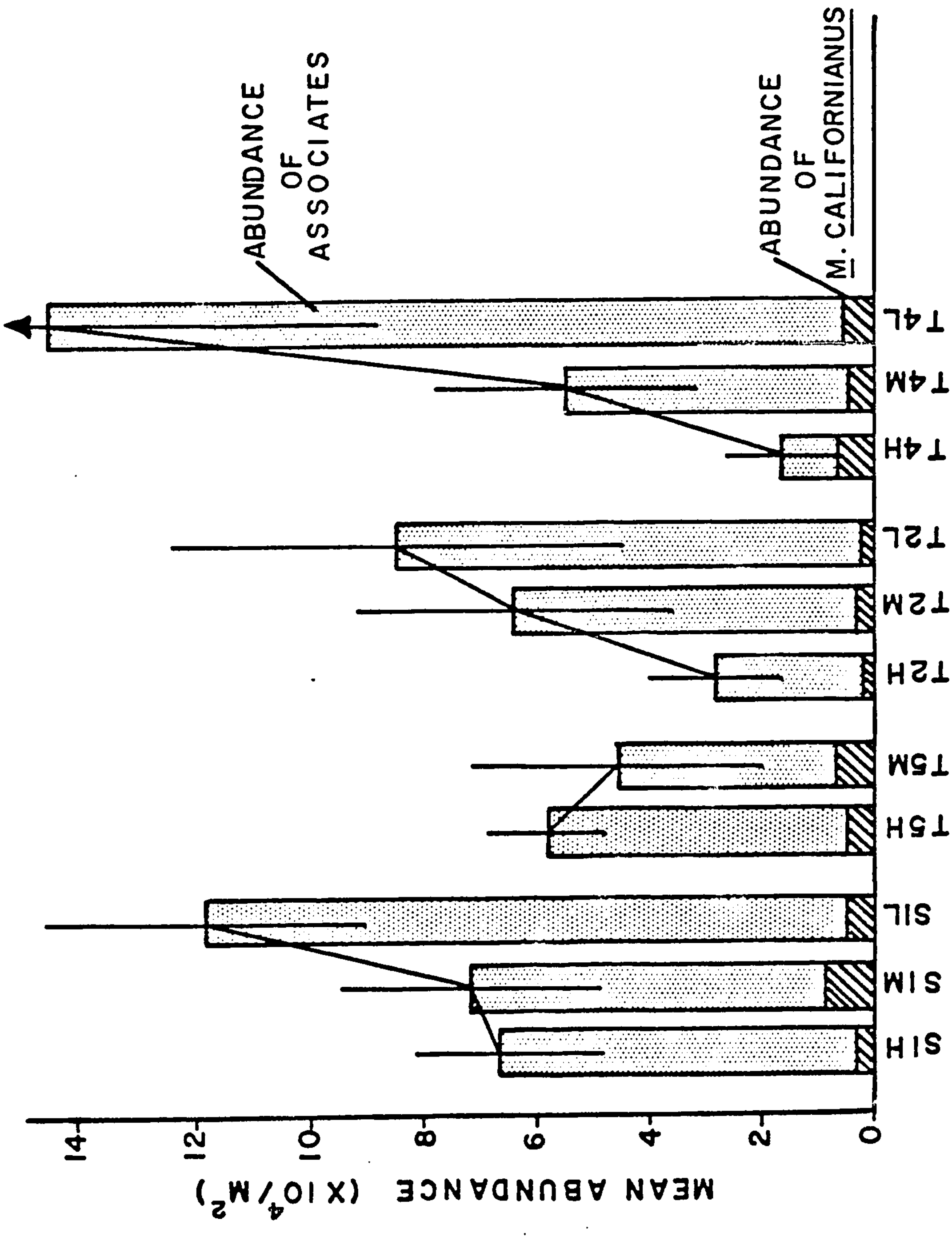

ABUNDANCE OF ASSOCIATES
ABUNDANCE OF M. CALIFORNIANUS
T4L
T4M
T4H
T2L
T2M
T2H
T5M
T5H
S1L
S1M
S1H
0
2
4
6
8
10
12
14
MEAN ABUNDANCE (X10^4/M^2)

Table VII. Significance levels for the Friedman's Rank Sums Test. Samples were analysed for trends between tidal heights and trends over time. The Friedman statistic is approximated by χ^2 values and here, critical values for p>0.10 were considered non-significant (ns).

		Shi-Shi	T2	T5	T4
Significant Trends with Tidal Height	(S)	**** (.01<p<.005)	*** (.02<p<.01)	ns (.50<p<.30)	**** (.01<p<.005)
	(H')	* (.10<p<.05)	ns (.50<p<.30)	** (.05<p<.02)	* (.10<p<.05)
	(J')	ns (.30<p<.20)	ns (.90<p<.80)	** (.05<p<.02)	* (.10<p<.05)
Significant Trends with Time	(S)	* (.10<p<.05)	* (.10<p<.05)	ns (.30<p<.20)	* (.10<p<.05)
	(H')	ns (.50<p<.30)	ns (.80<p<.70)	ns (.70<p<.50)	ns (.70<p<.50)
	(J')	ns (.50<p<.30)	ns (1.00<p<.90)	ns (.50<p<.30)	ns (.50<p<.30)

* = p<0.10
** = p<0.05
*** = p<0.02
**** = p<0.01

sampling period was relatively short (i.e., two years) a slight increase in the structural complexity is the most probable explanation for this rise in species richness.

A static analysis of the relationship between S, H', and J' and the structural complexity of various mussel beds yields a significant increase for species richness, the Shannon-Weaver index and the evenness index with increasing structural complexity (as measured by the depth of the beds). Fig. 29 shows that values for species richness range from around 30 species in shallow mussel beds to 135 species in deeper beds. This relationship is best described by the fitted line $Y = 3.15X + 39.98$, and the slope of the regression line is significantly positive at $p<.001$. Fig. 30 shows a similar trend for the Shannon-Weaver index with depth ($Y = 0.02X + 0.77$) with H' values ranging from 0.449 (a high intertidal shallow mussel bed at Shi-Shi -- least exposed) to 1.330 (a low intertidal deep bed at Tatoosh Site 4 -- most exposed). The slope of this regression line is also significantly positive at $p<.001$. One note of comparison here is that when calculating H' or H'', some authors use the natural logarithm rather than the logarithm to the base 10 as I have done (see above). When calculated with the natural logarithm, my H' diversity values range from a low of 1.034 at the Shi-Shi high intertidal site to 3.062 at the low intertidal site at Tatoosh Island. Finally, Fig. 31 shows how evenness (J') changes as a function of depth. Here, the fitted line has a positive slope and is significant at $p<.05$.

From the results of diversity trends in real mussel beds, it is apparent that species richness and the Shannon-Weaver index increase

Fig. 29. Relationship between species richness (S) and structural complexity of mussel beds (as measured by the depth of the beds).

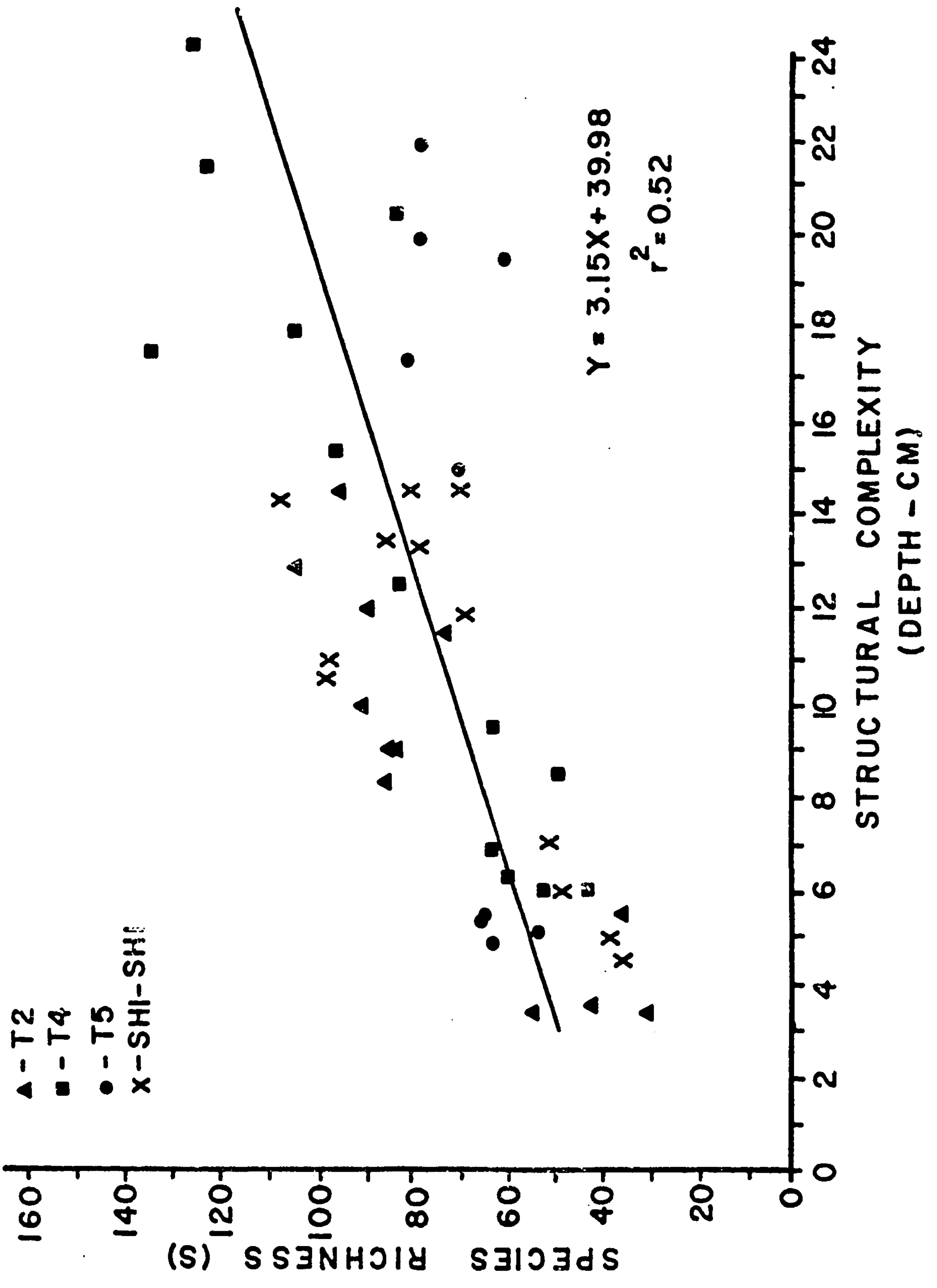

▲ - T2
■ - T4
● - T5
X - SHI-SHI
Y = 3.15X + 39.98
$r^2 = 0.52$
SPECIES RICHNESS (S)
0
20
40
60
80
100
120
140
160
STRUCTURAL COMPLEXITY
(DEPTH - CM)
0
2
4
6
8
10
12
14
16
18
20
22
24

Fig. 30. Relationship between the Shannon-Weaver index (H') and structural complexity of mussel beds (as measured by the depth of the beds).

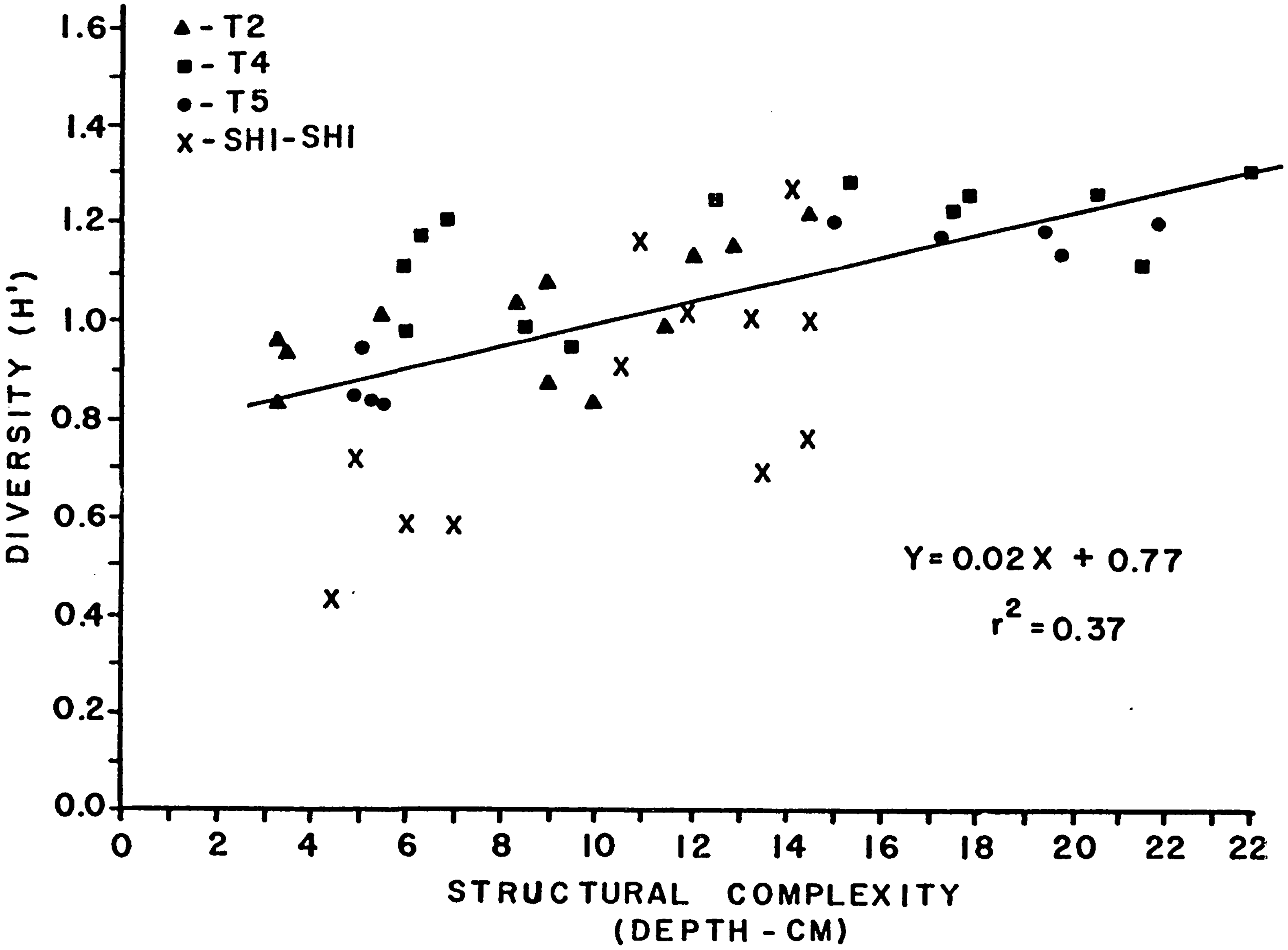
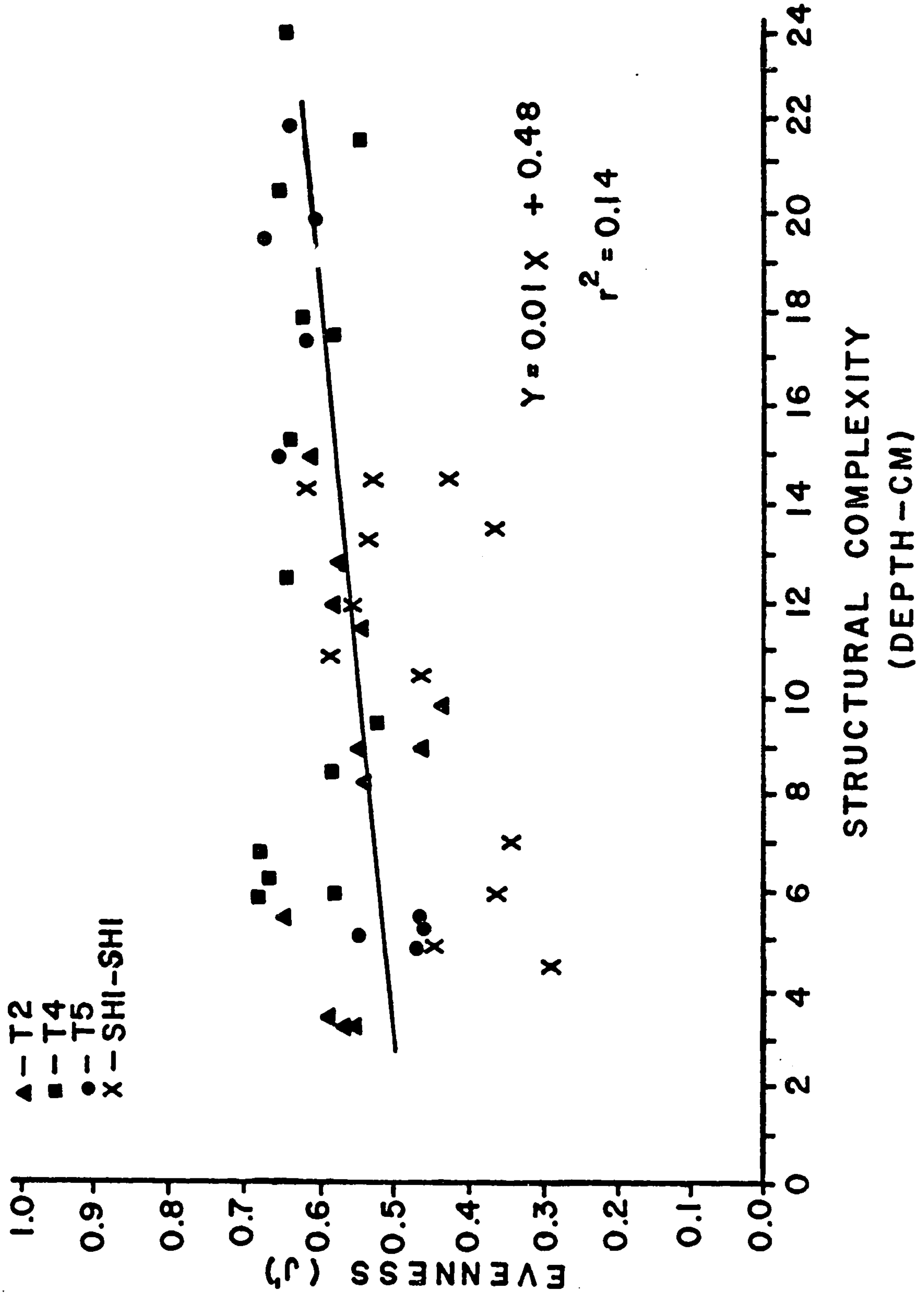

▲ - T2
■ - T4
● - T5
x - SHI-SHI
Y = 0.02 X + 0.77
r² = 0.37
DIVERSITY (H')
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
18
20
22
22
STRUCTURAL COMPLEXITY
(DEPTH - CM)

Fig. 31. Relationship between the evenness index (J') and structural complexity of mussel beds (as measured by the depth of the beds).


▲ – T2
■ – T4
● – T5
X – SHI-SHI
Y = 0.01 X + 0.48
r^2 = 0.14
EVENNESS (J')
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
16
18
20
22
24
STRUCTURAL COMPLEXITY
(DEPTH-CM)

as one proceeds from high to low intertidal mussel beds. However, confounded with decreasing intertidal height is the increasing structural complexity of the mussel bed matrix. Therefore, to determine which factor has the most influence on species diversity, I placed artificial structures of varying degrees of complexity (which physically resembled various sized mussel beds) in the high intertidal where mussel beds of high structural complexity never existed naturally, and in the low intertidal where mussel beds of low structural complexity rarely occur (see section on Artificial Mussel Beds).

An approach revealing more of the biological composition and variability of the taxa which comprise this diverse assemblage was taken by considering changes in the abundance of species and individuals in major taxonomic divisions. Appendix V provides a condensed taxonomic representation of the community for 29 major groupings primarily at the phylum and class level. It gives the total abundance of species and individuals within each of those divisions as well as the relative numerical importance of each division as represented by the proportion of species and the proportion of individuals for each group. For a more complete listing of the abundance of each species in any of the samples, the raw data are given in Appendix VI.

To understand better how individual species dominate each study site, I have extracted from the raw data the variation in the five most numerically abundant species. Table VIII gives the rank, abundance, and proportion (by numerical abundance) for these dominant species from each sample. In a few instances, a single species dominated the sample

Table VIII. Rank, absolute abundance, and relative abundance (by proportion) of the five most numerically abundant species for each sample. Numbers in parentheses indicate total abundance of associates in sample.

S1H	S1H3 (4036)			S1H4 (6246)			S1H5 (8022)			S1H6 (7435)			S1H7 (6418)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Chthamalus dalli	1	1842	.456	1	4166	.667	1	4762	.594	1	5393	.725	1	4223	.658
Balanus glandula	2	1043	.258	2	1382	.221	2	1885	.235	2	1181	.159	2	1070	.167
Hyale plumulosa	3	365	.090	5	103	.016	4	130	.016				5	110	.017
Littorina scutulata	4	284	.070	3	207	.033	3	544	.068	3	367	.049	3	288	.045
Collisella strigatella	5	133	.033	4	136	.022				4	188	.016	4	146	.023
Mytilus edulis							5	100	.012	5	102	.014			

S1M	S1M3 (11085)			S1M4 (6012)			S1M5 (4197)			S1M6 (6254)			S1M7 (7452)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Chthamalus dalli	1	4857	.438	1	2773	.461	1	1130	.269	1	2063	.330	1	2239	.300
Balanus glandula	2	3277	.296	2	1191	.198	3	671	.160	2	1063	.170	2	1600	.215
Hippothoa hyalina	3	649	.059	3	512	.085	4	609	.145	3	760	.122	3	879	.118
Barleeia sanjuanensis	4	403	.036				5	236	.056	5	410	.066			
Cucumaria pseudocurata	5	347	.031	4	281	.047	2	825	.197	4	472	.075	4	543	.073
Cirolana harfordi				5	265	.044									
Balanus cariosus													5	480	.064

S1L	S1L3 (14172)			S1L4 (11525)			S1L5 (9056)			S1L6 (15023)			S1L7 (7623)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Chthamalus dalli	1	9020	.636	1	7438	.645	1	2181	.241	1	7438	.495	4	479	.063
Balanus glandula	2	1875	.132	2	773	.067	3	793	.088	3	949	.063	2	820	.108
Cirolana harfordi	3	374	.026							5	533	.035			
Collisella strigatella	4	306	.022												
Hippothoa hyalina	5	293	.021	4	396	.034	4	398	.044	4	811	.054	5	412	.054
Spirorbidae sp. A				3	483	.042	2	2098	.232	2	1953	.130	1	2019	.265
Mytilus edulis				5	259	.022									
Balanus cariosus							5	384	.042				3	703	.092

T2H	T2H3 (1571)			T2H4 (1398)			T2H5 (1604)			T2H6 (3815)			T2H7 (5228)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Mytilus edulis	1	596	.379	1	599	.428	1	792	.494	1	1316	.345	2	1098	.210
Balanus glandula	2	183	.116												
Barleeia sanjuanensis	3	144	.092												
Hippothoa hyalina	4	119	.076												
Polysiphonia spp.	5	111	.071												
Musculus taylori				2	400	.286	5	75	.047	2	702	.184	1	1490	.285
Dynamenella sheareri				3	138	.099	2	232	.145	3	488	.128	5	461	.088
Littorina sitkana				4	61	.044				5	256	.067	3	585	.112
Hyale grandicornis				5	59	.042									
Ianiropsis kincaidi							3	96	.060						
Lasaea subviridis							4	85	.053	4	259	.068			
Oligochaeta sp. A													4	464	.089

T2M	T2M3 (4257)			T2M4 (2957)			T2M5 (7366)			T2M6 (7356)			T2M7 (9710)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Cucumaria pseudocurata	1	1276	.300	2	624	.211	1	2176	.295	3	916	.125	2	2168	.223
Barleeia sanjuanensis	2	935	.220	1	753	.255	2	1569	.213	1	2208	.300	1	2655	.273
Hippothoa hyalina	3	821	.193	4	260	.088	4	785	.107	4	753	.102	3	803	.083
Homalopoma lacunatum	4	208	.049	5	121	.041	5	178	.024				5	430	.044
Lasaea subviridis	5	145	.034	3	402	.136	3	1075	.146	2	1096	.149			
Cirolana harfordi										5	363	.049			
Balanus cariosus													4	691	.071

T2L	T2L3 (13285)			T2L4 (2560)			T2L5 (11268)			T2L6 (6829)			T2L7 (7246)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Barleeia sanjuanensis	1	7020	.528	1	905	.354	2	1502	.133	1	3812	.558	1	2171	.300
Cucumaria pseudocurata	2	1167	.088							5	207	.030	2	1477	.204
Balanus cariosus	3	1017	.077										3	963	.133
Hippothoa hyalina	4	770	.058	3	289	.113	4	1021	.091	2	779	.114	4	460	.063
Dynamenella sheareri	5	516	.039	5	107	.042									
Spirorbidae sp. A				2	293	.114	3	1455	.129						
Cirolana harfordi				4	189	.074							5	281	.039
Hyale frequens							1	2552	.226						
Sertularella fusiformis							5	460	.041						
Halichondria panicea										3	367	.054			
Homalopoma lacunatum										4	308	.045			

T4H

	T4H3 (667)			T4H4 (653)			T4H5 (1486)			T4H6 (2663)			T4H7 (1559)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Hippothoa hyalina	1	234	.351	1	187	.286	1	524	.353	1	735	.276	1	559	.353
Polysiphonia spp.	2	70	.105												
Mytilus edulis	3	62	.093	2	84	.129	4	68	.046	2	278	.104			
Hyale grandicornis	4	47	.070	3	58	.089									
Collisella strigatella	5	35	.052												
Chthamalus dalli				4	56	.086	3	92	.062				2	123	.079
Dynamenella sheareri				5	51	.078				3	250	.094			
Onchidella borealis							2	400	.269	4	187	.070	5	76	.049
Lasaea subviridis							5	63	.042	5	162	.061			
Cucumaria pseudocurata													3	92	.059
Nematoda sp. B													4	90	.058

T4M

	T4M3 (2478)			T4M4 (8640)			T4M5 (4451)			T4M6 (6760)			T4M7 (4701)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Barleeia sanjuanensis	1	684	.276	2	1364	.158	2	1038	.233	1	1184	.175	2	720	.153
Cucumaria pseudocurata	2	618	.249				1	1304	.293	4	572	.085	1	1154	.245
Hippothoa hyalina	3	414	.167	3	1205	.139	3	881	.198	3	784	.116	3	647	.138
Lasaea subviridis	4	150	.061	1	1985	.230									
Phascolosoma agassizii	5	101	.041							5	376	.056			
Pancolus californiensis				4	518	.060									
Nematoda sp. A				5	506	.059							4	261	.056
Cirolana harfordi							4	240	.054	2	1085	.161			
Homalopoma lacunatum							5	170	.038				5	250	.053

T4L

	T4L3 (20670)			T4L4 (6480)			T4L5 (16523)			T4L6 (18244)			T4L7 (10546)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Spirorbidae spp.	1	8215	.397	1	1191	.184	2	2697	.163	2	2789	.153	3	1146	.109
Cirolana harfordi	2	1836	.089	5	232	.036				4	1704	.093			
Ianiropsis kincaidi	3	1274	.062												
Jassa falcata	4	1211	.059				3	1558	.094	3	1857	.102			
Hippothoa hyalina	5	722	.035	3	484	.075				5	1378	.076	4	1123	.106
Barleeia sanjuanensis				2	636	.098	1	2773	.168	1	4417	.242	2	1385	.131
Dynamenella sheareri				4	240	.037									
Hyale frequens							4	1332	.081						
Chthamalus dalli							5	1232	.075				5	772	.073
Balanus cariosus													1	1736	.165

T5H	T5H3 (4771)			T5H4	T5H5 (6310)			T5H6 (4786)			T5H7 (6476)		
	RANK	ABUND.	PROP.		RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
				(NO DATA)									
Lasaea subviridis	1	1616	.339		1	3344	.530	1	2601	.543	1	3607	.557
Pancolus californiensis	2	1077	.226		3	420	.067						
Hippothoa hyalina	3	562	.118		2	546	.087	2	648	.135	2	540	.083
Nematoda sp. A	4	335	.070		5	266	.042	5	125	.026	3	391	.060
Barleeia sanjuanensis	5	228	.048					4	257	.054	4	379	.059
Musculus taylori					4	391	.062	3	.287	.060	5	279	.043

T5M	T2M3 (2977)			T5M4 (4132)			T5M5 (4595)			T5M6 (2424)			T5M7 (8424)		
	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.	RANK	ABUND.	PROP.
Hippothoa hyalina	1	785	.264	3	368	.089	1	1202	.262	1	615	.254	4	882	.105
Barleeia sanjuanensis	2	531	.178	2	733	.177	3	683	.149	3	298	.123	1	1782	.212
Balanus cariosus	3	265	.089	1	927	.224	4	280	.061				3	1173	.139
Lasaea subviridis	4	182	.061				5	109	.024						
Cucumaria pseudocurata	5	120	.040				2	896	.195	4	164	.068	2	1527	.181
Cirolana harfordi				4	309	.075				2	348	.144	5	365	.043
Pollicipes polymerus				5	265	.064									
Halichondria panicea										5	144	.060			

by more than 50 per cent. This disproportionate distribution of individuals was especially common at the Shi-Shi study area, accounting for the low evenness values found in that region (Fig. 31).

Nearly all of the associated species can be classified as either epibiota (including fauna and flora), mobile fauna, or infauna. Epibiota are defined here as those organisms which are sessile and attached to the valves of the mussels. Mobile fauna are those which have the facility to move freely throughout the interstices of the mussel matrix. Infauna exist in or on, and are generally dependent upon, the gorp (see above for definition) at the base of the mussel matrix.

The relationship between the mussels and each of the associated species may be negative, neutral, or positive. In general, infauna seem to be of negligible consequence to the health and well-being of the mussel beds. They are generally either filter feeders, deposit feeders, or scavengers. Because they are at the base of the mussel matrix, the infaunal filter feeders utilize sea-water already partially filtered by the mussels and therefore most likely do not compete for food resources with them. Deposit feeders utilize minute particles of organic matter which have settled to the bottom of the matrix. And scavengers generally consume larger bits of dead organic matter which have become lodged in the matrix, but occasionally may act as predators on smaller mobile fauna.

Epibiota are those invertebrates and algae which foul the shells of the mussels. Species such as hydroids, bryozoans, crustose red algae (or juvenile barnacles and algae) nearly always will have a neutral effect. However, when barnacles and macro-algae mature, they usually have a negative influence, either by interfering with food intake currents, growing into the aperture of the shell causing excessive desiccation during low tides, or by creating greater resistance to the shearing stresses of wave action thus making it increasingly more difficult for the mussels to remain fixed to the rock surface because of increased strain on the byssal thread attachment (see Chapter 5).

Mobile fauna represent the largest category of associated species and span the gamut of interactions with mussels from being lethal (through predation or parasitism) to being necessary for the mussels' survival. Table IX shows the type of effect that taxa in each of the three major categories of associated fauna and flora have on the mussels themselves. Because it was impossible to test or observe the interaction of each of the 300 plus species individually, the reliability of my interpretation of some interactions are questionable. These cases are designated with question-marks. Also, many taxa essentially form guilds (Root, 1967) in their response to and interaction with the mussels, and therefore I have lumped them accordingly in Table IX.

The relative percentage (by numbers of species) of these three functional groups remains quite constant over time, tidal height, and study areas. Approximately 20-30% of the species are epibiota, 60-70% are mobile fauna, and usually 10-15% are infauna. However, when one considers the numerical abundance of individuals rather than the number of species, there is a dramatic difference between the

Table IX Number of taxa that have a positive, neutral, or negative influence on M. *californianus*. (?) indicates uncertain influence.

	EPIFAUNA		MOBILE FAUNA		INFAUNA
(POSITIVE)	CHLOROPHYTA (2) PHAEOPHYTA (5) RHODOPHYTA (10)		PLATYHELMINTHES (1) NEMERTEA (1) POLYPLACOPHORA (4) ARCHAEOGASTROPODA (12) MESOGASTROPODA (1)+(2?) NEOGASTROPODA (3) OPISTHOBRANCHIA (1)	PULMONATA (1) ISOPODA (1)+(2?) INSECTA (1) ASTEROIDEA (2)+(1?) ECHINOIDEA (3) OSTEICHTHYS (2?)	
(NEUTRAL)	CHLOROPHYTA (1) PHAEOPHYTA (1) RHODOPHYTA (3) HYDROZOA (9)		ANTHOZOA (2?) NEMERTEA (2) NEMATODA (2?) MESOGASTROPODA (8) NEOGASTROPODA (4?) OPISTHOBRANCHIA (1?) OLIGOCHAETA (1?) PYCNOGONIDA (3?) PSEUDOSCORPIONIDAE (1?)	ACARI (10?) TANAIDACEA (4?) ISOPODA (13?) AMPHIPODA (32?) DECAPODA (7?) INSECTA (9?) HOLOTHUROIDEA (3) OSTEICHTHYES (3?)	MESOGASTROPODA (4) NEOGASTROPODA (1?) BIVALVIA (13) SIPUNCULIDA (1) OPHIUROIDEA (1)
(NEGATIVE)	CHLOROPHYTA (2) PHAEOPHYTA (7) RHODOPHYTA (13) PORIFERA (3) BIVALVIA (2)	POLYCHAETA (11) CIRRIPEDIA (6) BRYOZOA (17) ASCIDIACEA (1)	ANTHOZOA (1) NEOGASTROPODA (1)+(1?) BIVALVIA (1) POLYCHAETA (25?)	PYCNOGONIDA (1?) DECAPODA (1)+(2?) ASTEROIDEA (2)	POLYCHAETA (27?)

Shi-Shi and Tatoosh study areas. At Shi-Shi, the percentage of epibiotic individuals is relatively high (average = 78 ± 10%), whereas, the average for all sites at Tatoosh is 30 ± 16%. The abundance of mobile fauna is correspondingly reversed showing an average of 20 ± 8% at Shi-Shi and an average of 40 ± 14% at Tatoosh. This may be explainable if many of the mobile fauna are predators or grazers on epibiota growing on the mussel shells, and with an increased abundance of predators and/or grazers at Tatoosh in general, this could diminish the relative abundance of epibiota at that location. The percentage of individuals that are infauna averages only 2 ± 2% at Shi-Shi but shows over an order of magnitude difference at Tatoosh (average = 29 ± 19%). As yet, I have no explanation for this trend. These percentages for each sample by area are given in Table X.

Table X. Number of species and abundance of individuals that are epibiota (EPI), mobile fauna (MOB), or infauna (IN) for each sample. Percentage by number of species and by abundance of individuals is also given for each group.

SAMPLE CODE	NUMBER OF SPECIES			ABUNDANCE OF INDIVIDUALS			PERCENT BY NUMBER OF SPECIES	PERCENT BY ABUNDANCE OF INDIVIDUALS
	EPI	MOB	IN	EPI	MOB	IN	EPI/MOB/IN	EPI/MOB/IN
SHI-SHI								
S1H3	8	28	2	2957	1054	25	21/74/5	73/26/1
S1H4	7	23	6	5615	579	52	19/64/17	90/9/1
S1H5	11	35	4	6855	1143	24	22/70/8	86/14/0
S1H6	9	23	4	6714	692	29	25/64/11	90/9/1
S1H7	11	31	9	5490	812	116	21/61/18	85/13/2
S1M3	15	50	5	8953	1628	504	22/71/7	81/15/4
S1M4	9	38	8	4523	1318	171	16/69/15	75/22/3
S1M5	13	50	6	2511	1547	282	19/72/9	58/36/6
S1M6	17	54	8	3937	1882	435	22/68/10	63/30/7
S1M7	14	57	9	5400	1884	167	18/71/11	73/25/2
S1L3	19	59	7	11910	2100	161	22/69/9	84/15/1
S1L4	28	60	9	9899	1541	85	29/62/9	86/13/1
S1L5	29	64	6	6557	2370	129	29/65/6	72/26/2
S1L6	33	59	7	12159	2614	250	33/60/7	81/17/2
S1L7	34	63	10	5374	1926	322	32/59/9	71/25/4
TATOOSH								
T2H3	8	22	7	443	908	220	22/59/19	28/58/14
T2H4	4	15	5	11	942	445	17/62/21	1/67/32
T2H5	6	20	6	66	1336	202	19/62/19	4/83/13
T2H6	11	26	6	424	2384	1007	26/60/14	11/62/27
T2H7	10	39	6	298	2951	1979	18/71/11	6/56/38
T2M3	16	46	10	1095	1987	1174	22/64/14	26/47/27
T2M4	11	53	9	419	1275	1263	15/73/12	14/43/43
T2M5	19	59	8	1102	3320	2944	22/69/9	15/45/40
T2M6	20	61	8	1161	2596	3598	23/68/9	16/35/49
T2M7	24	70	11	2081	4475	3154	23/67/10	21/46/33
T2L3	22	53	9	2554	3542	7187	26/63/11	19/27/54
T2L4	22	52	8	886	738	936	27/63/10	35/29/36
T2L5	31	58	7	4152	5519	1597	32/61/7	37/49/15
T2L6	21	56	13	1637	1126	4065	23/62/15	24/16/60
T2L7	18	56	13	1998	2781	2467	21/65/15	28/38/34
T4H3	11	28	5	368	265	34	25/64/11	55/40/5
T4H4	10	22	5	322	304	27	27/59/14	49/47/4
T4H5	12	34	7	722	639	125	23/64/13	49/43/8
T4H6	13	42	9	1100	1138	425	20/66/14	41/43/16
T4H7	17	35	8	852	537	170	28/58/14	55/34/11
T4M3	14	30	6	501	1009	968	28/60/12	20/41/39
T4M4	18	53	8	1509	2925	4206	23/67/10	17/34/49
T4M5	12	44	7	1053	2070	1327	19/69/12	24/46/30
T4M6	23	61	11	1843	3063	1852	24/64/12	27/45/28
T4M7	19	55	9	1104	2335	1260	23/66/11	23/50/27
T4L3	31	79	13	12049	8088	531	25/64/11	58/39/3
T4L4	25	52	7	3776	2058	646	30/62/8	58/32/10
T4L5	31	80	14	6834	6605	3083	25/64/11	41/40/19
T4L6	35	83	15	7462	6143	4635	26/62/12	41/34/25
T4L7	28	66	10	6076	3041	1427	27/63/10	58/29/13
T5H3	10	36	8	674	1622	2475	18/67/15	14/34/52
T5H4	-	-	-	-	-	-	-	-
T5H5	13	43	8	808	1206	4296	20/67/13	13/19/68
T5H6	12	44	9	829	669	3288	18/68/14	17/14/69
T5H7	13	43	10	913	879	4684	20/65/15	14/14/72
T5M3	15	47	9	1272	908	797	21/66/13	43/30/27
T5M4	22	48	8	1972	1291	868	28/61/11	48/31/21
T5M5	19	52	9	1833	1914	848	24/65/11	40/42/18
T5M6	16	37	8	1040	1025	359	26/61/13	43/42/15
T5M7	19	52	11	2570	3907	1947	23/63/14	31/46/23

OBSERVATIONS ON THE COMMUNITY MEMBERS

Because the overall organization, functioning, and dynamics of a community such as the mussel bed system is so dependent upon the biology and natural history of the individual species within the assemblage, I have further considered these aspects for as many taxa as possible. Below, I present observations on the major functional and taxonomic groups and their possible significance within the mussel bed community. The information presented combines original observations and relevant literature on the resident species. Observations on living mussel bed communities were conducted from 1972-1978, usually at low tide. Occasionally SCUBA gear was used to observe interactions of species which are only active at high tides.

MARINE ALGAE:

All algal species considered in this survey were sessile (epiflora) and therefore partially dependent upon the surface of the mussel matrix for settlement and attachment sites. Their functional roles do not fall along strict taxonomic lines so I will make no attempt to consider separately effects of the three major taxonomic divisions.

Many of the smaller, filamentous algae such as _Endocladia_, _Microcladia_ and _Polysiphonia_ act as settlement sites for _M_. _edulis_ (see Chapter 2) and to a lesser degree for _M_. _californianus_ and therefore could play a beneficial role to the mussels. The filamentous _Cladophora_ could potentially act in this same manner, but I have never seen juvenile *Mytilus* spp. on it. Another beneficial feature which some algae undoubtedly impart is protection from desiccation. Since the upper intertidal limit of *M. californianus* is determined by physiological stresses to temperature and desiccation, moist blades of algae keep mussels shaded, cool, and moist, possibly extending their intertidal range where this occurs. Algae in this category are the ulvoids, *Alaria*, *Fucus*, *Haedophyllum*, *Laminaria*, *Pelvetiopsis*, *Callophyllus*, *Endocladia*, *Gigartina*, *Halosaccion*, *Iridaea*, *Microcladia*, *Polysiphonia*, *Porphyra*, and *Schizymenia*.

At the other end of the spectrum, some of these same algae and others can have a dramatic negative effect on the mussels as well. This happens primarily in two ways. First, encrusting algae (such as the corallines, *Analipus*, *Ralfsia*, *Hildenbrandia*, and *Petrocelis*) can grow between the valves, preventing total closure, thereby resulting in excessive desiccation and death for the mussel. Or they may grow over the aperture, preventing effective feeding and/or respiration (pers. obs.). The larger macro-algae (*Alaria*, *Fucus*, *Haedophyllum*, *Laminaria*, *Pelvetiopsis*), and to a lesser extent, the smaller macro-algae (*Cladophora*, *Analipus*, *Callophyllus*, *Endocladia*, *Gigartina*, *Hallosaccion*, *Iridaea*, *Microcladia*, *Polysiphonia*, *Porphyra*, and *Schizymenia*) can create increased shearing stresses to wave action, leading to the dislodgement of mussels from the rock surface.

PROTOZOA:

Because their size ranged from minute to ca. 2.0 mm, the Foraminifera were not formally considered in the species counts from the mussel bed system. However, one very common species (*Eponides columbiensis*) was found amongst the gorp.

PORIFERA:

Cliona has an obvious detrimental effect by boring into the shell, weakening it, and potentially causing death to the mussel. Although I have recorded *Cliona*'s presence, I have rarely observed it to cause massive damage in *M. californianus*. It appears to colonize regions of the shell from which the periostracum has been at least slightly eroded, and therefore is not common on small, young shells (≤ 20 mm). *Halichondria* and *Haliclona* are most commonly found in deep or low intertidal mussel beds and primarily have detrimental effects by the same process described above for encrusting algae which grow between the valves of the mussels, preventing closure. They are possibly consumed by *Henricia leviuscula* and *Diodora aspera* (see below).

CNIDARIA:

As epifauna, all eight species of hydroids appear to act similarly. They undoubtedly depend on and compete for space on the mussel shells, but I consider their effect on the mussels to be neutral.

In the intertidal, *Stylantheca* is rare, only found at the lowest, most exposed sites and therefore probably of little consequence here. However, on subtidal mussels, such as those on Duncan and Duntze Rocks (Paine, 1976b), this hydrocoral may cover as much as 80-90%

of the surface of the shell. The importance and direction of its interaction with those mussels is uncertain.

Both *Anthopleura elegantissima* and *A. xanthogrammica* appear to utilize the mussel beds as nursery grounds, the latter moving to lower intertidal and subtidal sites as it matures (Sebens, 1977). *A. elegantissima* seems capable of considerable mobility throughout the interstices of the mussel matrix, and its influence on mussels is most likely neutral, whereas *A. xanthogrammica* usually remains fixed to or near the primary substratum. *A. xanthogrammica* normally captures mussels when they are dislodged from the rock surface by predators or wave action (Dayton, 1971; Sebens, 1977); it also reportedly can bend its column over to capture live attached mussels *in situ* (Sebens, pers. comm.).

Diadumene's presence was noted but its role is unknown.

PLATYHELMINTHES:

Notoplana was moderately common in some regions (see Appendix VI) and where abundant, probably has a positive influence on mussels by removing settling barnacles from the valves. Egg capsules were found most commonly in mid-intertidal samples.

NEMERTEA:

The three nemerteans encountered were active during low tides and were all active predators. *Amphiporus* was observed, on several occasions, to capture stranded amphipods, which were unable to move about at low tide. Its direct influence is most likely neutral.

Paranemertes was observed to be feeding on small polychaetes in the families Nereidae and Syllidae, consistent with the information of Roe (1970, 1971, 1976) who found this nemertean to prey on at least five families of polychaetes.

Emplectonema was also seen crawling on exposed surfaces at low tide, often preying on barnacles (*Balanus glandula* and *Chthamalus*). In California, Glynn (1965) found this nemertean to be most active during night low tides, non-selectively feeding on barnacles, *Thais emarginata* eggs and *Nereis*. Kent (1976), using antisera of various potential prey items, also found *Notoplana acticola* to be a common food item of this nemertean in Oregon. It is uncertain whether the local *Notoplana* (?*inquieta*) is similarly consumed. Therefore, this nemertean may provide some benefits (by removing barnacles) as well as some detriment to the mussel matrix by removing *Notoplana* (which also feeds on barnacles).

NEMATODA:

Two distinctly different morphological forms were observed but neither their identification nor their role in this community is known.

MOLLUSCA:

Polyplacophora:

The chitons found most commonly in the mussel bed system (*Cyanoplax dentiens*, *Katharina tunicata*, *Mopalia ciliata*, and *Mopalia muscosa*) most likely function as a guild, preferentially consuming micro- and small macro-algae (Himmelman & Carefoot, 1975), but through their foraging activities also scrape some invertebrates such as bryozoa, hydroids and even barnacles from the substrate. In general, their effect on the mussels is strongly positive by removing epibiota.

Archaeogastropoda:

With the exception of Acmaea, Diodora, and possibly the Homalopoma species, the members of this group also perform similar functions as the Polyplacophora by grazing diatoms and algal spores and sporelings (for feeding habits, see Castenholz, 1961; Foster, 1962; Abbott, 1964; Dahl, 1964; Abbott et al., 1968; Craig, 1968; Buckland-Nicks et al., 1973; Nicotri, 1977), benefiting mussels by keeping the shells clean. Acmaea mitra is known to graze coralline algae (Raymore, 1971; Kozloff, 1973), Diodora aspera likely preys heavily on sessile invertebrates (Gonor, in Miller, 1968; Thompson, 1976) and the role of Homalopoma here is uncertain. The abundance of Homalopoma lacunatum often exceeded 2000/m^2. Tegula funebralis is another grazer feeding mostly on benthic diatoms at night (Hewatt, 1937; Best, 1964; Glynn, 1965). It is likely that the mussel bed acts as a nursery ground for Tegula. Only immature individuals (sensu Paine, 1971a) were found (with sizes never reaching over 12 mm). In addition, densities of these juveniles reached upwards of 250-300/m^2 at more protected mid-intertidal sites such as Shi-Shi Bench. For bioenergetics and population dynamics of Tegula, see Paine (1969b, 1971a).

Mesogastropoda:

The slipper limpets (Crepidula spp.) are filter feeders and although using the mussel shells for attachment, they are probably not detrimental even in terms of competing for food. *Alvinia* and *Barleeia* are commonly found in the gorp and therefore are most likely deposit feeders or scavengers. *Barleeia* was extremely common in some beds, and at times its abundance reached over 70,000/m^2. *Balcis* is is possibly ectoparasitic on echinoderms (Carlton & Roth, 1975). *Opalia* feeds on *Anthopleura xanthogrammica* (Thorson, 1958) and therefore may possibly be secondarily beneficial to mussels (see Cnidaria). The role of *Cerithiopsis stejnegeri* is unknown, but a close relative, *Cerithiopsis tubercularis* has been found in or on sponges (Lebour, 1933). *Velutina velutina* feeds on tunicates (Fretter & Graham, 1962). *Trichotropis* is a filter feeder (Yonge, 1962) but it is unlikely that it competes at all with *Mytilus*.

Neogastropoda:

Most members of this group are predators. *Ceratostoma* has been observed to feed on barnacles (*Balanus cariosus*), although as an adult it can consume *M. californianus* (A.R. Palmer, pers. comm.). Almost all *Ceratostoma* found were juveniles, indicating that the mussel bed may act as the nursery ground for this species. Lloyd (1971) showed that *Searlesia dira* preys on a wide variety of invertebrates. At a rocky intertidal site in the San Juan Islands, Lloyd observed the most common food items of *Searlesia* to be (in order of preference by abundance): *Littorina sitkana*, *Littorina scutulata*, *Notoacmea scutum*, *Collisella pelta*, *Collisella digitalis*, *Collisella strigatella*, and *Calliostoma ligatum*. Other observations were made of it feeding on *Lacuna* sp., other *Searlesia dira*, *Katharina tunicata*, *Mopalia muscosa*, *Mytilus edulis*, *Hemigrapsus nudus*, *Pagurus* spp. and *Balanus* spp. It also showed a preference for weakened or dead animals and undoubtedly acts as an effective scavenger as well. Paine (pers. comm.) has found it preying on Littorina sitkana at Tatoosh Island and at Mukkaw Bay observed it in the oral region of Pisaster ochraceus. The two Thais species concentrate mostly on barnacles and mussels. Thais will prefer Mytilus edulis over M. californianus and therefore may be a major factor in reducing competition for space between these congeneric mussels (see Chapter 2). Amphissa is primarily a scavenger.

Opisthobranchia:

Odostomia spp. have long been recognized as ectoparasites (Dall & Bartsch, 1909; Bullock & Boss, 1971). Although O. columbiana has been shown to parasitize Trichotropis cancellata in Washington waters (Clark, 1971) and O. bisuturalis is most commonly found on Nassarius and Mytilus edulis (Bullock & Boss, 1971), the host of O. delicosa to my knowledge is as yet unknown.

Onchidella is an active diatom grazer at low tide (Wilson, 1976). Like other Onchidiacea, this species has a functional lung and seeks the refuge of a "nest" at high tide (Arey & Crozier, 1921). Like Onchidella, Siphonaria is also found at the highest intertidal sites, exhibits homing behaviour, and grazes diatoms. These two species again impart a benefit to the mussels as "cleaners."

Bivalvia:

The mytilids obviously comprise the bulk of the biomass for this community, with Mytilus californianus being the dominant species in the mid to lower intertidal zone and M. edulis being dominant in the upper zone (see Chapter 2). Modiolus is not uncommon, and only reaches sizes of ca. 30 mm. *Modiolus* and *Adula* are filter feeders which pose no competitive threat to *M. californianus*. However, *Adula*, by the nature of its mechanical boring activities (Yonge, 1955) can weaken the shell of *Mytilus* in those places where it penetrates, but is usually found simply nestled in the antero-dorsal groove at the junction of the two valves. *Musculus taylori* is most likely identical to *M. pygmaeus* of Glynn (1965). It was very common at high intertidal sites, often exceeding 16,000/m^2. *Pododesmus* was rare and, when present, only small juveniles were found. *Kellia*, *Petricola*, *Hiatella*, and *Entodesma* appear to be nestling filter feeders occupying whatever crack or crevice is available. *Mysella* is also a filter feeder but its microhabitat is restricted to the trapped sediment at the base of the mussel bed. It has been shown to filter diatoms and copepods (Maurer, 1967); this food and smaller particles are also the likely diet of *Lasaea*, *Protothaca*, *Saxidomus*, and *Mya*, which share the sediment habitat. *Lasaea subviridis* was found most commonly at the byssus/rock or byssus/gorp interface, consistent with previous observations by Keen (1938) and Glynn (1965). It was fairly ubiquitous and at one station its abundance reached levels of over 19,000/m^2. *Macoma* is also restricted to the sediment but has the versatility to filter feed or deposit feed by sweeping its intake siphon over the sediment (Reid & Reid, 1969).

ANNELIDA:

Because of the destructive nature of the sampling scheme, and because of the difficulty of making observations on organisms within the interstices of the bed, natural histories of the Annelida are especially lacking.

Oligochaeta:

Oligochaeta are generally considered to be deposit or detritus feeders (Cook & Brinkhurst, 1975). Only one recognizable form was observed in this community and its role is unknown. In the following list I have simply recorded those polychaete families and the number of representative species (in parentheses) for which I have no observations or other information: Orbiniidae (1), Cirratulidae (2), Sigalionidae (1), Chrysopetalidae (2), Hesionidae (1), Sphaerodoridae (1), Lumbrineridae (1), Arabellidae (2), Ampharetidae (1).

Polychaeta:

Spionidae:

Polydora has long been recognized as a mollusc borer (Blake & Evans, 1973) and *Polydora* (*Boccardia*) *proboscidea* is believed to have caused the numerous spionid-like holes in the shells of *M. californianus*, having a negative influence on the mussels' survival.

Opheliidae:

This family was represented by the sand/mud dwelling *Armandia* and *Travisia* but no general observations were made. Woodin (1974) discusses the sediment burrower *Armandia* and its interactions with several other polychaete species.

Phyllodocidae:

No observations were made on the two *Eulalia* species encountered. Blake (1975) lists the habitat of *E. viridis* as algal holdfasts and under rocks.

Polynoidae:

As a group the scale worms are generally commensal or parasitic on molluscs (e.g., *Arctonoe* on *Diodora*), asteroids, crustaceans, holothuroids, or other polychaetes (see Blake, op. cit., for references). Since no detailed live observations were made on this group, their role is questionable. However, Thompson (1976) found other polychaete hard parts in the guts of *Arctonone vittata*.

Syllidae:

The ecological role of this singly most diverse group of polychaetes in the mussel bed has yet to be elucidated, although they are usually associated with fine sediments and are most probably deposit feeders. As Glynn (1965) found, many were associated with filamentous algae such as *Endocladia*, old barnacle tests, and other crevices. In the present study, they were often found in the gorp sediment at the base of the mussel bed.

Nereidae:

Cheilonereis cyclurus has been shown to be commensal with hermit crabs whereas *Nereis vexillosa* is more or less an herbivore (Roe, 1975) or an omnivore, but not a scavenger by preference. In feeding choice experiments, *Nereis* preferred other polychaete worms to mussels (Johnson, 1943). The role of *N. limnicola* is unknown.

Sabellariidae:

No information is available for *Idanthyrsus*, but tubes of the filter feeding *Sabellaria cementarium* were most often found cemented to the inside surface of old mussel shells and occasionally on live mussels. Unless allowed to form massive colonies, *S. cementarium* seems to pose little threat to the mussel matrix.

Pectinariidae:

This family of deposit feeders was represented by three species. They remained restricted to the gorp and seemed to have limited impact on the mussels.

Terebellidae:

The three representative genera, *Eupolymnia*, *Laphania*, and *Streblosoma* are parchment-tube building forms, dependent on sediments and detritus for their nutrition. Again, this group appears neutral in terms of impact on the mussel populations.

Sabellidae:

This group of filter feeding worms is well represented with 10 identified species present, but again, because most inhabit the deeper interstices, little other information was obtained.

Serpulidae:

Most commonly found on the interior of old mussel shells and occasionally on live shells, the filter feeder *Serpula vermicularis* appears not to be detrimental or beneficial to *Mytilus*.

Spirobidae:

Even though this group was extremely common on broken mussel shell fragments as well as on live mussels, it does not appear to reach high enough abundance to be detrimental to live mussels. Both sinistral and dextrally coiled species were found.

SIPUNCULA:

Phascolosoma agassizii is a deposit feeder closely associated with and dependent upon the organic detritus material bound up in the gorp sediments. It was often found at the mussel/gorp interface and at some locations (usually in very deep beds) reached densities of over 2000-3000/m^2. For reproductive cycle and development, see Rice (1967, 1973) and Towle & Giese (1967).

ARTHROPODA:

Pycnogonida:

Achelia latifrons may be parasitic on *Mytilus californianus* like its congener *A. chelata* in California. The occurrence of *Pycnogonum stearnsi* (an anemone predator) represents a range extension for this species, previously known only from Monterey to Oregon (Hedgpeth, 1975). Its ecological role, as well as that of *Nymphopsis spinosissima* and *Phoxichilidium femoratum* is unknown.

Arachnida:

The well known pseudoscorpion *Halobissium occidentale* is an active predator (see Weygoldt, 1969 for details). The marine mites are an extremely ecologically diverse group which functionally may be herbivores, predators, and parasites. The role(s) of the ten unidentified taxa found in this survey is unknown. Because of their small size and the nature of the sorting techniques, their abundance is undoubtedly underestimated.

Crustacea:

Cirripedia:

All of the six species of barnacles impose a negative influence on the mussels by fouling their shells. If left unchecked, the excessive growth and weight on the *Mytilus* shells will cause either 1) occlusion of the current siphon resulting in lower food intake and respiratory currents, or 2) increased shearing stress against waves causing mussels to be ripped from the rock surface more easily (see Chapter 5). In addition to fouling their shells, *Pollicipes polymerus* actually competes for space with the mussels, and on vertical surfaces is the dominant space occupier (Paine, 1974).

Tanaidacea:

Not much is known of the ecology of tanaids other than that they function as filter feeders and are found in fouling communities often associated with hydroids, algae and sponges (Hatch, 1947; Miller, 1968). Highsmith (1977) has shown that *Leptochelia* prey on juvenile sand dollars (*Dendraster*) and Jumars (pers. comm.) noted them feeding on polychaetes.

Isopoda:

Cirolana harfordi has long been known as a mussel bed inhabitant (Hewatt, 1935). It is an active carnivorous scavenger, and on occasion I have observed in its gut contents, nearly intact *Nereis vexillosa*. However, active predation or immobilization of such a polychaete has not been observed. Little is known of the life histories of *Dynamenella dilitata*, *Dynamenella sheareri*, and *Edotea sublittoralis*. Hatch (1947) noted *Exosphaeroma amplicauda* in intertidal regions among and under rocks whereas Rees (1968) did a choice chamber experiment in the laboratory showing that it preferred gravelly substrates. It is certainly a mobile species but probably is dependent upon the gorp sediments. I have no other information on the other two species of *Exosphaeroma* (*octoncum* and *rhomburum*). *Gnorimosphaeroma oregonensis* also prefers coarse gravel substrates and can withstand extremely low salinities (Menzies, 1954; Riegel, 1959; Rees, 1968; Hoestlandt, 1973). In the past, *Ianiropsis analoga* has been found associated with the holdfasts of *Laminaria* and in gravelly substrates in the low intertidal, usually being reproductively active during February and May (Menzies, 1952). *Ianiropsis* (*Janiropsis*) *kincaidi* also seeks refuges in the intertidal, and has been reported from tide pools in the past (op. cit.). The previous two congeners obviously prefer or need protective sites to survive in the intertidal and the mussel beds offer an excellent habitat for them. *Idotea* (=*Pentidotea*) *schmitti* has long been known from the rocky intertidal, generally being found in the *Laminaria* zone (Menzies, 1950). *Idotea wosnesenskii* is a very common member of the mussel bed complex and is most often found in the mid-intertidal region (op. cit.). It can easily match the color of its background, generally mimicking the colors of its preferred food items such as *Fucus*, *Ulva*, *Enteromorpha*, *Porphyra*, *Haedophyllum*, and epiphytic diatoms (Chien, 1968). It also has been shown to be sexually active in July-August (op. cit.). When first described, *Jaeropsis dubia* was known from Dillon Beach, Calif. to Newport Bay, Calif. (Menzies, 1951) and I know of no other reports extending its range this far north. It has been reported from exposed rocky coasts on algal holdfasts, bryozoans, tunicates, hydroids, and barnacles (op. cit.). Jaeropsis lobata is also known only to occur as far north as Coos Bay, Oregon (Hatch, 1947) and to my knowledge nothing is known of its ecological role. Even when first described, Munna chromatocephala was a well recognized component of the mussel bed ecosystem (Menzies, 1952). Ovigerous specimens were found during May. Synidotea bicuspida is an arctic-boreal-temperate species known from Monterey, Calif. to Point Barrow, Alaska, generally found on sandy bottoms (Menzies & Miller, 1972). Little is known of its ecology. Other members of this genus are all benthic, typically cold-water species living on open coasts, and many feed on hydroids and bryozoans but the food preference of this species is unknown (op. cit.).

Amphipoda:

Relatively little is known of the habits and ecological significance of most amphipod species, and this extremely diverse group is still undergoing considerable taxonomic revision in the Pacific Northwest (C. Staude, unpubl. ms.). The following key and subsequent information on the general habitats in which these species are found are taken mostly from Barnard (1975).

(A): Nesting in algae or surfgrass

(B): Burrower in sand or mud bottoms or sedimentary patches of intertidal rocky regions

(D): Free-living, amongst organic debris

(I): Inquilinous, ectocommensal or ectoparasitic, usually with sucking or mucus-lapping mouthparts, hosts poorly known

(TA): Tube builder attaching tube to algae

(TB): Tube builder attaching tube to debris on mud bottom

Table XI gives a condensed representation of the function-type/ habitat information on those species for which I have no other data.

Ampithoe simulans (TA). Generally builds tubes on surfgrass, kelp, or smaller algae. This species is known from Oregon to Coal Oil Point, Calif. (Barnard, 1965) and thus this probably represents a range extention.

Caprella angusta (?). The caprellids are not uncommon in the mussel bed community. They primarily feed upon diatoms, but may also consume small invertebrates and perhaps detritus (McCain, 1975).

Caprella greenleyi (?). This species has been found associated with *Henricia leviuscula*, hydroids, and algae (McCain, 1975) and has been shown to feed by scraping and filter-feeding (Caine, 1978).

Deutella ?*californica* (?). Caine (1977) describes this species as a sit-and-wait predator which is often found on algae and hydroids. Its gut contents contained nearly 20% copepod and nematode parts and about 60% detritus.

Hyale anceps (A). Glynn (1965) found *Endocladia* fragments and green algal cells in the guts of some unidentified *Hyale* species. Also, some *Hyale* species are known from under the edges of limpet shells (Barnard, 1975).

Hyale grandicornis californica (A). This species may be synonomous with *H. pugettensis*.

Table XI. Habitats and functional types for amphipod species in *M. californianus* beds.

(A): Nesting in algae or surfgrass
(B): Burrower in sand or mud bottoms or sedimentary patches of intertidal rocky regions
(D): Free-living, amongst organic debris
(I): Inquilinous, ectocommensal or ectoparasitic, usually with sucking or mucus-lapping mouthparts, hosts poorly known
(TA): Tube builder attaching tube to algae
(TB): Tube builder attaching tube to debris on mud bottom

	A	B	D	I	TA	TB	?
Aeroides columbiae					X		
Corophium brevis						X	
Deutella ?californica							X
Hyale frequens	X						
Hyale plumulosa	X						
Ischyrocerus anguipes					X		
Jassa falcata					X	X	
Melita californica	X						
Melita desdichada	X?						
Metopa cistella				X			
Najna californica	X?						
Oligochinus lighti	X						
Orchestia sp. A			X				
Parallorchestes ochotensis	X						
Paraphaxus cf. obtusidens		X					
Parapleustes den	X?						
Parapleustes nautilus							
Parapleustes pugettensis	X						
Photis sp. A					X?		
Pontogeneia intermedia	X						
Stenothoides burbanki				X			

Ischyrecerus serratus (TA?). To my knowledge this species has not been reported in North America, but it has been recorded from N.W. Pacific waters by Gurjanova (1938).

Najna ?consiliorum (A). Found especially on kelp (Barnard, 1975).

Orchomene sp. A, sp. B (?). Many other *Orchomene* species are mud ingesters, facultative diatom feeders, and scavengers.

Paramoera cf. *mohri* (A?). This almost certainly represents an undescribed species (C. Staude, pers. comm.).

Paramoera sp. B (A?). This is identical to the undescribed species of Armstrong *et al*. (1976).

Decapoda:

Cancer branneri is known from Alaska to Santa Catalina Island, Calif. (Rathbun, 1930), but its role in the mussel bed system is unknown. *Fabia subquadrata* has long been recognized as an internal commensal (parasite?) of bivalves and other invertebrates. Wells (1928) describes its presence in *Mytilus edulis*, *Mytilus californianus*, *Modiolus modiolus*, *Venericardia ventricosa*, and in a tunicate *Styela gibbsii*. Hart (cited in Pearce, 1966) found it in *Saxidomus* and Pearce (1966) describes its biology from *Modiolus rectus* from the San Juan Archipelago. Giles (cited in Pearce, 1966) noted less than one percent *Fabia* infestation in *M. californianus* from Tomales Bay and Bodega Bay, Calif. Ricketts *et al*. (1968) found up to three percent infestation at various locations in California, and Pearce (1966) found no infestation in some 300 *M. edulis* and over 100 *M. californianus* examined. In contrast to these low levels of infestation, Fabia is moderately common in mussel beds from the outer coast of Washington and some samples yield infestations of ca. 30% for all M. californianus over 50 mm. I have found that infestation was much more common amongst larger mussels; large M. californianus from subtidal sites down to 100 ft. depth (from Duncan Rock or in the San Juan Archipelago) had infestations of up to 50%. Hemigrapsus nudus is a common intertidal crab usually found in exposed rocky areas. Its preferred micro-habitat is coarse sand or gravel. It is probably a scavenger but may also nip at the feed of M. californianus in the same manner as Petrolisthes cinctipes, possibly contributing to the formation of hummocks (see Petrolisthes). Oedignathus inermis is sometimes found in the interstices of the mussel bed system, often in crevices or old Balanus nubilus tests (but always in the lowest intertidal sites). Little is known of its ecology. Pachycheles rudis is also a crevice or hole dweller, but again nothing is known of its role in this system. Several Pagurus species (unidentifiable because of their small size) were found in the mussel beds. They are generally scavengers and/or deposit feeders; Nyblade (1974) analysed their distribution and ecology in Washington waters. Petrolisthes cinctipes is fairly common, but its abundance is often patchy. It moves easily through the mussel bed matrix because of its flattened shape. Like Hemigrapsus nudus, it may also nip at the feet of M. californianus. (It is possible that to a Petrolisthes, a wiggling mussel foot attempting to place down a byssal thread may look like a tasty polychaete.) If they nip at the mussels' feet, they could prevent them from securing byssal threads to the primary substratum, resulting in a hollow hummocked region. Many such hummocks were observed at Tatoosh Island and Shi-Shi; almost inevitably they were occupied by considerable numbers of *Petrolisthes* or sometimes *Hemigrapsus* (see Fig. 32). These raised hummock regions were common at both major study areas in Washington. They range up to 20-30 cm in diameter, contain up to 100 crabs each, and appear to be less stable than the main contiguous portion of the mussel beds. As a result, they may more easily be ripped loose by wave action. If these hummocked regions are formed by the crabs, then they may impart a negative influence on the mussels. *Petrolisthes eriomeris* was very low in abundance. Normally found in kelp holdfasts and gravelly substrates (Carlton & Kuris, 1975), its role is unknown. *Pugettia gracilis* ranges from the Aleutian Islands to California and previously has been known mostly from low intertidal eel grass habitats whereas *Pugettia richii*'s range is from Vancouver Island, B.C. to San Diego Bay, California and has been found in regions of coralline algae, again from the low intertidal (Carlton & Kuris, 1975).

Insecta:

Diptera:

Larvae of *Coelopa* sp. (a member of the kelpflies) were found but further identification was not possible without an adult fly. Kompfner (1974) found that *Coelopa vanduzeei* (Cresson, 1914) in California occurred in the surface layers of deep piles of beach wrack composed of *Phyllospadix* or *Macrocystis* in the lower tide zones. The larvae appeared to feed preferentially on partially decomposed

Fig. 32. Diagram of typical mussel bed hummock containing numerous crabs (*Petrolisthes* or *Hemigrapsus*).

Macrocystis over other algae, and their activities help to further the decomposition process (Egglishaw, 1960). Their abundance also coincided with neap tides. Poinar (1977) also found that C. vanduzeei larvae pupate in the upper few centimeters of sand and adult flies emerge in five to six days (his work was done in August).

Pupae of Oedoparena glauca, a dryomyzid fly, were not uncommon. The larvae have been shown to be predatory on Balanus glandula and Chthamalus (Knudsen, 1968 - cited in Schlinger, 1975) and apparently the adults feed on diatoms.

Paraclunio alaskensis were found as adults, larvae, and pupae, and may be important algae consumers (Morley & Ring, 1972). In spring and early summer, oviposition occurs by the insertion of single eggs in filamentous algae (Saunders, 1928). I observed larvae seeking shelter most commonly in the junctures between Balanus spp. plates, and in crevices between adjacent barnacles.

Both adults and larvae of Paraphrosylus nigripennis were observed. To my knowledge almost nothing is known of this species which has been recorded from Alaska as well as Washington (Cole, 1969).

Coleoptera:

The staphylinid beetle, Diaulota densissima, was present as adults and larvae. It is strictly an intertidal beetle and maintains itself at high tide by seeking the refuge of a crevice or some other heterogeneity which might trap an air bubble. Glynn (1965) found their eggs laid in the crevices between barnacles during February, March, April, May, October, and December and suggested that they reproduce at least during the autumn, winter, and spring months. His analysis of gut contents revealed numerous diatoms (Navicula spp.), blue-green and green algal cells and possibly Gigartina. They also feed on damaged animal tissue, suggesting an omnivorous diet.

To my knowledge not much is known of the other identified staphylinid, Liparocephalus brevipennis. In general, its distribution in the intertidal is similar to that of D. densissima.

BRYOZOA:

In general, the bryozoa tend to function in similar ways relative to their effect on the mussels. With the exception of Cellaria mandibulata, all are low encrusting forms which tend to foul the shells. I never observed excessive enough fouling by bryozoa to restrict the feeding currents in a mussel. Bryozoa usually colonize anterior portions of the shell. In larger mussels, bryozoans can cover up to 50% or more of the shell, but the posterior portions are still usually the cleanest. This is undoubtedly due to at least two factors: 1) The anterior end of the shell is more protected within the bed since the byssal thread attachments originate from this region. This affords better protection from desiccation or temperature stress; 2) The anterior portion is also the oldest and obviously has had the longest opportunity to be colonized.

Hippothoa hyalina was the most common bryozoan encountered, being found at all tidal levels and on all sizes of mussels. It was also fairly common on the byssal threads as well, and at times completely encased them.

In general, the bryozoa colonized most available hard substrata within the mussel bed system including live shells, shell fragments, and even many mobile invertebrates. Considerable attention has been directed towards aspects of bryozoan-mollusk relationships. Duncan (1957) claims that there is considerable substrate specificity in bryozoan settlement patterns whereas Osburn (1957) and Adegoke (1967) claim that there is none. I have found a range of responses from generalists to specialists which appear to be micro-habitat related rather than specifically substrate related. At one end of this spectrum is the ubiquitous *Hippothoa* mentioned above encrusting everything from pebbles to byssal threads and live mussels. On the other end are species like *Alcyonidium polyoum*, *Callopora horrida*, and *Crisia pugetti*, almost inevitably found in the deepest reaches of the mussel bed and often on the interior of empty *Mytilus* shells, which likely afford them some protection from wandering predators as well as an optimal microclimate. The details of these relationships still need considerable work. Table XII lists the most common habitats where the various species of bryozoa were found within the mussel bed matrix.

ECHINODERMATA:

Asteroidea:

Henricia leviuscula is a relatively common intertidal starfish on the exposed outer coast of Washington which is occasionally found in the mussel bed complex. It has been described as a

Table XII. Common habitats for bryozoa found in *M. californianus* beds.

	Most protected habitats (e.g. inside old mussel shells)	Pebbles and small shell debris	Mussel shells	Byssus	Other mobile fauna
Alcyonidium polyoum	X	X	X		
Bugula pugeti	X				
Callopora horrida	X				
Cellaria mandibulata	X				
Crisia occidentalis	X				
Crisia pugeti	X				
Dendrobeania curvirostrata	X				
Dendrobeania (?*laxa*)	X				
Flustrella corniculata	X				
Hippodiplosia insculpta		X	X	X	
Hippothoa hyalina		X	X	X	X
Microporella californica			X		
Microporella (?*marsupiata*)			X		
Schizoporella linearis			X		
Smittina retifrons	X				
Tricellaria ternata	X				
Tubulipora pacifica			X		

ciliary plankton feeder (Rasmussen, 1965), and primarily a suspension feeder also capable of preying on sponges and bryozoa as well (Mauzey *et al.*, 1968).

The brooding six-armed starfish *Leptasterias hexactis* is often abundant and in some mussel bed regions reaches densities of over 1000/m^2. This figure may be somewhat misleading, however, for a large number of these can be young which are being brooded. Dayton (1973a) and Paine (1976a) have reported densities as high as 160/m^2 and 523/m^2 (respectively) on the Washington outer coast and Paine suggests that it may simplify the mussel bed structure by preying on *M. californianus*, thus enhancing the probability of mussel bed persistence. *Leptasterias* is an active predator and a true generalist which switches its preferred prey items from one location to another. Among its most common prey items are littorinids, limpets, *Balanus* spp., small chitons, *Thais* spp. and *Mytilus edulis*. For details, see Menge (1972a, b, 1974, 1975) and Menge & Menge (1974). It does consume *M. edulis* but whether it feeds on small *M. californianus* and has a significant impact on this species is not known. Its overall contribution to the relative status of the mussel bed community is therefore difficult to assess.

Pisaster ochraceus undoubtedly has the greatest impact in structuring the mussel bed system. Indeed, it restricts the lower limit of intertidal *M. californianus* beds on mainland areas by its predatory activities (Paris, 1960; Paine, 1974, 1976a). Details of its feeding activities can be found in papers by Feder (1959), Mauzey

(1966), Landenberger (1968), Mauzey *et al*. (1968) and Paine (1969a, 1974, 1976a). In the study by Mauzey *et al*. (1968), *Pisaster* was shown to choose the following prey items in decreasing order of preference: *Mytilus* spp., *Balanus* spp., limpets ("*Acmaea*" spp.), and *Thais* spp., although Paine (1966) and Mauzey (1966) showed that they consume considerable numbers of chitons as well. From my own observations at Shi-Shi, *Pisaster* also appears to prefer *M. edulis* over *M. californianus*. Again, because of the wide variety of its diet and because of second order and third order interactive effects (such as the results of its preying on *Balanus* spp., limpets, and *Thais* spp.), I hesitate to place an overall value on its contribution to the mussel bed matrix, although Paine (1966, 1969a) has shown that it increases the diversity of primary substrate occupiers by its predatory activities on mussels.

Echinoidea:

The urchins *Stronglyocentrotus* spp. were relatively rare, usually occurring at the lowest tidal sites. Always found at the bottom of the beds, near the primary substrate, they likely graze on whatever food items are available to them. Because their preferrred food items (diatoms and algae) are absent in the depths of the beds, I presume they also graze on hydroids or encrusting organisms such as bryozoa or sponges.

Holothuroidea:

Cucumaria pseudocurata ranges from at least the Queen Charlotte Islands, Canada to Monterey, Calif. (Rutherford, 1973). This cucumber was one of the most conspicuous members of deep mussel beds and at times its abundance was over $20,000/m^2$. Although Rutherford (op. cit.) found them growing profusely on open rock surfaces in California, they seem to be relatively confined to mussel beds on the outer coast of Washington. This is most likely due to the extreme wave action which would wash them off any open rock surface. Therefore, their existence here seems dependent on the mussel bed structure for at least protection. They may also depend on the mussels for some portion of their nutrition. In laboratory observations of isolated portions of mussel beds kept in running sea water tanks, *C. pseudocurata* was found to be highly photo-negative and tended to lodge itself just below the surface of the mussel bed. In this position, it aptly caught and consumed feces and pseudo-feces from *M. californianus*. Whether this can supply enough nutrition for the cucumbers or whether this happened in nature (with much more severe turbulence) was not ascertained. I suspect that on calm days the situation is fairly comparable. All of Rutherford's populations (op. cit.) were black, whereas all of the individuals I observed were pure gray in color. It has been hypothesized that the dark pigmentation (probably a melanin) of a closely related species (*Cucumaria curata* Cowles, 1907) protects it from excessive light penetration (Smith, 1962). He found that those cucumbers under mussel beds were lighter in color. My observations on the photo-negative behaviour and light color of *C. pseudocurata* in Washington supports this contention. *C. pseudocurata* also broods its young and colonizes new areas by wave action spreading juveniles to other mussel beds (Rutherford, 1973).

Cucumaria miniata was uncommon in the mussel bed system, usually being found only at the lowest intertidal sites. It occurs from Alaska to Carmel, California in crevices and between mussels. It breeds in the spring and is a passive filter feeder, probably feeding on phytoplankton (Engstrom, 1974).

Eupentacta quinquesemita was only slightly more common than Cucumaria miniata. Its distribution ranges from Sitka, Alaska to central California and in the mussel beds it occurs in similar habitats to that of its congener. Laboratory spawning was obtained in the spring and newly settled Eupentacta spp. were collected from among sabellid tubes in the San Juan Archipelago (Engstrom, op. cit.). Engstrom did not observe it filtering during winter months but when it did, it ingested non-living seston and plankton. In the mussel bed it is probably a filter feeder and deposit feeder.

Ophiuroidea:

Ophiopholus aculeata was the only brittle star encountered in the mussel bed complex. It is a suspension feeder which can capture particles in all size classes at least 30-360 micrometers in diameter (LaBarbera, 1978). The influence of O. aculeata on the mussels is most likely neutral.

CHORDATA:

Ascidiacea:

Pyura haustor is a fouling organism which was so rare that it seemed to have no significant negative effect. It was only found at the lowest intertidal levels.

Osteichthyes:

Several fishes were collected from the mussel bed matrix but many were so mobile that they escaped during sampling. Therefore, the species listed below are a minimum representation of species and their numbers in the raw data list (Appendix VI) are undoubtedly underestimated.

Other pelagic, demersal and epibenthic fishes are undoubtedly important as predators and grazers in the mussel beds at high tide but because of the inherent problems in sampling them, they have not been considered here. The three species identified below are all active generalist predators, mainly specializing on gammarid amphipods. The information on their food preferences was obtained from gut content analyses from fish collected in the Strait of Juan de Fuca by Cross *et al*. (1978). Their estimates for the relative importance of various food items was calculated as an equally weighted average of three values: The relative frequency of occurrence of stomachs with that particular food item, the total abundance of that food item from those stomachs, and the total biomass of that food item. This is referred to as the Index of Relative Importance (IRI).

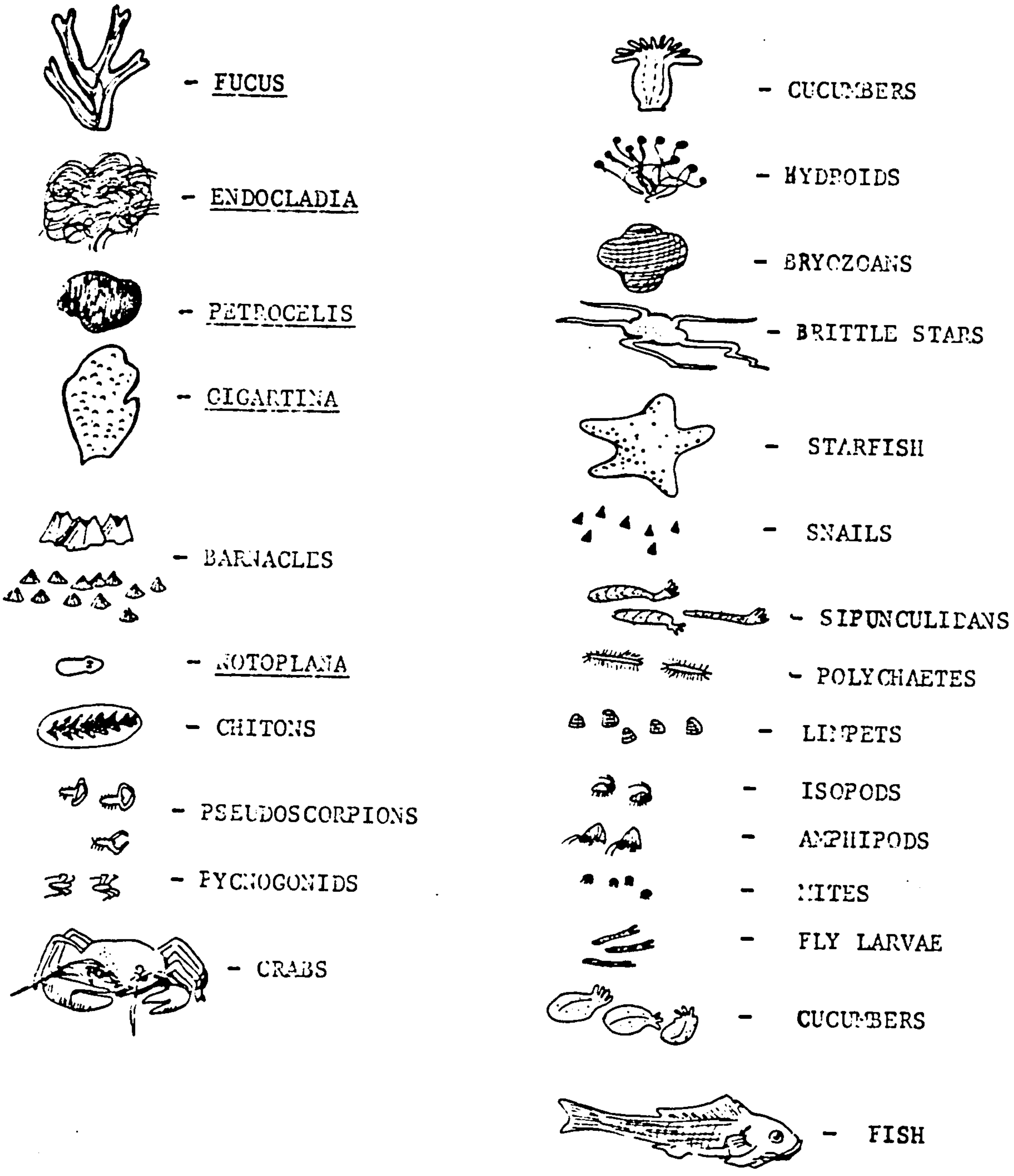
Clinocottus embryum (the calico sculpin) had an IRI value of 66% for gammarid amphipods and over 20% for isopods (of which the majority were *Gnorimosphaeroma oregonensis* and *Exosphaeroma amplicauda*). Barnacles comprised ca. 13% of the diet.

Phytichthys chirus (the ribbon prickleback) also preferred gammarid amphipods (represented by an IRI value of 79%). Polychaetes were secondarily preferred food items, comprising 15% of the diet. The remainder consisted of Natantia and algae.

Xiphister atropurpureus (the black prickleback) is also a generalist but gammarids comprised over 75% of its diet. Algae and Sabellid polychaetes were each scored at about 10%.

There are specific sites within the mussel bed matrix where one can predictably find many of the component species. Algae obviously prefer and require the lighted surface of the mussel shells and other epibionts such as barnacles, bryozoans, hydroids, burrowing bivalves, sponges, and tube-building polychaetes are found generally throughout all levels of the bed, attached to the valves. Anemones, although appearing to be relatively stationary, undergo a fair amount of movement from surface levels to deeper regions. Some mobile fauna (see Table VIII) generally move more freely throughout all levels but many others are restricted to particular levels for most of their activities. For example, the holothuroid Cucumaria pseudocurata usually exists about mid-level in the bed barely reaching the surface layers, but its congener C. miniata is almost exclusively restricted to the bottom level. The sipunculan Phascolosoma exists at the surface of the gorp sediment layer, as do many of the syllid polychaetes. A whole host of other polychaetes and bivalves are found relatively exclusively within the bottom most sediment layers. Fig. 33 shows a cut-away diagrammatic representation of this zonation within the various levels of the mussel bed matrix for the major groups of associated organisms.

Fig. 33. Cut-away diagram showing zonation of associated organisms within various levels of the M. californianus bed.



ARTIFICIAL MUSSEL BEDS: Materials and Methods

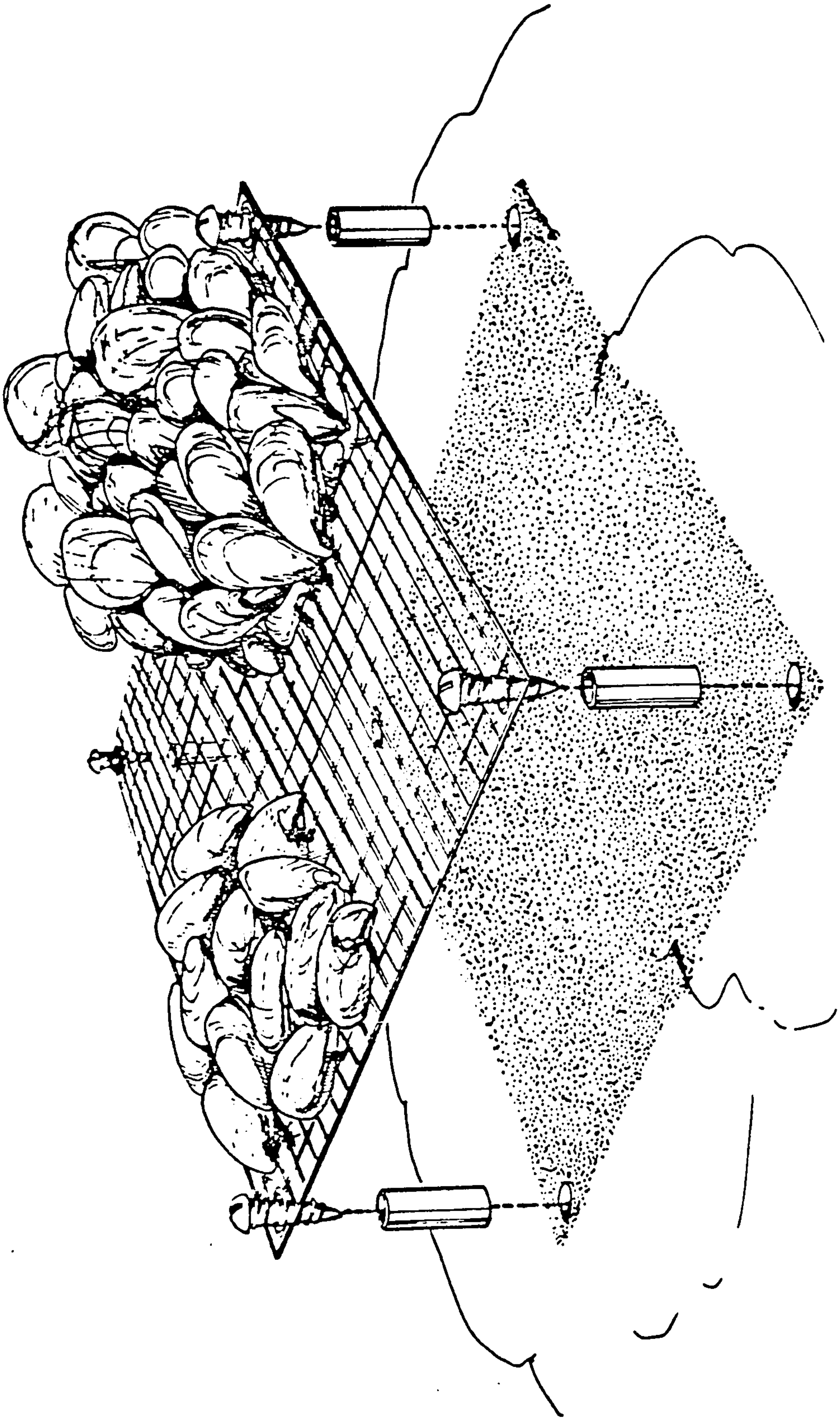
To test the influence of structural heterogeneity on the development of a diverse community of associated organisms, artificial mussel "bedlets" were constructed which resembled real mussels in their physical nature. Artificial mussels were constructed as follows: A silicone rubber mold was prepared around a real mussel shell. The mold was cut open and the real shell removed. A fast-drying, non-toxic polyester resin compound (Aqua-Zap ^{TM}) was then poured into the rubber molds and a set of artificial byssal threads, made of 40 lb. test monofilament fishing line, was incorporated into each mold. The monofilament line approximated the diameter of byssal threads (0.4 - 0.6 mm) from medium to large (100-150 mm) mussels. The physical rugosity of the surface of the real mussels was mimicked almost precisely because of the high quality of the molding material. A blue-black coloring compound was also added to the resin so that the Aqua-Zap mussels had the same general appearance and coloration as real mussels.

Three size classes of Aqua-Zap mussels were molded: 50 mm, 100 mm, and 150 mm in length. Aqua-Zap mussels were then tied to 0.10 m^2 plates of ¼" stainless steel wire mesh by their monofilament byssal threads. The resulting Aqua-Zap bedlets were composed of monolayers of either fifty 50 mm "mussels", thirty 100 mm "mussels", or twenty 150 mm "mussels". One set of a mixture of all three size classes was constructed with the following proportions: fifteen 50 mm, ten 100 mm, and eight 150 mm "mussels". Finally, one set of multilayered Aqua-Zap bedlets was formed with fifty 50 mm "mussels" on the bottom and middle layers, interspersed with thirty 100 mm "mussels" on the upper layer.

Replicated Aqua-Zap bedlets representing the three monolayer categories, the mixed category, and the multilayered category were anchored with stainless steel screws and washers secured to nylon masonry sleeves inserted into holes drilled into the rock substrate (see Fig. 34).

These replicates were placed at a high (11.3 ft, 3.5 m) and a low (5.7 ft, 1.7 m) intertidal height at Strawberry Point, Tatoosh Island (see Chapter 1) in May 1976, resulting in 10 Aqua-Zap bedlets at each of the two tidal heights. Associated organisms were allowed to colonize for one year (the bedlets were collected in May 1977), and the associates were picked, sorted, and preserved in the same manner as described above for real mussel bed samples.

Fig. 34. Diagram of Aqua-Zap^{TM} artificial mussel bedlets, showing a monolayer of medium sized (100 mm) "mussels" on the left and a cluster of the multilayered arrangement (comprised of 50 mm and 100 mm mussels) on the right. The stainless steel screen and screws and the masonry sleeves used for attachment are also shown.

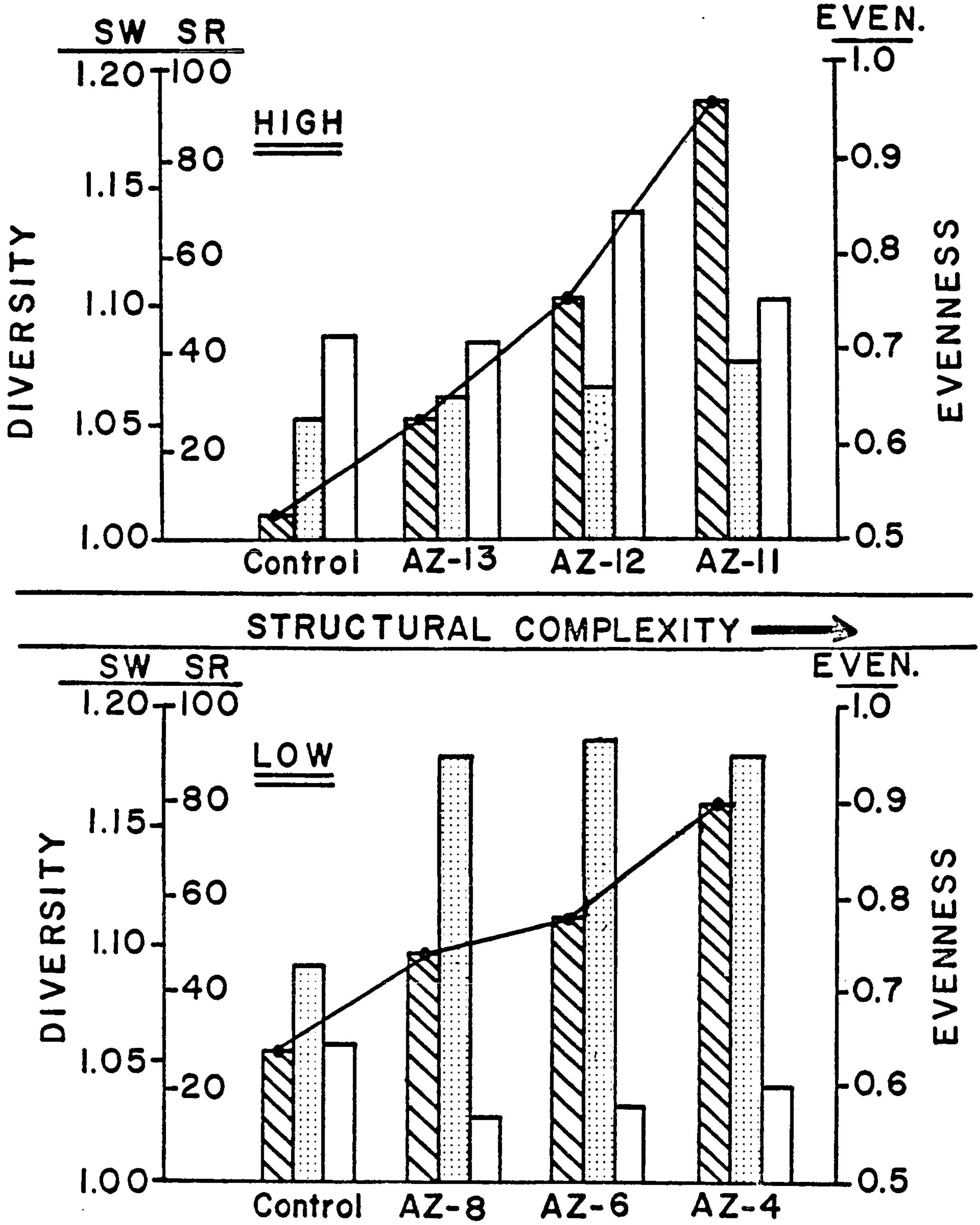


ARTIFICIAL MUSSEL BEDS: Results

During the winter of 1976-1977, storms detached many of the Aqua-Zap mussels from their positions. Most of the 150 mm size class, some of the 100 mm size class, but almost none of the 500 mm size class Aqua-Zap mussels were destroyed. Nevertheless, a gradient of structural complexity could still be obtained from the surviving bedlets.

In May 1977, after the one year period, during which colonization of associated organisms occurred, the bedlets were collected and organisms identified and counted. The resulting levels of species richness, the Shannon-Weaver index and the evenness index for various degrees of structural heterogeneity and for a control sample (indicating the complement of species occurring in the absence of mussels, naturally at each site) are given in Fig. 35. From these results, it is clear that for both high and low intertidal sites, the levels of diversity found in the artificially created physically complex structures are higher than for the natural community (control) found at each site. In addition, these results show that the species richness and Shannon-Weaver index clearly increase with increasing structural complexity ($p<.01$, Friedman's Rank Sums Test). The evenness index yields no significant trends. It is clear from these results that structural complexity can increase diversity above ambient levels of physical structure, and that given the same levels of physical structure, a low intertidal site can support twice the number of species (species richness) as a high intertidal site, even though the information theory index (H') may be very similar.

Fig. 35. Shannon-Weaver, species richness, and evenness index values obtained from Aqua-Zap TM mussel bedlets after 1 year of colonization in the high and low intertidal, along a gradient of structural complexity (see text for explanation).


SW SR
1.20 100
1.15 80
60
1.10 40
1.05 20
1.00
DIVERSITY
HIGH
EVEN.
1.0
0.9
0.8
0.7
0.6
0.5
EVENNESS
Control AZ-13 AZ-12 AZ-11
STRUCTURAL COMPLEXITY
SW SR
1.20 100
1.15 80
60
1.10 40
1.05 20
1.00
DIVERSITY
LOW
EVEN.
1.0
0.9
0.8
0.7
0.6
0.5
EVENNESS
Control AZ-8 AZ-6 AZ-4

Structural complexity appears to be of greater importance than the age of the mussel bed, although for real beds, these are confounded. The artificial mussel bedlets were allowed to colonize for only one year, but resulted in diversity levels (both in terms of species richness and the Shannon-Weaver index) at least equal to those found in real mussel beds.

DISCUSSION AND CONCLUSIONS:

Although a few studies have shown no relationship between physical and/or microenvironmental complexity and diversity (Cameron, 1972; Fleming, 1973), the vast majority of authors report a strong positive relationship for a wide variety of fauna and flora (MacArthur & MacArthur, 1961; Kohn, 1967; Kohn & Leviten, 1976; Harman, 1972; Abele, 1974; Tomoff, 1975; Harner & Harper, 1976). The results reported here strongly indicate that as the physical complexity of the mussel bed matrix increases, microenvironmental parameters are altered to accommodate more specialized species. As a mussel bed ages, it becomes deeper and structurally more complex. At the interface between the mussels and the primary substratum wave action, sunlight, and temperature are decreased as surface area, relative humidity, and sedimentation are increased. More and more unique microhabitats and food resources are thus probably created, allowing more uniquely specialized species to enter the system, resulting in an increase in community-wide species diversity.

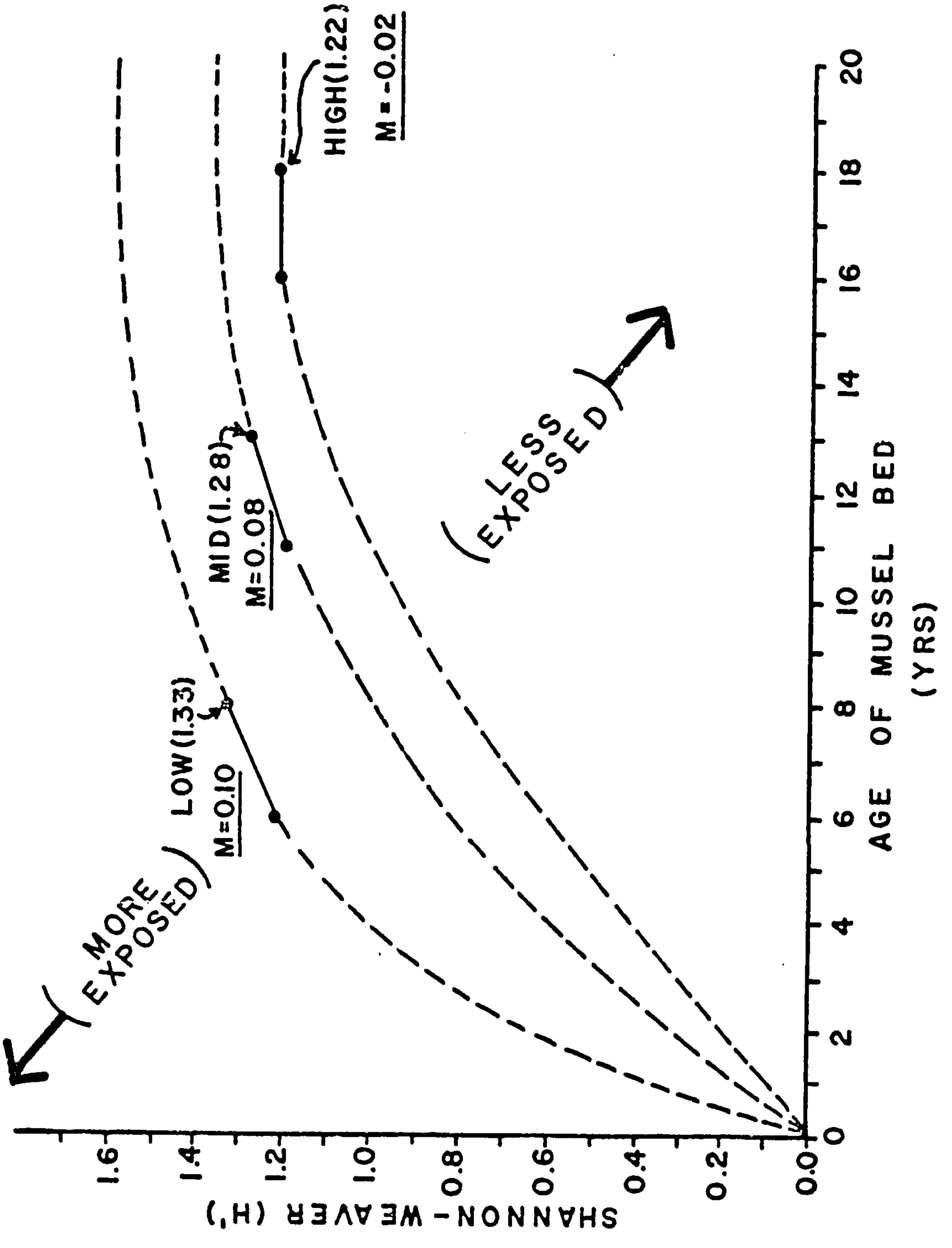
Associated fauna inhabiting physically complex structures are known for a variety of natural substrates (Colman, 1939; Glynn, 1965; Hagerman, 1966; and Haage & Jansson, 1970 for marine algae; Glime & Clemons, 1972 for mosses; Maclean, 1973 for sociable weaver nests; Ricketts _et al_., 1968 and Penchaszadeh, 1973 for mussels).

I suggest that the same type of phenomena should be occurring with these other physically complex structures as well. Some species will be attracted by food resources, others will utilize the space as a refuge from physically imposed stresses (such as wave action or desiccation) or biological stresses (such as predation). As higher order consumers find these initial colonizers and other competitors enter the system, trophic links become more complex, habitat specialization allows species packing, and community diversity increases at all trophic levels (supporting the contentions of Menge & Sutherland, 1976).

It is clear from the results of the Aqua-Zap mussels, that for both high and low intertidal sites, greater structural complexity begets greater diversity, and for the one year period allowed for colonization, diversity levels equalled or surpassed those of some real mussel beds. I have interpreted these results to represent the initial phase of diversity change during early colonization of a new or recently disturbed habitat (MacArthur & Wilson, 1967; Wilson & Simberloff, 1969a, b). Allowed to equilibrate, I suspect that these diversity levels might decline somewhat for this fixed level of structural heterogeneity. However, for real mussel beds, the diversity would gradually and steadily rise as the structural heterogeneity of the matrix increased with age.

Periodically, a region of mussel bed is destroyed by wave-driven logs or severe wave action during winter storms (Dayton, 1971; Levin & Paine, 1974). Initial indications are that the life span of a particular local region of mussel bed community ranges from 8-20 years or more, depending on tidal height and the chance occurrence of violent storms disrupting the mussel bed matrix. The samples taken for diversity analyses spanned a two year period, representing anywhere from 1/4 to 1/10th or less of the full developmental and replacement cycle of a complete mussel bed community (i.e., before it becomes destroyed by natural processes). However, even during this proportionately short period of time, significant diversity increases where noted for most study sites. The maximum diversity found at each intertidal level, as well as predicted curves for increasing diversity are given in Fig. 36. All maximum diversity levels were found at the T4 site (most exposed study site) but again it is not known what the exact ages of these beds were. I have assumed that the maximum diversity levels found represent relatively older mussel beds. I have also assumed that the relative maximum diversity levels and the rate of change in diversity are characteristic for each intertidal level (i.e., on the average, low intertidal levels have the highest diversity and the fastest rate of change). Because low intertidal mussel beds are perturbed most frequently, and high beds least frequently, I have positioned the real diversity trend data obtained in this survey for each intertidal height at different

Fig. 36. Actual and predicted changes in species diversity (H') over time for mussel beds from high, mid, and low intertidal regions. Solid lines represent actual changes documented in this study (m = slope for 2 year change) and dashed lines indicate projected curves of diversity change over time.


SHANNON - WEAVER (H')
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
AGE OF MUSSEL BED
(YRS)
0
2
4
6
8
10
12
14
16
18
20
MORE EXPOSED
LESS EXPOSED
LOW(1.33)
M=0.10
MID(1.28)
M=0.08
HIGH(1.22)
M= -0.02

relative ages along the developmental "cycle." I have speculated that on the average, mid-intertidal beds are at least five years older than low-level beds and that high-level beds are at least five years older than mid-level beds. No other assumptions are made as to the shape of the diversity curves, other than their being monotonically increasing functions. The slope (m) for the two-year changes in diversity levels at each intertidal height was obtained by averaging the two-year changes in the Shannon-Weaver index from all four study sites. The solid lines represent these averaged real values and the dashed lines represent a predicted diversity trend over time for each intertidal level. I have predicted that all three levels, if undisturbed, would continue to increase in diversity with the same relative, but declining, rates of change as noted during this two year study, resulting in highest diversity in the lowest intertidal mussel beds and the lowest diversity in the highest mussel beds. The values of H' obtained in this study probably represent close to the maximum value obtainable for high intertidal mussel beds since the slope for the two year average change was actually -0.02. For more exposed habitats, I suggest that all three curves would be shifted up and in less exposed habitats, the curves would be shifted down. In more exposed habitats, mussel beds become perturbed at a more frequent rate and may be terminated before reaching full diversity potential. Therefore, on the average, mussel beds of comparable intertidal height should be older in more protected habitats but not necessarily more diverse.

To my knowledge, the species richness values found here are the highest yet reported for any single temperate community and are comparable to those reported by Hessler & Sanders (1967) and Sanders & Hessler (1969) for the temperate deep sea environments, but in this case the richness is clearly related to structural complexity. The results are probably not directly comparable, however, for the sampling technique used by Sanders & Hessler (1967) involved dragging an 80 cm wide epibenthic sled over the sea bottom for one hour, probably sampling more than one environment. They sampled an area of about 1854 m^2, finding a maximum of 365 taxa. My sampling technique involved the collection of 0.1 m^2 samples, with a total of only 5.5 m^2 sampled in the entire study, yielding a total of 303 taxa. The results presented here refute their claim (op. cit.) that "...the diversity of benthic invertebrates in the deep-sea well exceeds that of temperate, shallow water, benthic communities...". They are, at the least, of comparable level and probably represent much higher levels. Further, the intertidal community is clearly much richer in visible structure, phyletic representation, standing crop biomass, and probably productivity.

In summary, the primary factor controlling diversity in mussel bed communities is the structural complexity of the mussel bed matrix. For real mussel beds, this structural complexity is in turn a function of the age of the mussel bed, its tidal height, and relative degree of exposure to wave action. As a mussel bed gets older, its physical structure becomes increasingly more complex, creating unique microhabitats and food resources which probably further allow the survival of more specialized species dependent upon these unique resources.

CHAPTER 5

MAINTENANCE OF COMMUNITY STABILITY BY MUTUALISM BETWEEN MUSSELS (*MYTILUS CALIFORNIANUS*) AND THEIR ASSOCIATES

INTRODUCTION

The notion of ecosystem change and stability has intrigued and bewildered biologists for decades (for discussions, see MacArthur, 1955; Dunbar, 1960; Cunningham, 1963; Frank, 1968; Holling, 1969, 1973; Lewontin, 1969; Margalef, 1969; Preston, 1969; Watt, 1969, May, 1972a, Smith, 1972). Even the earliest developments of the theories on succession were an attempt to deal with the concept of a community approaching some prescribed stable end point, to be disturbed or perturbed from this ideal "stable" state only by some catastrophe or disaster such as a flood, a fire, or massive predation. The major problems with the concept of stability have been how to define it, how to measure it, and how to compare it. An endless supply of jargon has accompanied attempts to resolve the first point, that is, how to define it. Words such as "stayability," "zero-stability," "constancy," "ability to bounce back," "persistence," and "resilience" are among the many and as yet we still lack a quantitative or qualitative handle on the concept. The second and third points, how to measure and compare it, have met with varied success from different disciplines. Mathematically, the stability of a system with, say, *n* interacting species, can be modeled, and the component interactions varied according to some prescribed "game plan." The ability of this type of system to withstand perturbations or persist through time can indeed be quantified (May, 1972b, 1973a, b, 1974). But, as May (1973c) himself aptly points out "...the models aim not at realism in detail, but rather at providing mathematical metaphors for broad classes of phenomena." It is the application of this body of theory to natural conditions which has proven problematical, hence a large gap between theory and reality still exists.

Ecologically, the prime considerations which must be dealt with in any discussion of stability are those of scale, both temporal and spatial. The spatial arena under consideration may range from a local, fixed point in space (yielding ideas of neighborhood stability) to a regional phenomenon which may extend to a boulder, a field, a coastline, or a continent (global stability). The temporal aspects have the same unbounded limits which may span over physiological time, ecological time, or evolutionary time (Slobodkin, 1961), hence the profound problem in comparing stability between ecosystems.

The common thread through nearly all discussions of ecosystem stability has been that if a particular system is stable, it either 1) maintains relatively constant numbers of taxa and/or individuals over time, 2) if disrupted from this state, it can, in some specified period of time, return to previous condition, or 3) fluctuates widely, but in a predictable manner. The end result is that the extinction or drastic reduction of one or more taxa does not occur.

In Chapter 4, I presented a detailed account of observations dealing with interactions of functional or ecological roles of the associated members of the Mytilus californianus community. In this chapter I describe experiments on this spatially well-defined ecosystem which demonstrate that its stability (indeed, perhaps its very existence) is dependent upon a mutualism between the dominant structure-forming species (mussels) and a number of associated species which inhabit the mussel bed matrix.

Here I use stability to refer to any or all of the three points mentioned above. The spatial scale of the experimental manipulations involved only a few mussel beds several meters in length along no more than 1 kilometer of rocky coastline, but the results are generalizable to the entire range of the mussel's distribution (i.e., along the West Coast of North America). The manipulations were performed in ecological time, covering a three year period, but again, the results may be relevant and extendable to evolutionary time.

These experiments were conducted primarily at Tatoosh Island (mostly on the south and west sides) and at Shi-Shi (at Shi-Shi Bench and Wreck Cove). Chapters 1 and 4 give detailed descriptions and maps for these study sites. Map label codes and tidal heights for the experimental manipulations are provided in the Methods section for each experiment.

GENERAL OBSERVATIONS

The unique nature of the isolated mussel beds on hillocks at Wreck Cove (Shi-Shi) made it relatively easy to study interactions at the interface between mussel beds and other intertidal communities such as the *Fucus*-zone assemblage. The perimeter of mussels at each of these hillock beds is remarkably constant over time and the lower limit of mussels is kept in check by the predatory activity of *Pisaster* in the manner identical to that described by Paine (1974) for continuous mussel beds along the Washington coast. Predation therefore limits the mussels' distribution to a cap or crown over each of the hillocks. Surrounding each of these isolated mussel beds, I observed a halo or zone of relatively bare space where neither mussels nor *Fucus* grew (Fig. 37) and where there was a paucity of barnacles as well. The width of these halos varied from 5-100 cm but most were approximately 20 cm with wider halos usually found lower in the intertidal zone. An average of 100 random measurements of the halo zone yielded a value of 29.69 (± 22.10 S.E.) cm. For three years (1974-1976) the halos did not appear to vary according to season, but during the summers of 1977 and 1978, the *Fucus* populations as a whole diminished considerably, resulting in less well defined halos in general.

Two possible mechanims which could explain the existence of these halos and the absence of *Fucus* are 1) allelochemicals emitted from the mussels and 2) mobile grazers living in the interstices of the mussel matrix. At low tide, I collected two (.01 m^2) replicate

Fig. 37. Photograph of a typical hillock mussel bed at Shi-Shi with a distinct halo (approx. 20 cm) surrounding it. Algae at the perimeter of the halo is *Fucus distichus*.

samples from the central region of one hillock mussel bed and two from the edge region adjacent to the halo. The results (Table XIII) indicate that there are twice the number of mobile grazers (and an abundance of _Thais_, a significant barnacle predator) at the edge as compared to the central region of the bed. This strongly supports the notion that mobile grazers are utilizing the food resources surrounding the bed at high tide and possibly using the bed as a refuge at low tide.

The experimental manipulations described in the next sections were performed to test hypotheses concerning the origin of the halos (which indeed are browse zones, see Ch. 2) and to determine the overall significance of associated grazers and predators on the stability of the mussel bed structure and associated community.

Each experiment was designed and executed to test a particular hypothesis and therefore I have followed each methods section with results in order to maintain the logic of the experimental design.

Table XIII. Grazer densities from the center and edge of a hillock mussel bed at Shi-Shi. Numbers represent counts per m^2 (±S.E.) from two replicates each from the center and the edge.

	LIMPETS	LITTORINES	*TEGULA*	*ONCHIDELLA*	ALL GRAZERS (TOTAL)	*THAIS EMARTINATA* (barnacle predator)
EDGE OF BED	4100 (±141)	400 (±141)	0	0	4500	300 (±141)
CENTER OF BED	1900 (±283)	140 (±71)	200 (±141)	250 (±354)	2500	0

BARRIER EXPERIMENT

METHODS: Map Code = (B)

Here I test the hypothesis that the halos surrounding mussel beds are due to the influence of mobile grazers and not to the presence of allelochemicals being emitted from the mussels. To test this, I have constructed a barrier at the edge of an isolated mussel bed located on one of the hillocks at Wreck Cove to prevent movement of these grazers from the bed into the halo region. In May 1974, a 1.0 meter barrier made of stainless steel screen (mesh size approx. 5 mm) was bolted to the rock substratum with stainless steel wood screws fastened to nylon masonry sleeves. In addition to the screws, quick-drying (Jet-Set ^{TM}) cement was used to secure the base and prevent gaps between it and the irregular rock surface. The barrier showed significant results within eight months time, with a disappearance of the browse zone and a luxuriant growth of algae. The barrier was maintained for nearly 2½ years and then removed in August, 1976 to test the ability of the grazers to affect these fully grown macroalgae. This experiment was conducted at 6.0 ft (1.8 m) tidal height.

RESULTS:

The barrier successfully prohibited the movement of limpets and other large grazers such as chitons from the mussel matrix out into the browse zone region. Within a few months after erection of the barrier, algae (primarily *Fucus* and some *Porphyra*) began to settle.

By the end of 10 months, the region, which was previously part of the halo, but subsequently protected from mussel bed associated grazers, was completely overgrown by macroalgae. Fig. 38A represents the condition at the initiation of the experiment in the early summer of 1974 when the barrier (crescent-shaped structure in the foreground) was erected. Fig. 38B shows the elimination of the browse zone by subsequent growth of _Fucus_ in the exclusion area one year hence. The browse zone returned nearly one year after removal (July, 1977) (Fig. 38C). Note that the browse zone surrounding the rest of the bed remained distinct throughout the experiment, being virtually devoid of macro-algae. Table XIV gives the percent primary and secondary cover (see Chapter 2 for definitions) occupied one year after the erection of the barrier (the condition in Fig. 38B). This demonstrates the significant influence which the associated grazers have on structuring the plant (and animal) communities surrounding mussel beds, for _Fucus_ increased from 5% to 75% secondary cover in one year. This also allows me conclusively to discount the hypothesis that the browse zone may be caused by allelochemicals being emitted from the mussel bed.

Fig. 38A. Photograph of 1.0 m barrier (crescent-shaped structure in foreground) at intiation of experiment at the edge of a hillock bed at Wreck Cove, Shi-Shi (June 1974). Other circular structures are part of the Circle Cage experiment (see text).

Fig. 38 B. Photograph of Barrier 1 year later (June 1975) demonstrating elimination of halo by growth of *Fucus distichus* in the exclusion area.

Fig. 38C. Photograph of same hillock bed 1 year after removal of barrier (removed in July 1977), showing reestablishment of browse zone at the perimeter.

Table XIV. Percent primary (1^{o}) and secondary (2^{o}) cover of dominant space occupiers holding greater than 1% of the space in the barrier zone and from the remaining browse zone (control) one year after the barrier was erected (the condition in Fig. 38B).

	REMAINING BROWSE ZONE (control)	BARRIER ZONE
FUCUS DISTICHUS	1% 1^{o} (5% 2^{o})	10% 1^{o} (75% 2^{o})
PETROCELIS SP.	0	2% 1^{o}
BALANUS CARIOSUS	10% 1^{o}	20% 1^{o}
BALANUS GLANDULA	30% 1^{o}	35% 1^{o}
CHTHAMALUS DALLI	10% 1^{o}	10% 1^{o}
BARE ROCK	45%	20%

CIRCLE CAGE EXPERIMENT

METHODS: Map code = (CC)

Similar in purpose and design to the Barrier Experiment, this manipulation allowed me to examine how grazers affect the biology of recolonizing organisms in patches which have formed internally in the matrix of a mussel bed. Various sized patches of cleared space occur naturally in the mussel bed matrix (see Chapters 2 and 3) and I have simulated the formation of these patches by clearing away mussels and associates from circular (0.1 m^2) areas in the central region of the mussel bed. These patches were created at Tatoosh Island (CC1) at a tidal height of 8.4 ft (2.6 m) and at Shi-Shi (CC2) at a tidal height of 4.8 ft (1.8 m) above MLLW (see map in Ch. 1 for exact locations).

At each location, two patches were created; one control and one experimental. The control patches were cleared and then only monitored for patterns of recolonization within the patch. The experimental patches were cleared, a stainless steel screen cage (mesh size approx. 5 mm) was secured at the perimeter of the patch and Jet-Set ^{TM} Cement placed at the base to fill in irregularities from the rock surface. This prevented the larger mobile grazers within the mussel matrix from moving into the patch and affecting subsequent colonization. These cages were established and dismantled on the same time schedule as the Barrier Experiment, being bolted in place in May, 1974 and removed in August, 1976. Grazers which managed to crawl over the fencing material were removed upon monitoring during each visit. Fig. 38A gives a generalized perspective of the experimental set up at Shi-Shi.

RESULTS:

The results of this experiment are even more dramatic than those of the Barrier Experiment. Again, the mobile grazers decimated any algae which settled into the small patch within the mussel bed. Figs. 39A and 39C represent the open circles from Tatoosh Island and Shi-Shi respectively (one year after scraping) where mobile grazers were free to roam. Figs. 39B and 39D are photographs of the caged circles taken at the same time (one year after scraping and establishment of the cages) showing that substantial algal growth had taken place within the exclosures. At Tatoosh Island, Ulva dominated the substrate within the cage; Fucus dominated at Shi-Shi. Table XV gives the results of monitoring the major space occupiers of greater than 1% primary and secondary cover for both Tatoosh Island and Shi-Shi in June, 1975 (one year after erection of the cages). And Fig. 40 shows that total cover remained constant throughout the remainder of the experiment.

These results confirm those obtained by Dayton (1971) in his Dog-Dish Experiments (which were similar in design but performed on open intertidal surfaces) where he showed the ability of limpets to influence both algal and barnacle populations.

Fig. 40 demonstrates algal colonization and growth at the two study sites (Tatoosh Island and Shi-Shi) within the caged circles,

Fig. 39A. Photograph from Tatoosh Island of the open circle (control patch) in June 1975 (one year after scraping), where grazers were free to roam showing maintenance of a denuded substrate.

Fig. 39B. Photograph of the circle cage (experimental patch) at Tatoosh Island in June 1975 (same date as above, one year after scraping) where grazers were eliminated showing dominant cover of *Ulva* and some *Fucus*.

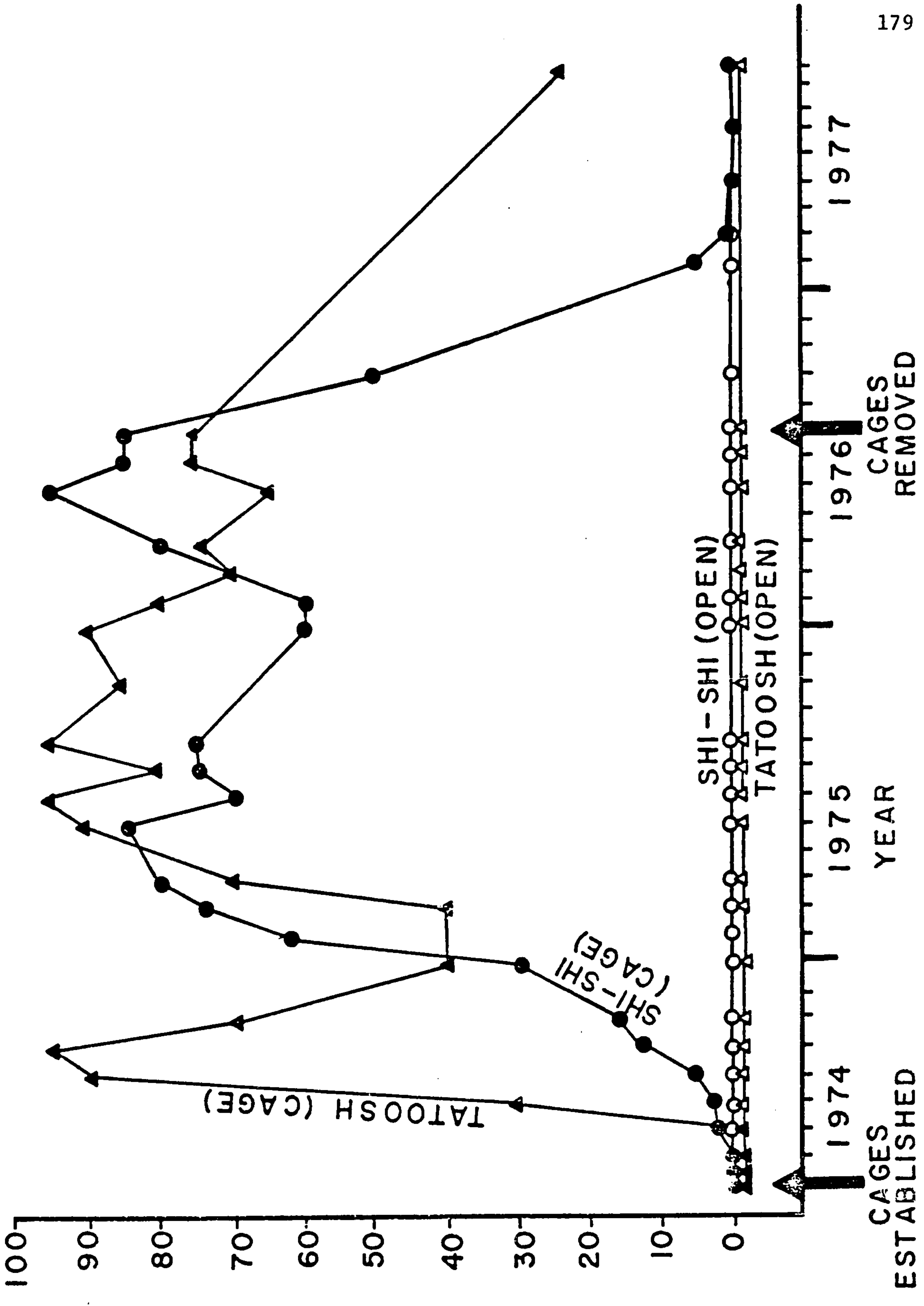
Fig. 39C. Photograph of the open circle (control) from Shi-Shi in June 1975 (one year after scraping) where grazers were free to roam showing maintenance of a denuded substrate.

Fig. 39D. Photograph from Shi-Shi of the circle cage (experimental patch) in June 1975 (same date as above, one year after scraping) where grazers were eliminated showing dominant cover of Fucus.

Table XV. Percent primary (1^o) and secondary (2^o) cover of dominant space occupiers holding greater than 1% of the space in the open circles (where grazers were free to roam) and in the circle cages (where grazers were excluded), in June 1975 (one year after scraping and establishment of cages).

	TATOOSH		SHI-SHI	
	OPEN CIRCLE	CIRCLE CAGE	OPEN CIRCLE	CIRCLE CAGE
FUCUS DISTICHUS	0	15% 1^o (85% 2^o)	0	3% 1^o (8% 2^o)
ULVOIDS	0	2% 1^o (5% 2^o)	0	40% 1^o (90% 2^o)
ANALIPUS JAPONICA	0	5% 1^o	0	2% 1^o
BALANUS CARIOSUS	0	0	10% 1^o	10% 1^o
BALANUS GLANDULA	35% 1^o	50% 1^o	0	30% 1^o
CHTHAMALUS DALLI	25% 1^o	5% 1^o	20% 1^o	0
MYTILUS EDULIS	0	5% 1^o	0	0
BARE ROCK	35%	10%	65%	5%

Fig. 40. Percent cover of secondary substrate (i.e. map area) by algae in open circle patches (controls) and caged circle patches at Tatoosh Island and Shi-Shi during the course of the Circle Cage experiment. Scraping and establishment of cages was done in May 1974. Cages were maintained for over 2 years and removed in late summer 1976.


% COVER
100
90
80
70
60
50
40
30
20
10
0
TATOOSH (CAGE)
SHI-SHI (CAGE)
SHI-SHI (OPEN)
TATOOSH (OPEN)
CAGES ESTABLISHED
1974
1975
1976
1977
CAGES REMOVED
YEAR

and the absence of any algal growth in the circles open to grazing by mussel bed associated herbivores. The cages were maintained for over two calendar years and in August, 1976 were removed. This was done in order to determine if the grazers could effecitvely crop macro-algae which had established themselves within the exclosures as well as the young succulent shoots of recently settled algae. Soon after removal of the cages, algal cover declined dramatically at both study sties (Fig. 40) falling to zero within seven months at Shi-Shi. When last observed (September, 1977) the Tatoosh patch was declining rapidly as well.

BROWSE ZONE EXPERIMENT

METHODS: Map code = (BZ)

The effect of grazers on recolonization events in various sized patches was determined by creating four replicated series of three different sized patches during April, 1976 at Tatoosh Island (BZ1 at 6.0 ft (1.8 m) and BZ2 at 5.0 ft (1.5 m) above MLLW) and at Shi-Shi (BZ3 at Wreck Cove was 6.3 ft (1.9 m) and BZ4 near Shi-Shi Bench was 5.8 ft (1.8 m) above MLLW). In order to test whether grazers are capable of affecting internal colonization patterns within a patch 20 cm from each edge of the mussel matrix, at each site I created one set of patches smaller than this critical size (20 x 20 cm), one set of patches equal to this critical size (40 x 40 cm), and one set of patches larger than this size (80 x 80 cm). Subsequent recolonization patterns were monitored for a period of two years.

RESULTS:

In three out of the four replicates of this experiment, the results were conclusive, yielding no growth of macro-algae in the small (20 x 20 cm) patches, little growth in the medium (40 x 40 cm) patches, and substantial growth in the central region of the large (80 x 80 cm) patches. Figs. 41A, 41B, and 41C show the trend for these various sized patches. This result supports the hypothesis that there is an effective limit to the ability of grazers to control the colonization of algae within patches. This limit is essentially 20-30 cm from the edge of the mussel bed from which they emerge, no

Fig. 41A. Photograph of 20 x 20 cm patch in June 1977, showing complete grazing of all algae by associated grazers.

Fig. 41B. Photograph of 40 x 40 cm patch in June 1977, showing minimal algal growth.

Fig. 41C. Photograph of 80 x 80 cm patch in June 1977, showing the limited browse zone on internal patches, resulting in substantial algal growth in the central region which was rarely reached by grazers.

matter whether that edge is on the interior or the exterior of the bed. Experiments BZ1, BZ2, and BZ3 all showed similar results, but BZ4 had no successful algal survival. _Collisella digitalis_ was very abundant in the BZ4 region and because of its superior abilities to withstand desiccation, it was probably able to completely graze the experimental patch.

POISON BED EXPERIMENT

METHODS: Map code = (P)

An experiment designed to determine the influence of the majority of associated species on the stability of the mussel matrix was initiated in March, 1975 at Wreck Cove. One of the isolated hillock mussel beds (tidal height approx. 5.5 ft (1.7 m) above MLLW) was designated as a control and another (same tidal height) was treated with a selective poison, para-dichloro-benzene (=PDB=POLYSTREAM ^{TM}). PDB is used in the commercial oyster industry for the removal of oyster drills without harm to the oysters themselves (Harvey *et al.*, 1966; Mackenzie, 1970). This poison was used to remove as many associated fauna from the interstices of the bed as possible without disruption of the physical matrix of the mussels. Because many herbivorous mollusks such as limpets could secure their shells against the mussel valves until the next tide washed the poison away, any other associated organisms visible from the surface were also removed by hand using forceps. The poisoning and manual removal of associated fauna was performed approximately each month during the summer and every other month during the winter season for a duration of two years. The control and experimental beds were separated by more than 20 meters to prevent accidental poisoning of the control bed.

RESULTS:

Removal of all associated mobile fauna had dramatic effects on the mussel bed matrix. Not only did the browse zone disappear, but the mussels became fouled with heavy encrustations of barnacles (*Balanus glandula*) and macroalgae (*Fucus* and *Porphyra*). Even though the experiment was only continued for a period of two years, the results suggest a further direction of continued fouling and overgrowth. Eventually this would result in mussels being torn from the rock surface by excessive shearing stresses due to the fouling organisms. Figs. 42A and 42B show the initial condition of the control bed and Poison bed (respectively) and Figs. 42C and 42D show them after nearly two years of manipulation of the latter.

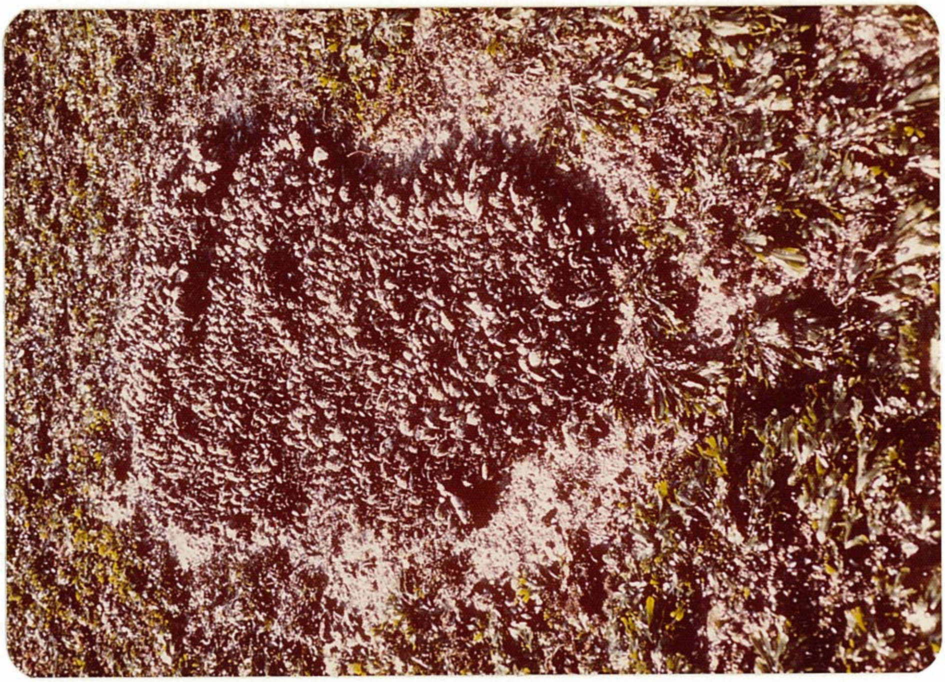
These results confirm those of the Barrier Experiment in showing how influential the associated mobile grazers are on the maintenance of the browse zone. In addition, they demonstrate that the grazers keep the mussels free of fouling organisms. Note in Fig. 42D that the Poison Bed mussels are heavily encrusted with barnacles (light color), whereas the control bed mussels (Fig. 42C) are relatively clean. By keeping the fouling organisms from overloading the shells, the associates enable the mussel matrix to persist for long periods of time.

Fig. 42A. Photograph of initial condition of control bed at Shi-Shi showing extent of browse zone in March 1975.

Fig. 42B. Photograph of initial condition of Poison Bed at Shi-Shi showing similar extent of browse zone as in the control bed in March 1975.

Fig. 42C. Photograph of control bed in October 1976. Note the continued presence of the browse zone.

Fig. 42D. Photograph of Poison Bed in October 1976, after 1.5 years of application of PDB and manual removal of grazers. Note disappearance of browse zone and heavy encrustations of barnacles on the mussels.



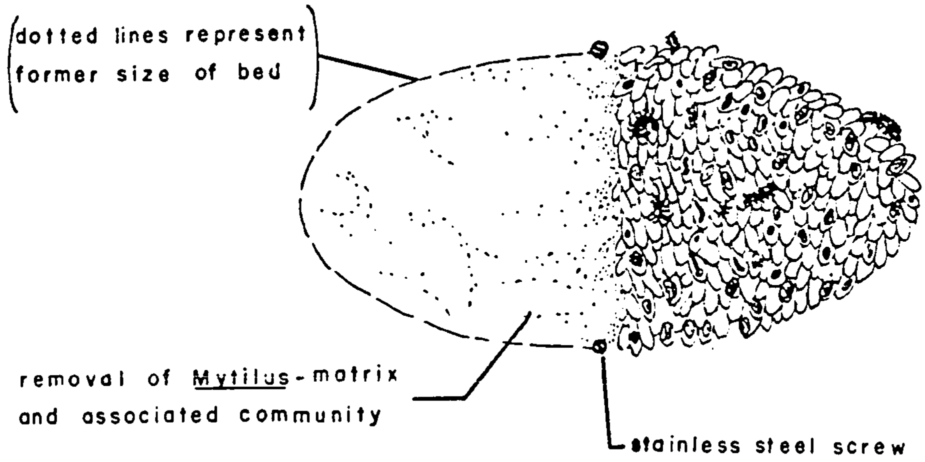
HALF-BED EXPERIMENT

METHODS: Map code = (H)

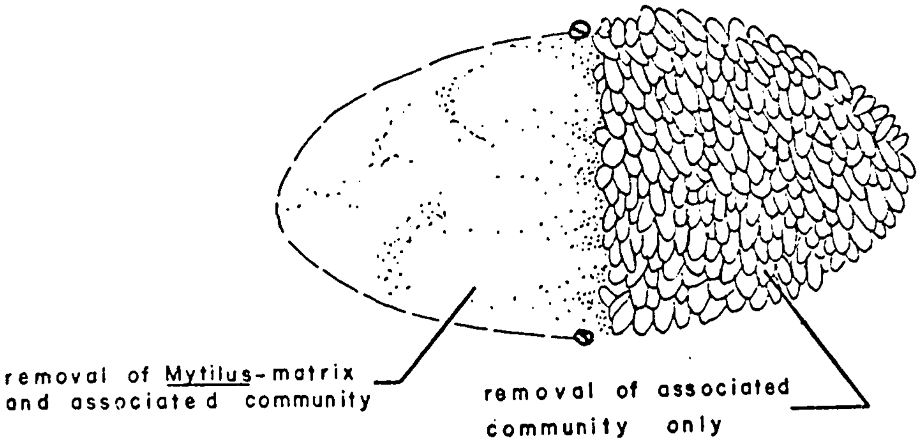
A final experiment in which I also applied PDB and manually removed associated organisms from isolated hillock beds at Wreck Cove was designed to test the influence of the assoicates on affecting the ability of *M. californianus* beds not only to persist, but also to expand. One control bed and one experimental bed were established in August, 1976 at each of two sites in Wreck Cove and were followed for a one year period. The two beds at H1 were 6.0 ft (1.8 m) and those at H2 were 5.5 ft (1.7 m) above MLLW. From each bed, half of all the mussel matrix and associated community was removed completely. In the control bed the remaining half was left intact with all the associates. On the experimental bed I applied PDB and manually removed as many associated fauna as possible on a monthly or bi-monthly schedule as described for the Poison Bed Experiment. Stainless steel screws were placed at each side of the leading edge of the newly created half-bed (see Fig. 43) and measurements were taken on the movement of the mussels from this point by stretching a line tightly between the two stainless steel screws at each site. Values for the movement of the front of mussels were an indicator of the relative success of mussels at recolonizing area lost (e.g. through wave action and log damage during storms) by movement alone.

Fig. 43. Diagram of the control and experimental plots for the Half-Bed experiment showing the removal of the *Mytilus* matrix and associated community from the beds. Experiment initiated in August 1976.

CONTROL PLOT:



EXPERIMENTAL PLOT:



RESULTS:

Table XVI gives the results of organisms colonizing the removal half areas and the fouling organisms that settled on the valves of the mussels. This table shows conclusively that where associated organisms are lacking, considerable overgrowth occurs by a variety of algae and barnacles. But, where the full complement of associates is present, grazing pressures are intense on algae settling in the removal half regions and on mussels of control beds. Figs. 44A and 44B show the differences between a control bed and an experimentally manipulated half-bed (respectively) one year after the initiation of the experiment. From these photographs one can also observe that the front of mussels has moved substantially forward in the control beds whereas it has barely moved at all in the experimental beds (note the stretched line at the leading edge). Table XVII gives the results of measurements taken on the leading edge of the mussel beds for both control and experimental plots. The results indicate that the leading edge moved considerably farther in the control plots than in the experimental ones, supporting the idea that an associated fauna may be extremely beneficial not only in cleaning fouling organisms from the shell but potentially as an aid to mussel bed expansion. The mechanism by which the experimental bed could have been inhibited may be involved with the placement of byssal threads onto the primary substratum. Where the associated grazers keep diatoms and settling algae off the primary substratum, the mussels have no problem securing byssus. However, where the primary substratum is extensively covered with algae, mussels

Table XVI. Results of Half-Bed experiments H1 and H2. Percent primary (1^{o}) and secondary (2^{o}) cover of major space occupiers holding greater than 1% cover.

	H1				H2			
	REMOVAL AREA		ON MUSSELS		REMOVAL AREA		ON MUSSELS	
	CONTROL	EXPERIMENTAL	CONTROL	EXPERIMENTAL	CONTROL	EXPERIMENTAL	CONTROL	EXPERIMENTAL
Fucus distichus	2% 2^{o}	5% 1^{o} (60% 2^{o})	0	10% 1^{o} (75% 2^{o})	1% 2^{o}	5% 1^{o} (75% 2^{o})	0	1% 2^{o}
Endocladia muricata	1% 2^{o}	10% 1^{o} (25% 2^{o})	0	5% 2^{o}		15% 1^{o} (60% 2^{o})	0	3% 2^{o}
Gigartina sp.	0	3% 2^{o}	0	0	1% 2^{o}	5% 1^{o} (5% 2^{o})	0	2% 2^{o}
ulvoids	0	0	0	1% 2^{o}	0	2% 2^{o}	0	1% 2^{o}
Cladophora sp.	0	0	0	0	1% 2^{o}	15% 1^{o} (25% 2^{o})	0	2% 2^{o}
Iridaea cornucopiae	0	0	0	0	0	1% 1^{o} (1% 2^{o})	0	0
Petrocelis sp.	0	0	0	0	0	1% 1^{o} (1% 2^{o})	0	0
Leathesia difformis	0	0	0	0	0	1% 1^{o}	0	0
Priontis sp.	0	0	0	0	0	1% 1^{o}	0	0
Balanus cariosus	1% 1^{o}	20% 1^{o}	1% 1^{o}	1% 1^{o}	20% 1^{o}	5% 1^{o}	0	0
Balanus glandula	10% 1^{o}	15% 1^{o}	1% 1^{o}	30% 1^{o}	35% 1^{o}	10% 1^{o}	5% 1^{o}	60% 1^{o}
Chthamalus dalli	80% 1^{o}	40% 1^{o}	15% 1^{o}	15% 1^{o}	35% 1^{o}	40% 1^{o}	15% 1^{o}	20% 1^{o}
Bare rock or bare mussels	5%	10%	80%	40%	2%	10%	80%	10%

Fig. 44A. Photograph of Half-Bed control plot (i.e., with the normal complement of associates) one year after initiation of experiment. Note distinct browse zone and advance of mussels to the stretched line.

Fig. 44B. Photograph of Half-Bed experimental plot (i.e., with the associates removed) one year after initiation of the experiment. Note heavy algal cover in removal half and minimal expansion of mussel bed.

Table XVII. Results of mussel bed expansion in control and experimental plots in the Half-Bed experiment. Distances (in cm) were measured from a fixed line determined by a string stretched between the two screws on either side of the leading edge (see Figs. 43 and 44).

	DISTANCE MOVED FROM FIXED LINE AFTER ONE YEAR (cm) (N=10)		AVERAGE DISTANCE MOVED AFTER ONE YEAR
	H1	H2	
CONTROL	4.10	8.96	+6.53
EXPERIMENT	1.10	0.58	+0.84

may find it difficult locating attachment sites, thus slowing the bed expansion process. Observations on the conditions of the half-beds demonstrated more hummocking in the experimental beds as opposed to the controls. Whether this observation is a significant correlate of the inability of the bed to expand is not known.

DISCUSSION AND CONCLUSIONS

Observations on the relationship between mussels and the diverse group of invertebrates found associated with them make it clear that a strong interdependence has developed between the two. The existence of browse zones is evidence of one aspect of this interaction (i.e., the influence of mobile grazers and predators). Browse zones have been noticed in other systems in the past and when they occur, they usually indicate that a significant and active process is occurring on a regular basis. Although it need not be, the interaction is often a dependent one.

Randall (1961, 1965) claimed that conspicuous bands of bare sand separating reefs and beds of sea grasses (Thalassia and Cymodocea) in the West Indies were caused by overgrazing of herbivorous fishes (which seek shelter in the reefs from predaceous fishes). However, Ogden et al. (1973) gave conclusive evidence that the urchin Diadema antillarum can also be responsible for similar patterns, at least in the Virgin Islands. The urchins travel out into the halo zone at night and return to the protection of the reef by day. Ogden suggested that the nocturnal/diurnal behavioral patterns observed in these urchins are a response to predator pressures from 15 species of fish and a gastropod. Elimination of all urchins from one of these patch reefs resulted in the elimination of the halo within 8 months time. Around other Thalassia beds in Florida, Zieman (1972) described halos which were caused by the burrowing activities of worms and callianassid shrimps but gave no details of this phenomenon.

Terrestrial counterparts to the marine halos occur between shrub and grassland communities in the chaparral regions of coastal California (Bartholomew, 1970; Rood, 1970). Rodents, rabbits, and birds which seek shelter in the sage shrubs forage primarily at night (presumably to avoid diurnal predators), overgrazing the grasses adjacent to the shrubs. Bartholomew (1970), erecting exclosures around the bare zones, prohibited grazing and found significant growth of annual plants in these regions, but again did not discuss any interactive effects between the grazers and the shrubs.

The most detailed studies which have dealt with interactions between associated fauna and their host structures have been those on the tropical ant-plants. The close relationship between the neotropical myrmecophytes Cecropia and Acacia and their associated ants has long been recognized (Müller, 1874; Bequaert, 1922; Wheeler, 1942) but the question of whether this association is one involving exploitation or protection has been heavily debated (Bailey, 1922; Bequaert, 1922; Brown, 1960). Recently this association has been generally accepted as a co-evolved interdependence (Janzen, 1966, 1967, 1969; Hocking, 1970). The plants usually provide extrafloral nectaries to attract the ants, easily inhabitable swollen internodes or spines as nesting sites, and a nearly continual food source. The ants in turn provide protection for the plant from various parasitic plants, phytophagous insects or browsing mammals.

The mobile grazers and predators of the mussel bed community appear to function in much the same way as do the Acacia ants, and for similar reasons. The mussel bed matrix provides a continual source of food and acts as a refuge. It has a lighted surface area which is at least double that of flat rock substratum, and as a consequence settling diatoms and other algae are twice as concentrated per unit area of intertidal space. This in turn supplies more abundant food for grazers (limpets and chitons, etc.). The same condition exists for the barnacle predators. In addition to this extremely rich food supply, associates are protected at low tide from predation by shorebirds such as oystercatchers, surfbirds, and wandering tattlers.

Results of the Barrier and Circle Cage experiments show conclusively the negative influence of mobile grazers on the surrounding algal cover. At high tide these grazers venture out from the protection of the bed, utilizing still more food resources around the perimeter (or in patches within the bed). As the tidal cycle is completed, they again seek shelter. Since limpets at low tide are twice as abundant at the edge of the mussel bed as in the interior regions, it is reasonable that this skewed distribution represents the refugees which forage away from the bed only at high tide.

The results of the Poison Bed and Half-Bed experiments show that by their grazing activities, limpets (and for that matter, all other grazers and predators on epibiota) fortuitously, but effectively, clean the shells of _M. californianus_. In so doing, they protect them from excessive fouling and allow the mussels to maintain a stable population. Because _M. californianus_ does not have the ability to clean its own shell (as does _M. edulis_, Theisen, 1972) by sweeping off settling epibionts with its foot, it would become rapidly encrusted. This behavioral difference between these congeners was apparent after an enormous barnacle settlement of Balanus cariosus in the spring of 1977. Nearly all of the M. californianus shells were entirely encrusted with barnacles but M. edulis shells immediately adjacent to them were perfectly clean. Fig. 45 shows this event after the spring settlement on Tatoosh Island (photograph was taken in June, 1977). The dark, clean mussels to the left are M. edulis, whereas the ones with white barnacle encrustations to the right are M. californianus. Left unchecked, this fouling would add increased surface area and weight to the mussel shell, resulting in excessive shearing stresses from waves which would eventually tear the byssal threads loose from the rock substrata. Fig. 46 shows the result of unchecked fouling by Balanus cariosus on a M. californianus shell (18 cm in length). Barnacles have been removed from the left valve to show the unfouled condition. Once torn loose mussels would either 1) wash into tide pools and probably be captured by Anthopleura xanthogrammica (Dayton, 1973b; Sebens, 1977), 2) wash into subtidal regions where they would become easy prey for Pisaster, 3) wash up into the high intertidal where they would succumb to desiccation, or 4) occasionally reattach (Paine, 1974). A survey of M. californianus shells washed up on Shi-Shi Beach after storms (n = 363) revealed that over 75% still contained intact body tissues and were either heavily fouled by Balanus cariosus or Fucus, or were inexorably bound by byssus to other mussels that were fouled. Again, this is a strong indicator that fouling is a substantial source of mortality for M. californianus.

Fig. 45. Photograph of a low intertidal patch at Tatoosh Island in June 1977 with *M. edulis* (dark, clean mussels) to the left and *M. californianus* (with white *Balanus cariosus* encrustations) to the right, showing the result of shell-cleaning by *M. edulis*, and the inability to shell-clean by *M. californianus*.

Fig. 46. Photograph showing the results of unchecked fouling by *Balanus cariosus* on *M. californianus*. The shell is 18 cm in length and each *B. cariosus* is up to 8 cm in height. The left valve has been cleaned of barnacles to show the unfouled condition.

In addition to cleaning the fouling organisms from the shell, the associated grazers and predators aid M. californianus in expanding the area of intertidal space covered by mussel beds. As the mussels continually readjust their positions, by detaching and reattaching byssal threads, they expand into new regions basically by "crawling" (one byssal thread length at a time). As the Half-Bed experiment showed, those beds with a normal complement of associated fauna were able to expand into new territories more quickly than those beds without associates. Again, the reason may be that when the primary rock substratum is covered heavily with algae, the mussels cannot effectively place down byssal threads.

From my observations I can detect no extra incentives that M. californianus produces to attract its associated grazers. The interaction is clearly a mutualism, but is not coevolved in the sense that a demonstrable obligate interdependence has developed. However, since both participants can be shown to benefit from the association, the conditions for such evolution are present.

In summary, an interdependence between M. californianus and a number of its associated grazers and predators has developed which provides food and protection for the associated species, an anti-fouling mechanism to protect the mussels, and possibly a means by which this mussel can expand its populations. In this way the mussels avoid a potentially significant source of mortality and are able to maintain a substantially more stable structure (i.e., the mussel bed matrix) which in turn provides the structural heterogeneity necessary to support a complex, diverse community of over 300 associated species.

CHAPTER 6

SUMMARY AND CONCLUSIONS

In an attempt to understand and delineate the complex of interactions which structure and control the mussel bed community, I have focused upon several different aspects of this system. First, I have studied and described the basic competitive interactions between *Mytilus californianus* and its congener *Mytilus edulis*. I have shown that *M. edulis*, not previously known to be an important component of exposed rocky coast communities, and for the most part not known to occur in those habitats at all, is an abundant and significant member of the intertidal zone in those regions. I have defined its upper and lower limits and have made observations on the control of these boundaries.

M. edulis has escaped competition from *M. californianus* and predation by gastropods and sea stars by occupying a high intertidal band averaging 1.0 ft. in vertical height, above the level of the *M. californianus* zone (from 9.6 to 10.6 ft. above MLLW). However, this habitat is sub-optimal in several respects. It is subject to intense desiccation during summer months, and many *M. edulis* from the upper edge of this zone die each year. In addition, the individuals are so small (from lack of food resources) that they make only a minimal reproductive contribution towards the next generation. Alternatively, other *M. edulis* find settling sites in patches of cleared space in the lower intertidal which form during the winter months when regions of the *M. californianus* bed matrix are exfoliated.

Here, M. edulis is subject to predation by at least two carnivorous gastropods (Thais canaliculata and T. emarginata) and by Pisaster ochraceus, and it must compete for primary space with the superior competitor M. californianus. These lower patches represent a relatively high risk, and usually only temporary, habitat because of mortality from competitive exclusion and predation. Individuals colonizing these low intertidal patches contribute nearly 45 times as much (calculated on a population-wide basis) as their high intertidal counterparts in terms of reproductive fitness.

I have analysed many aspects of the life histories of these two Mytilus species, concluding that their strategies have diverged in several important ways. Differences in size, growth rate, age at first reproduction, mode of reproduction and life span have resulted in M. californianus taking on the role of a larger, slower growing mussel, devoting considerable energy into long-term growth, predator-deterring mechanisms, and overall competitive superiority, whereas M. edulis is a classic fugitive species which directs its energies not toward growth, but into maximum reproductive output and efficient dispersal mechanisms. I have also shown how disturbance may act as a cue to the timing of reproduction in M. edulis, allowing it to colonize recently perturbed habitats in the intertidal zone.

Having established the ecological and evolutionary basis behind the present distribution of M. californianus, I then focus on the dynamics of the mussel beds themselves. I have described the mechanisms involved in the recruitment of juvenile M. californianus, how the physical matrix of mussels develops, and have defined the basic physical attributes of the beds such as size, depth, and intertidal distribution. This matrix in turn supports a wealth of associated organisms (at least 303 taxa). These exist as either epibionts that can colonize the mussels' shells, mobile fauna that can move freely throughout the interstices of the bed, and infauna, that live in or on (and are generally dependent upon) the organic and inorganic sediments at the base of the mussel bed.

Through the use of artificial mussels made of a polyester resin, I have created physical entities that mimic the structural complexity and dimensions of real mussel beds. I have used these non-biological structures to demonstrate that this high level of species diversity is strictly a function of the structural heterogeneity of the environment.

I have given considerable natural history information on the resident associated organisms in an attempt to judge their relative significance and impact on the other community members as well as on the physical matrix of mussels. Many of the larger epibionts such as barnacles and algae are serious fouling organisms which, if left unchecked, cause considerable mortality for the mussels. This occurs by increasing surface area and therefore creating excessive shearing stresses against wave action, eventually causing mussels to be ripped loose from their attachment sites. Once torn free, they would most likely succumb to desiccation stress in the high intertidal or be consumed by predators in the shallow subtidal. However, many of the mobile fauna which seek shelter in the bed from desiccation and predation, are herbivores or predators on the epibiota, which impart an obvious benefit to the mussels. I have performed a series of experimental manipulations which have helped to define the ecological roles and probable evolutionary significance of this mutualistic relationship. Not only does this mutualism benefit the mussels, but in so doing, allows the existence of a biologically derived physical structure which supports a community of over 300 associated species.

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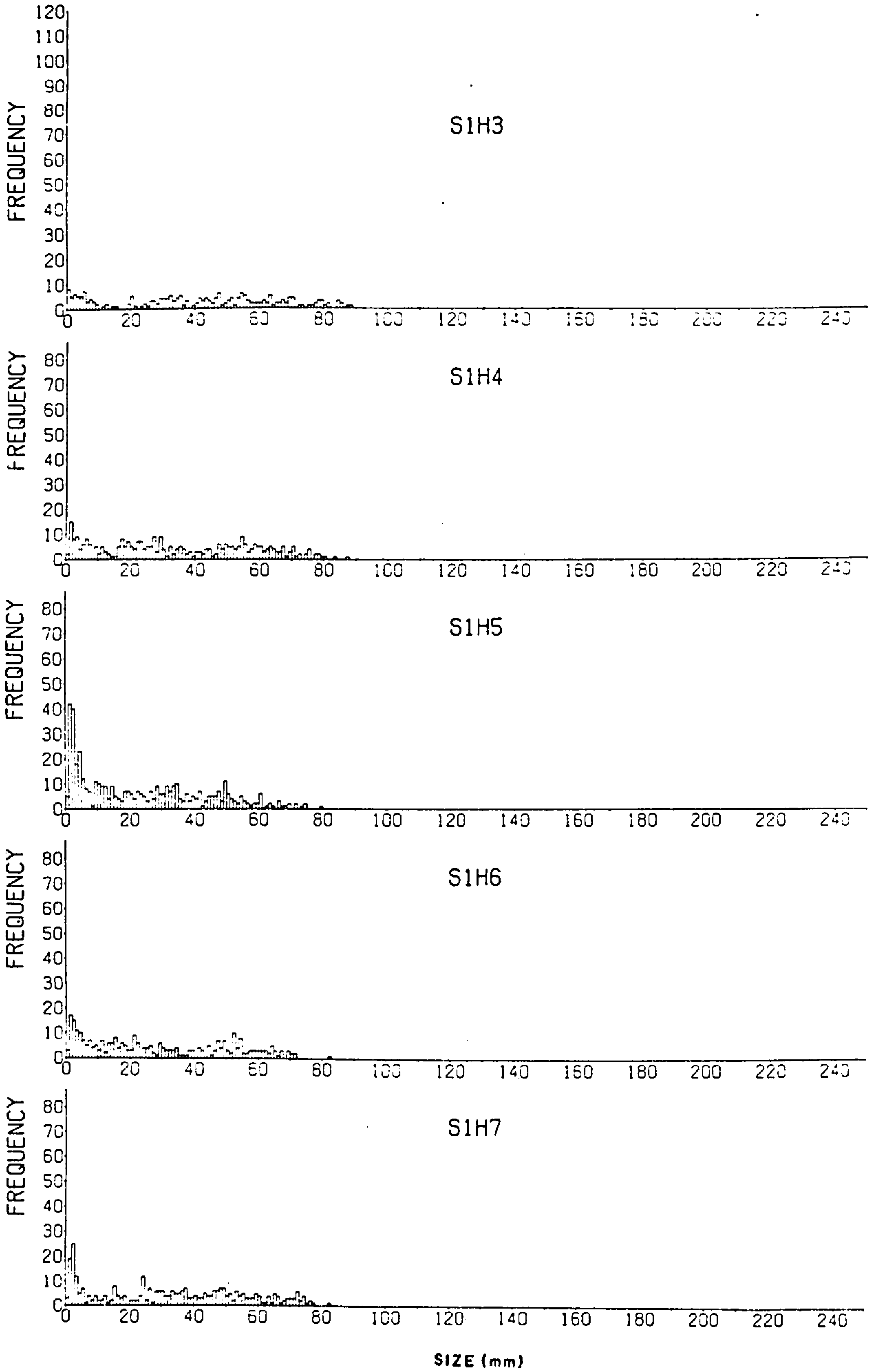
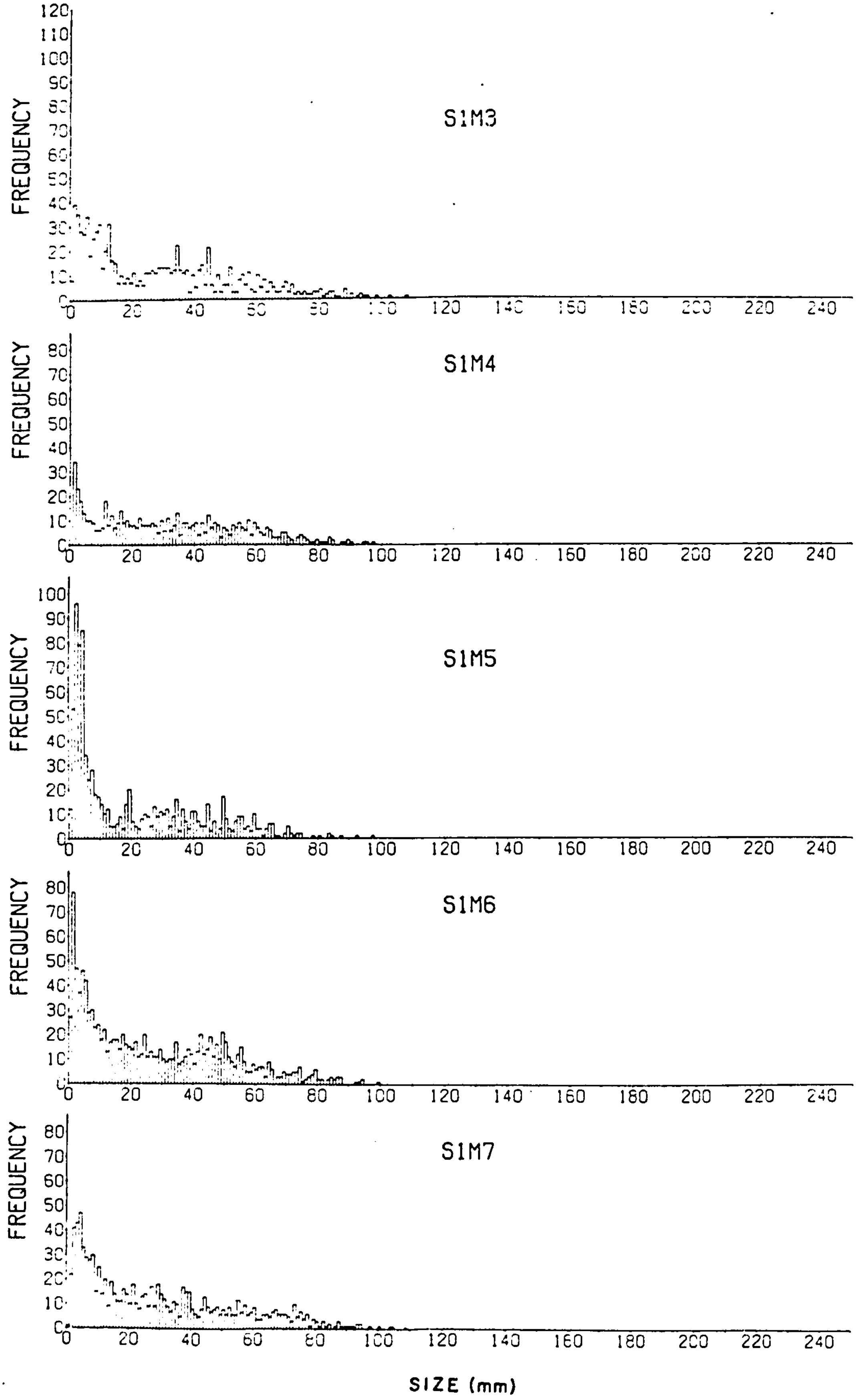
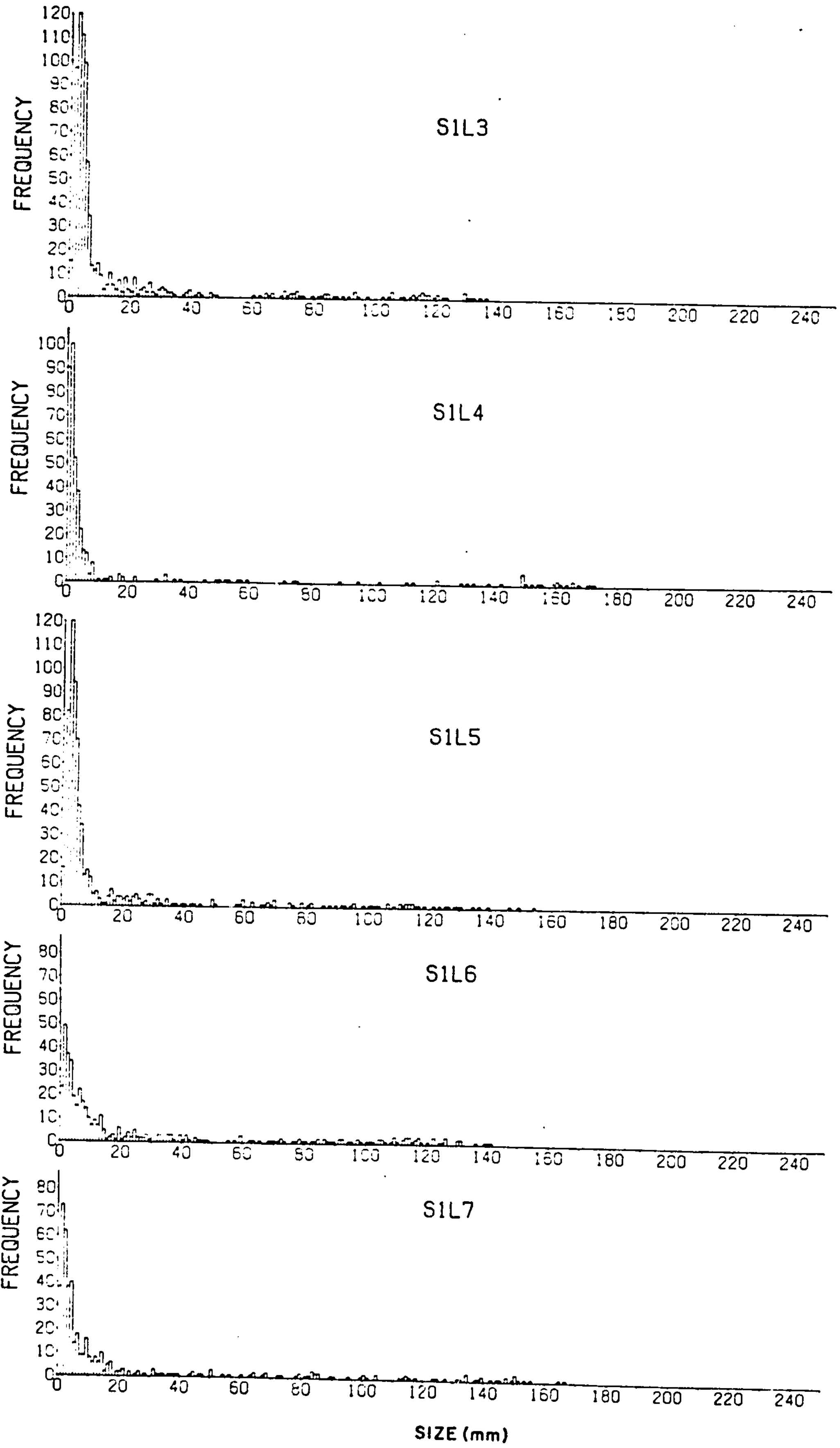
Appendix I. Number of daily visits to each study site.

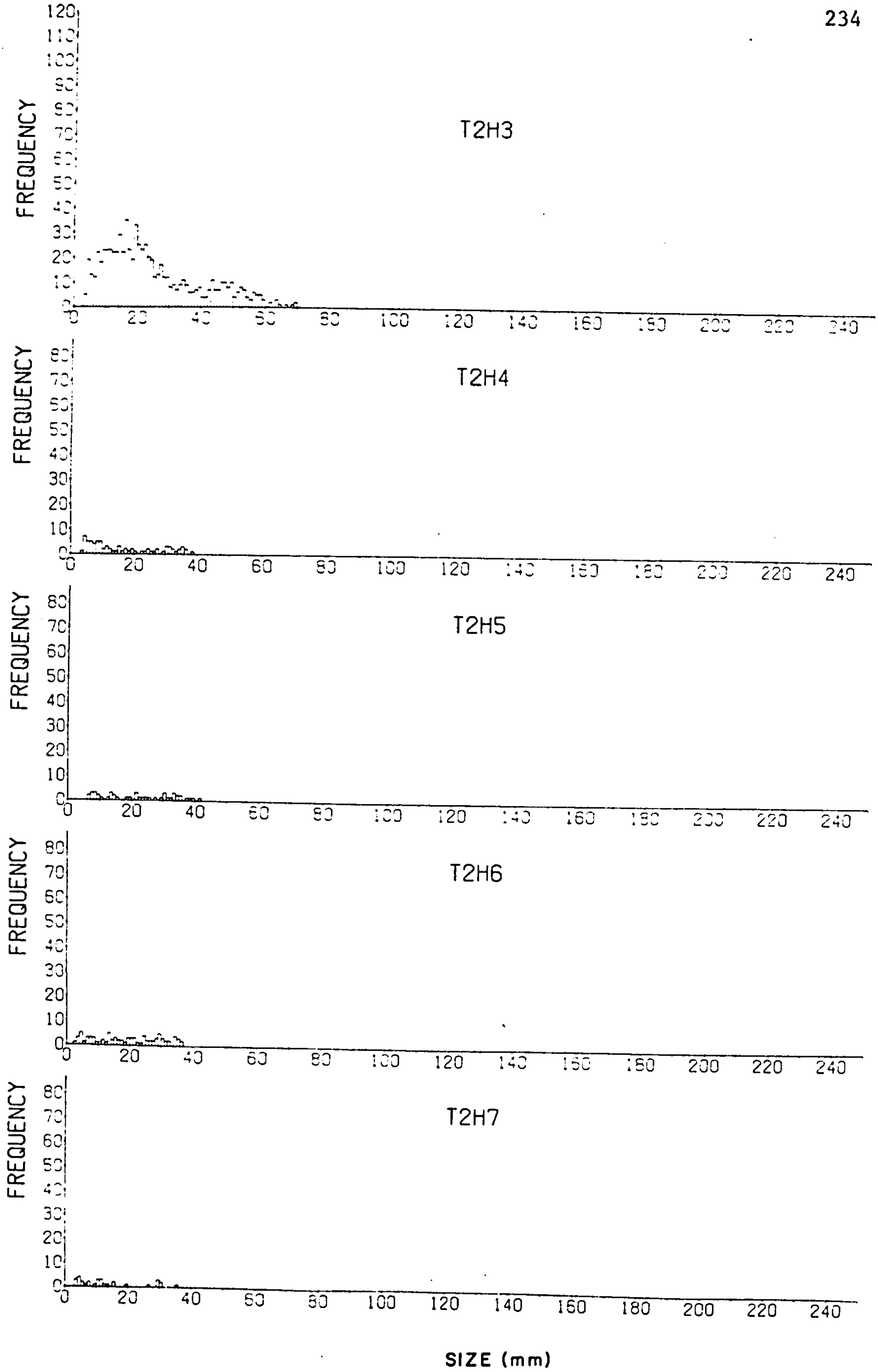
	1973		1974		1975		1976		1977		1978	
	SHI SHI	TATOOSH	SHI SHI	TATOOSH	SHI SHI	TATOOSH	SHI SHI	TATOOSH	SHI SHI	TATOOSH	SHI SHI	TATOOSH
JAN.		3	1				1	2	2			
FEB.							2	4	2			
MAR.				3	2	3			2		2	2
APR.					2	2	3	2		3		
MAY		1	2			1	1	3	2			
JUNE		6	1	4	2	4	2	4	3	3		
JULY		5	2	5	2	3	3	2	2			
AUG.			1	3	2	3	2	3			2	2
SEP.		6	2	4	2	5			4	4		
OCT.		3	1	3			2	4				
NOV.		3	2	4								
DEC.	2		2									

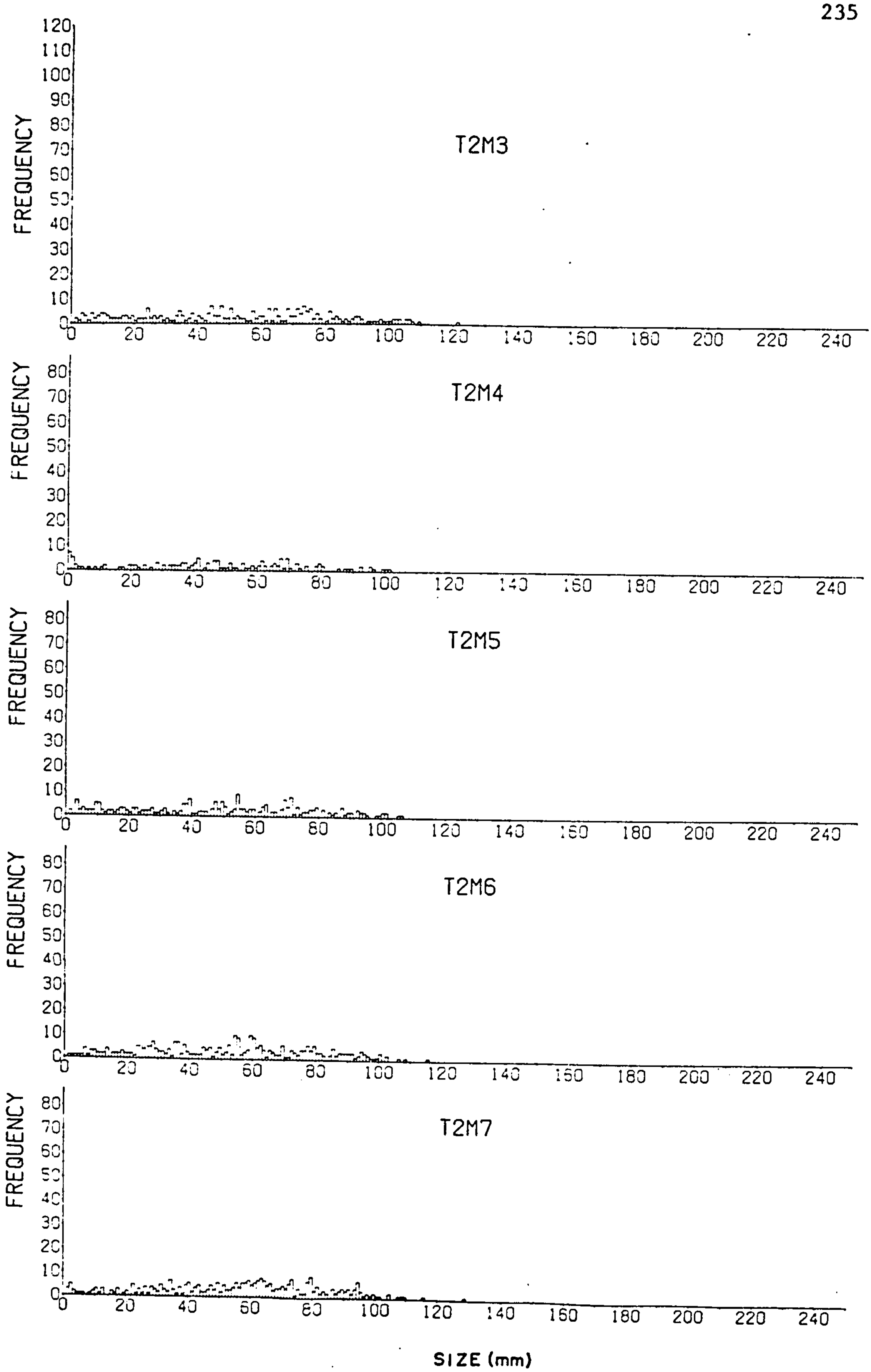
Appendix II. Size-frequency distributions for each sample.

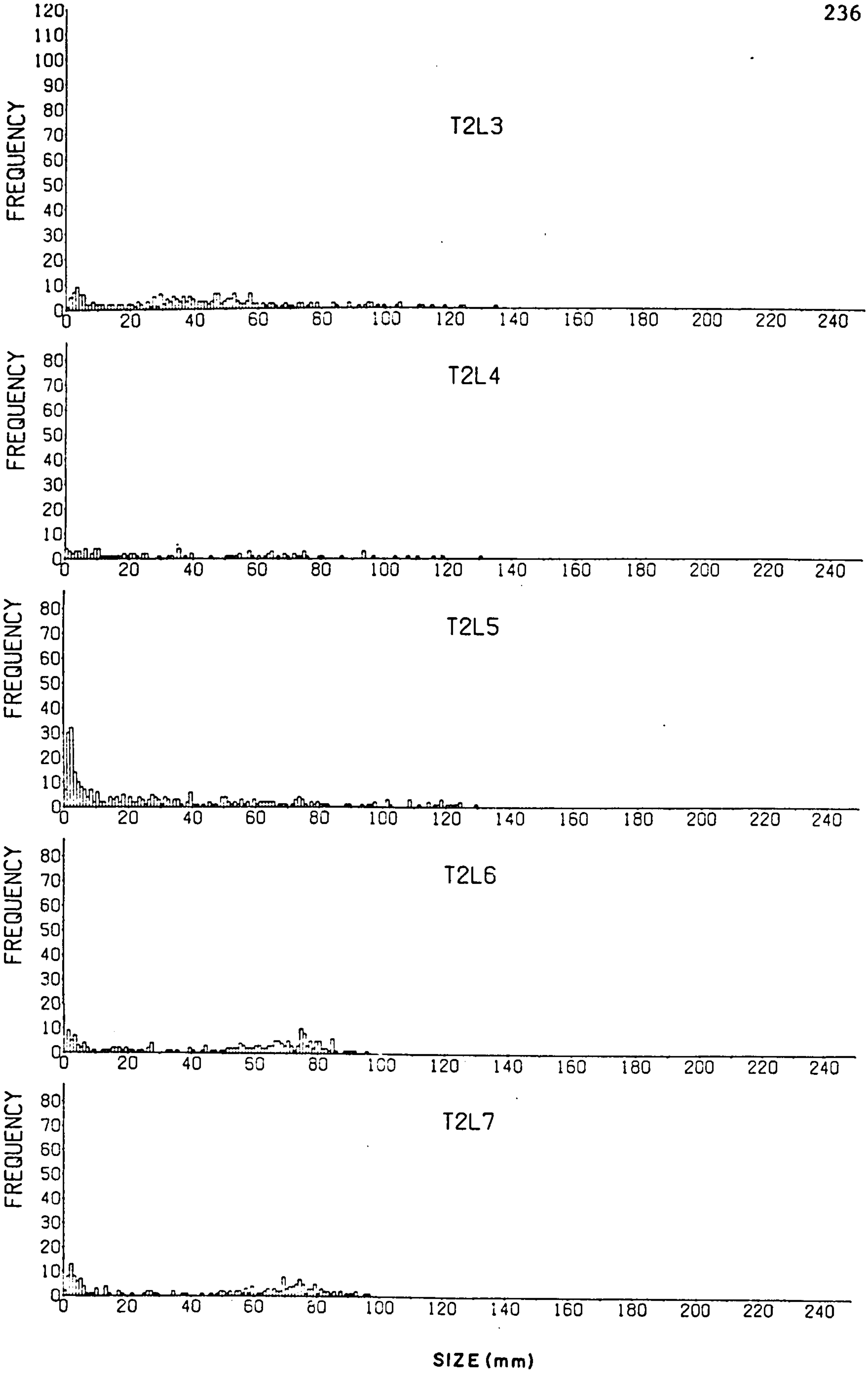

S1H3
S1H4
S1H5
S1H6
S1H7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

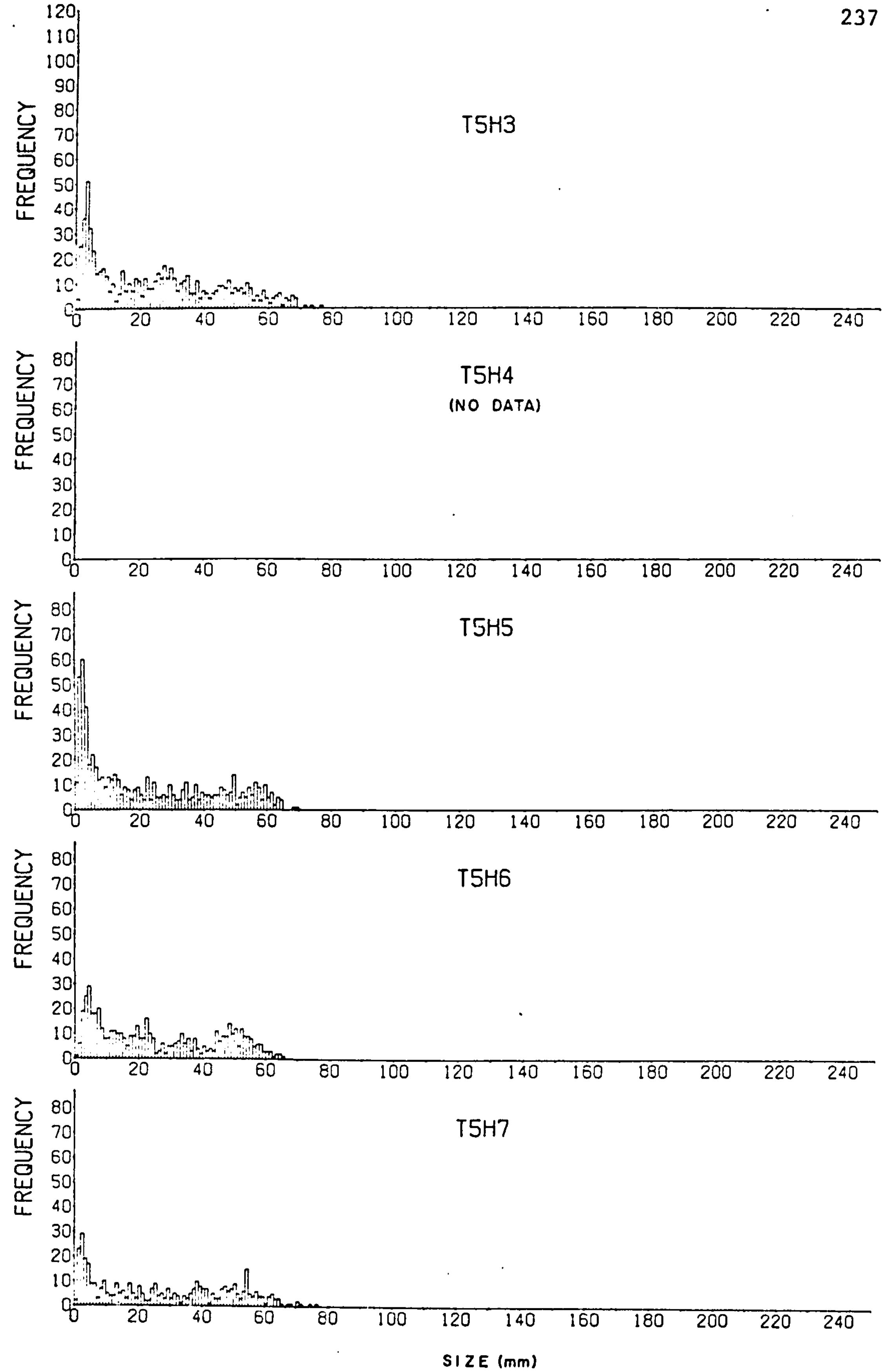

S1M3
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
S1M4
FREQUENCY
0
10
20
30
40
50
60
70
80
S1M5
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
S1M6
FREQUENCY
0
10
20
30
40
50
60
70
80
S1M7
FREQUENCY
0
10
20
30
40
50
60
70
80
SIZE (mm)

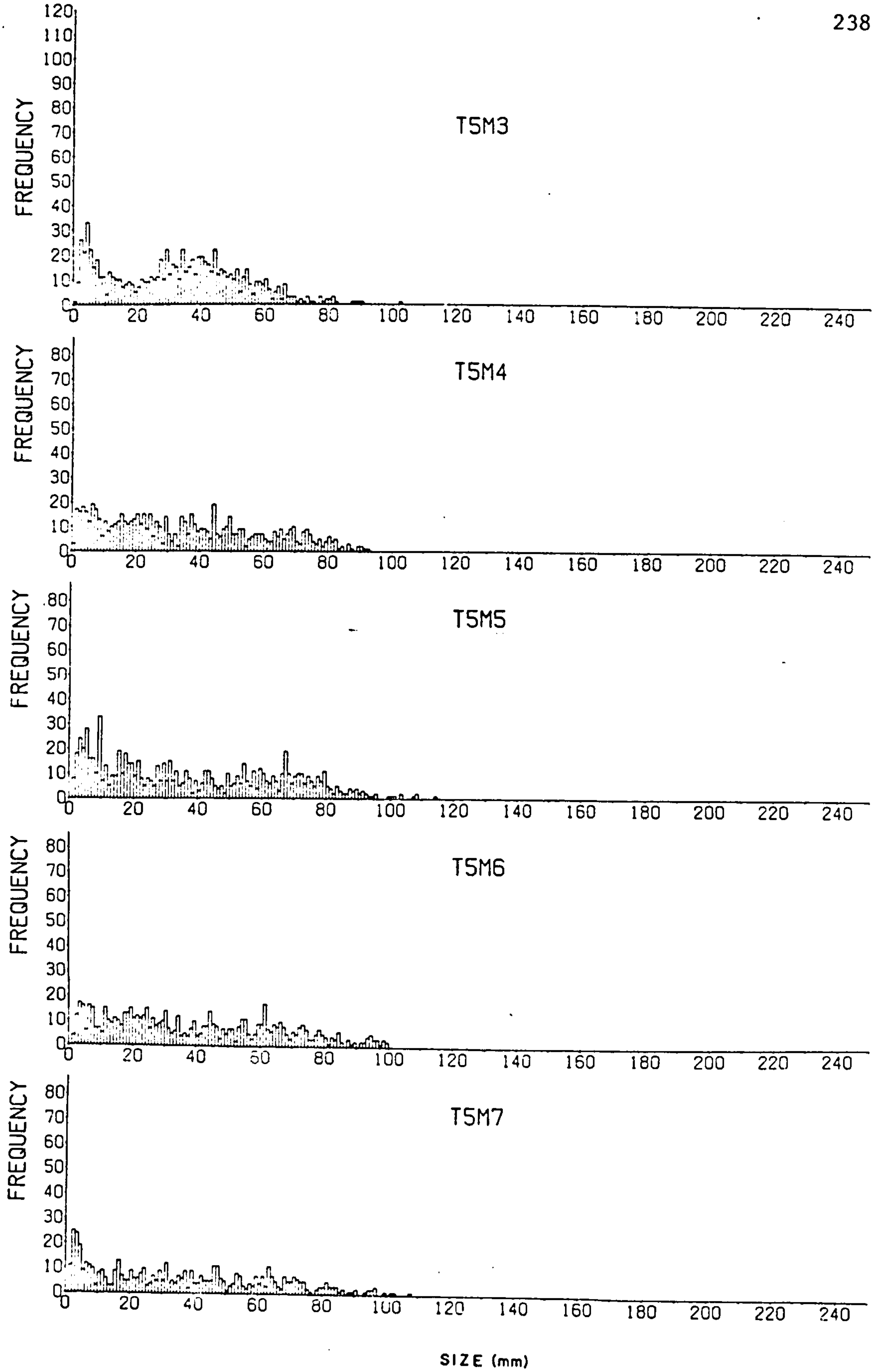

S1L3
S1L4
S1L5
S1L6
S1L7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

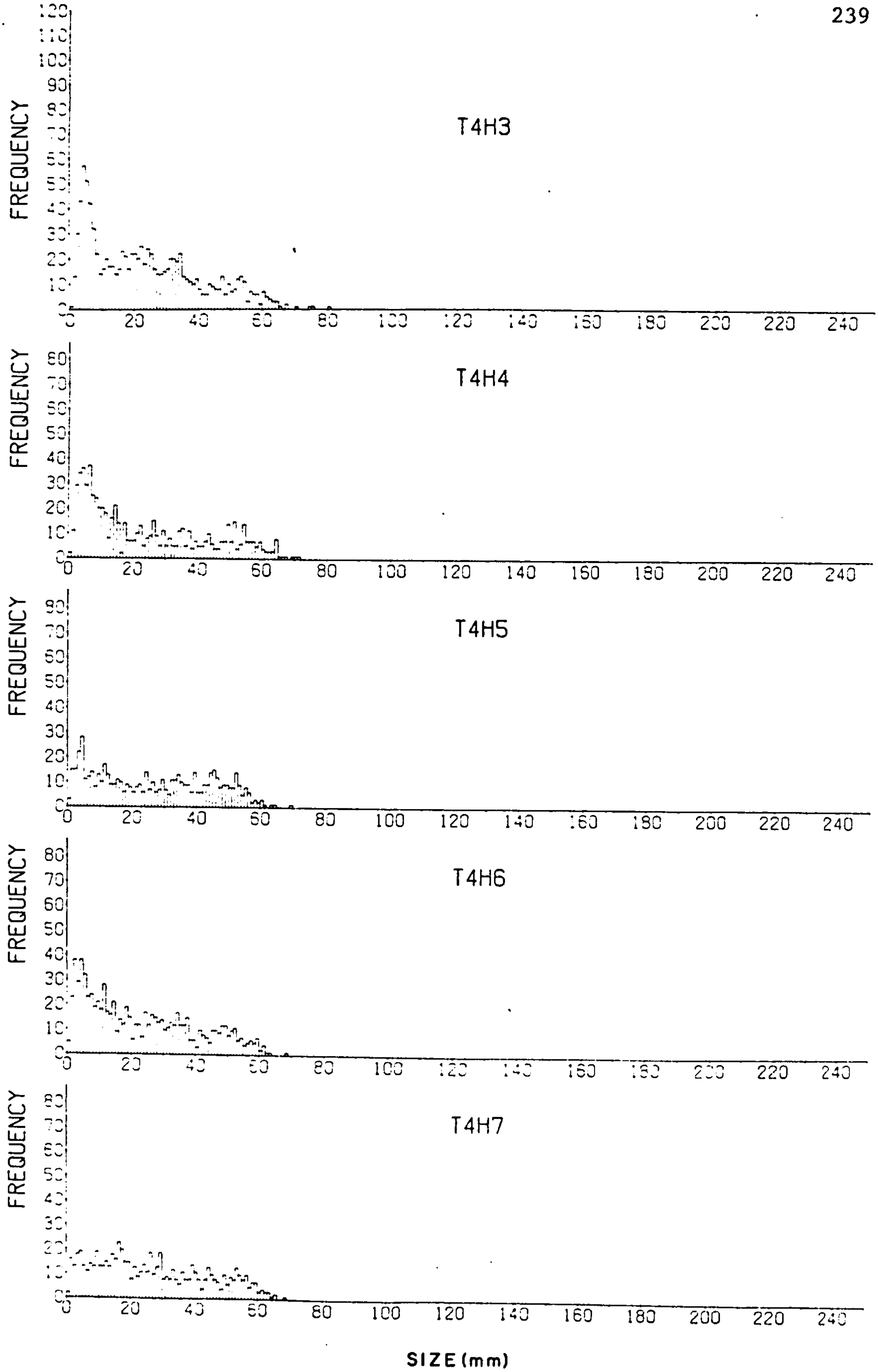

T2H3
T2H4
T2H5
T2H6
T2H7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

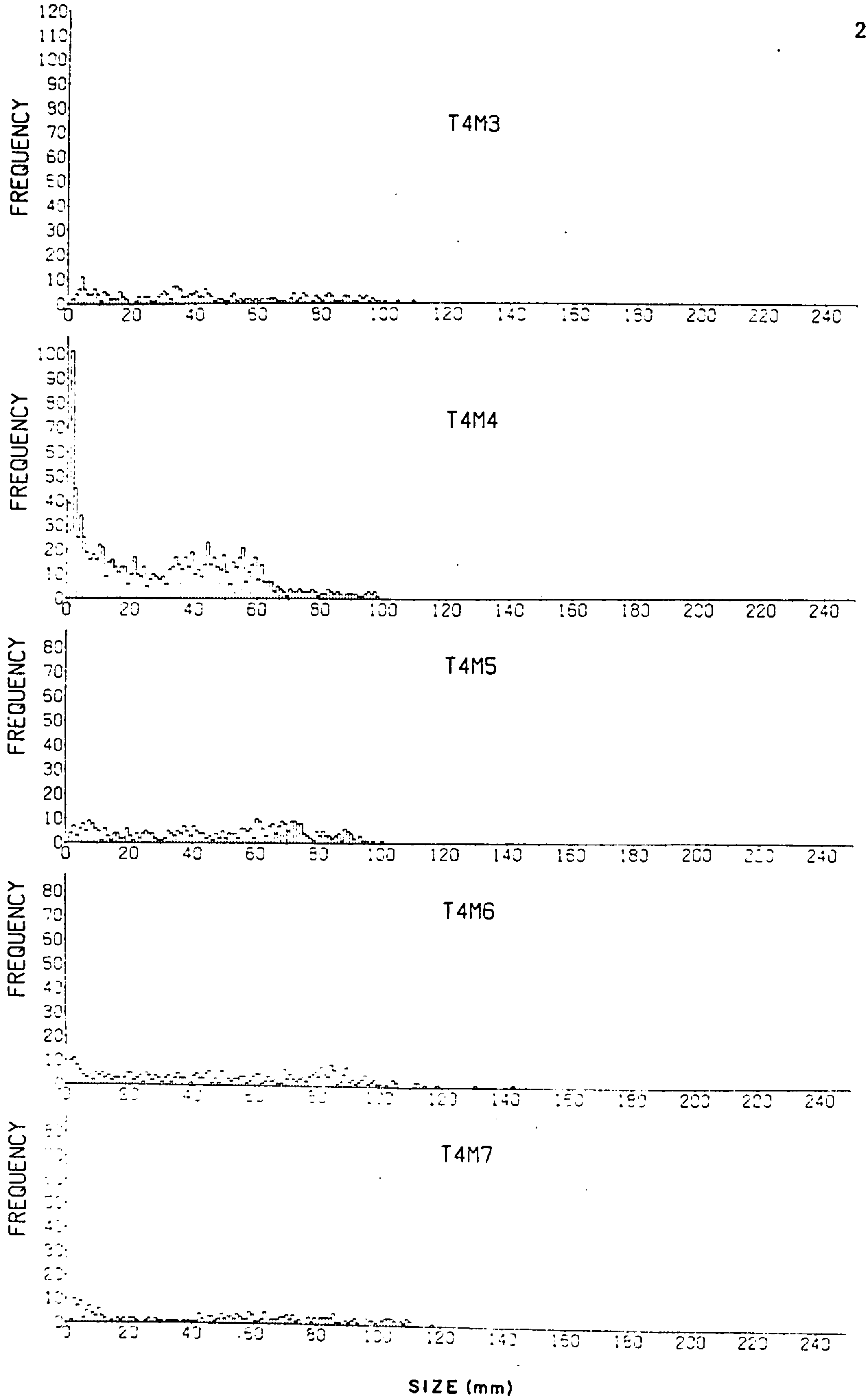

FREQUENCY
120
110
100
90
80
70
60
50
40
30
20
10
0
T2M3
0
20
40
60
80
100
120
140
160
180
200
220
240
FREQUENCY
80
70
60
50
40
30
20
10
0
T2M4
FREQUENCY
T2M5
FREQUENCY
T2M6
FREQUENCY
T2M7
SIZE (mm)

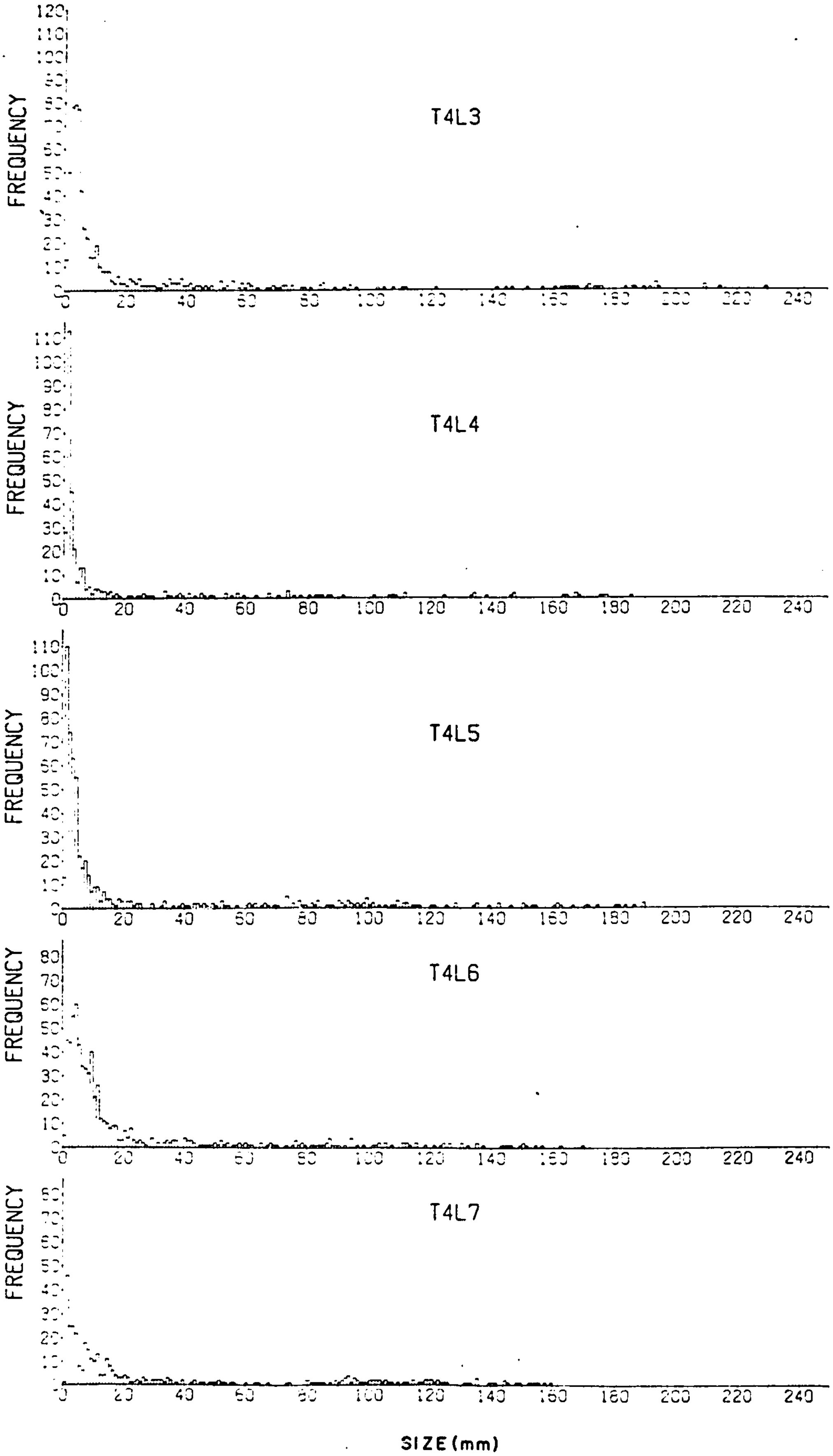

T2L3
FREQUENCY
120
110
100
90
80
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
180
200
220
240
T2L4
FREQUENCY
80
70
60
50
40
30
20
10
0
T2L5
FREQUENCY
T2L6
FREQUENCY
T2L7
FREQUENCY
SIZE (mm)


T5H3
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
T5H4
(NO DATA)
T5H5
T5H6
T5H7
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

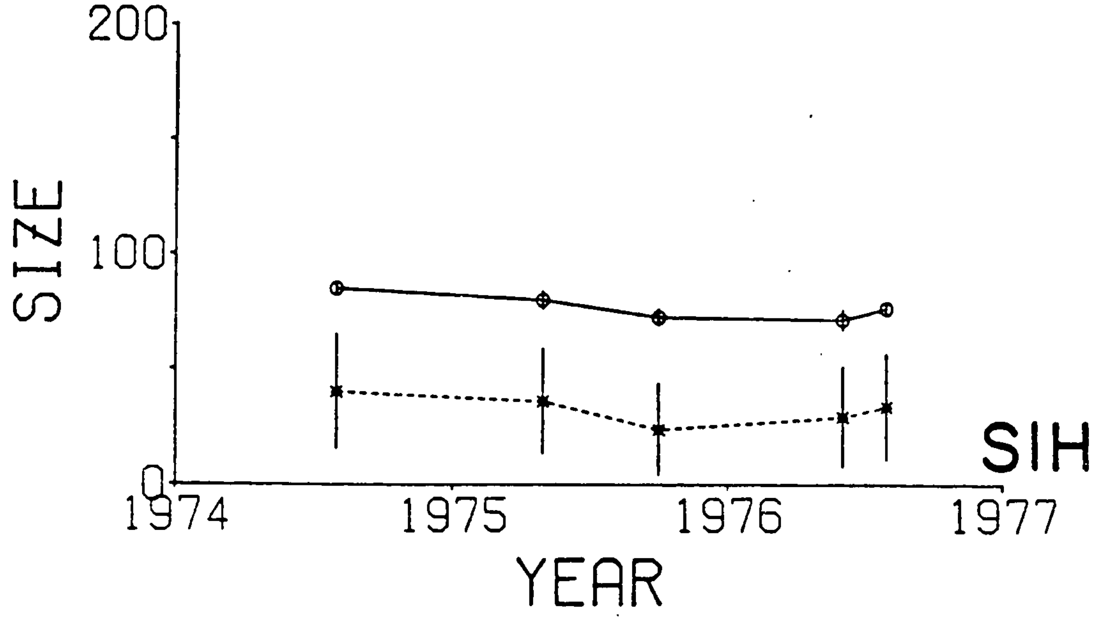

T5M3
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
T5M4
FREQUENCY
0
10
20
30
40
50
60
70
80
T5M5
FREQUENCY
T5M6
FREQUENCY
T5M7
FREQUENCY
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

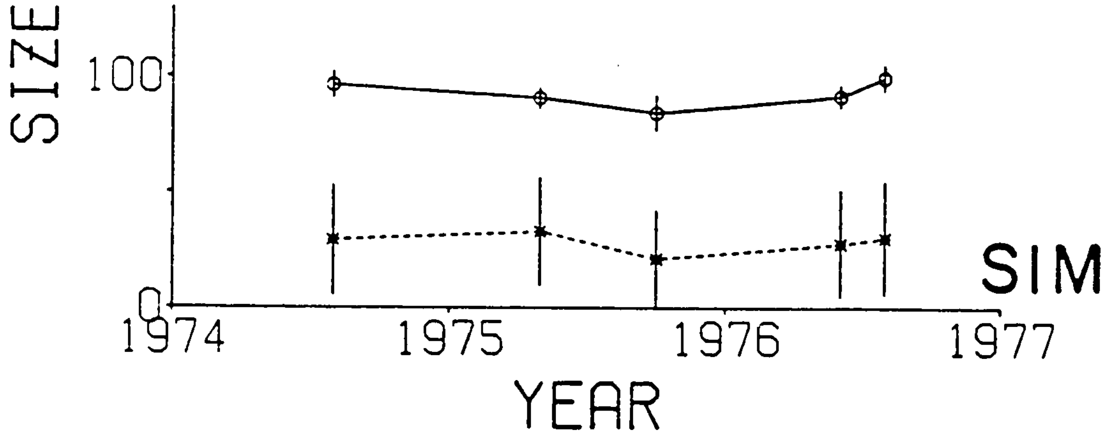

T4H3
T4H4
T4H5
T4H6
T4H7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

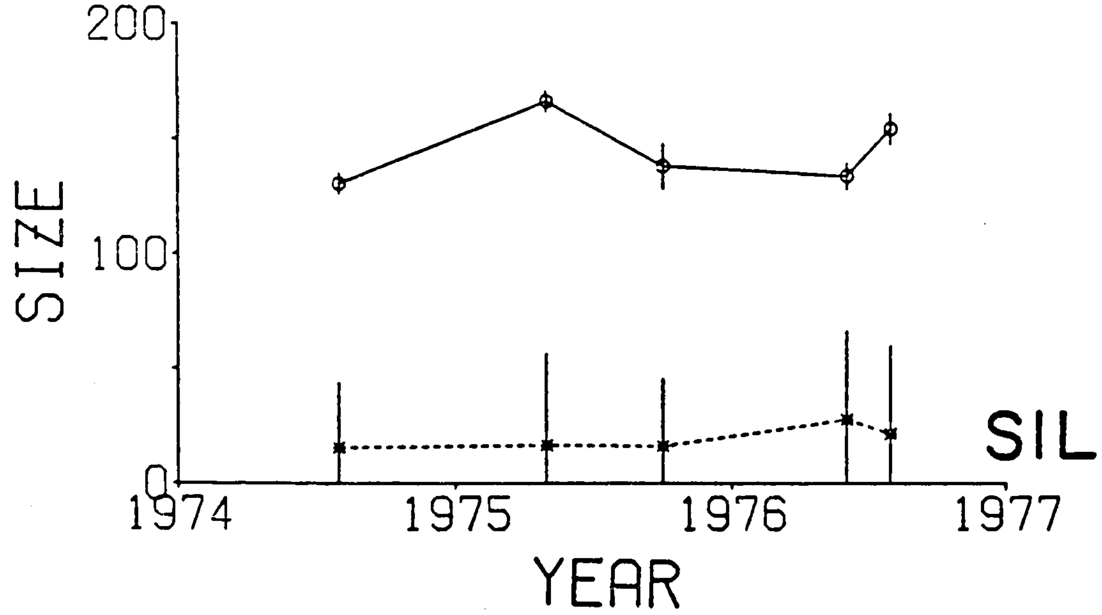

T4M3
T4M4
T4M5
T4M6
T4M7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

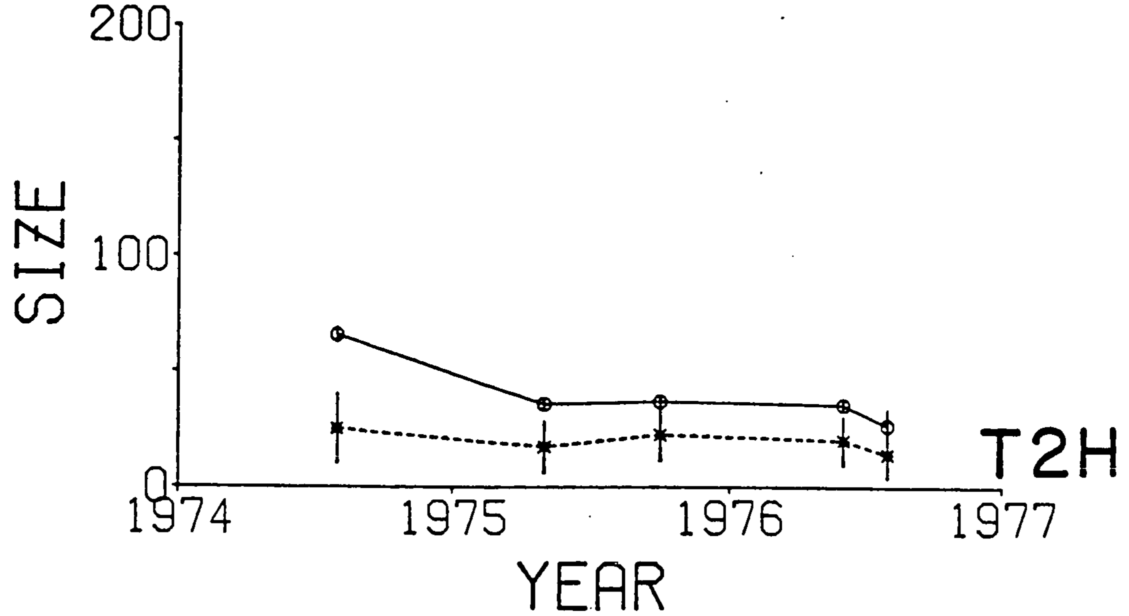

T4L3
T4L4
T4L5
T4L6
T4L7
FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
110
120
0
20
40
60
80
100
120
140
160
180
200
220
240
SIZE (mm)

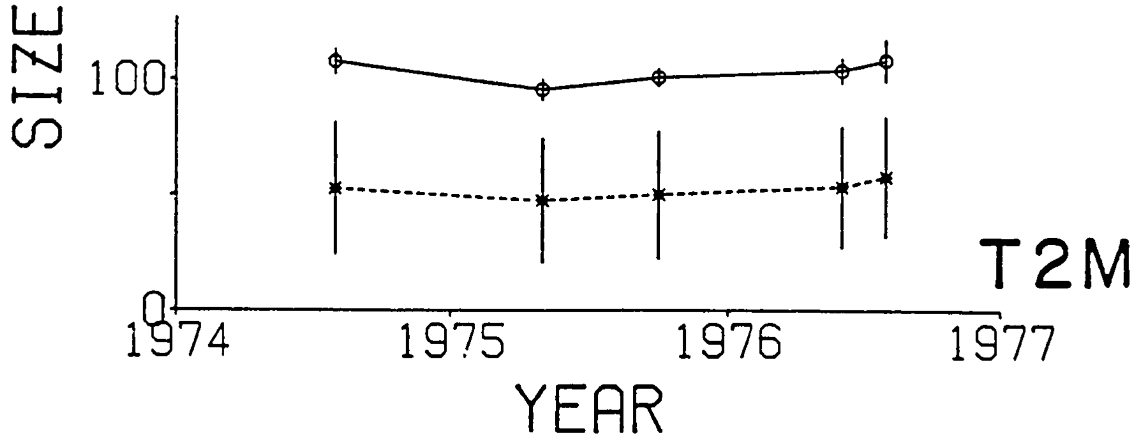
Appendix III. Mean size (mm) for entire sample (dashed lines) and for 10 largest mussels (solid lines) at each site over time.

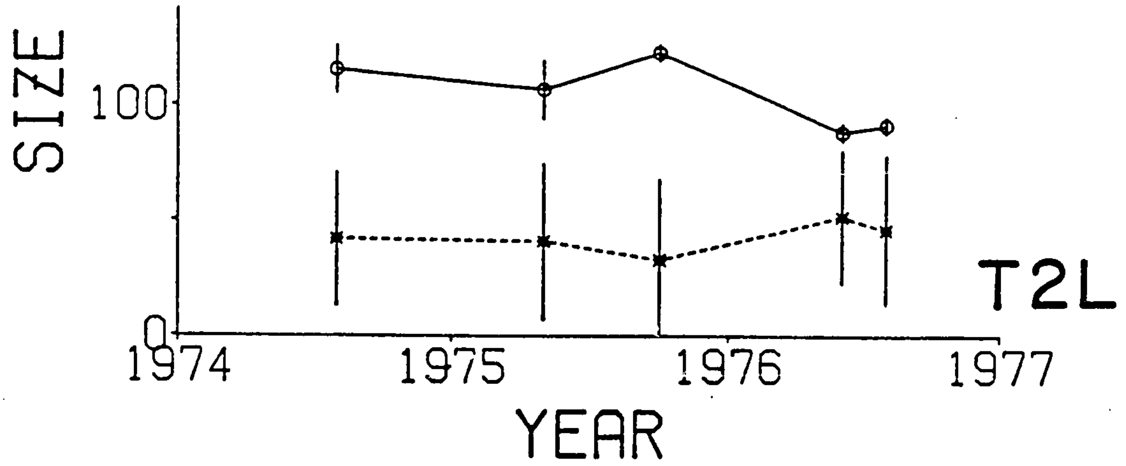

200
100
0
SIZE
1974
1975
1976
1977
YEAR
SIH

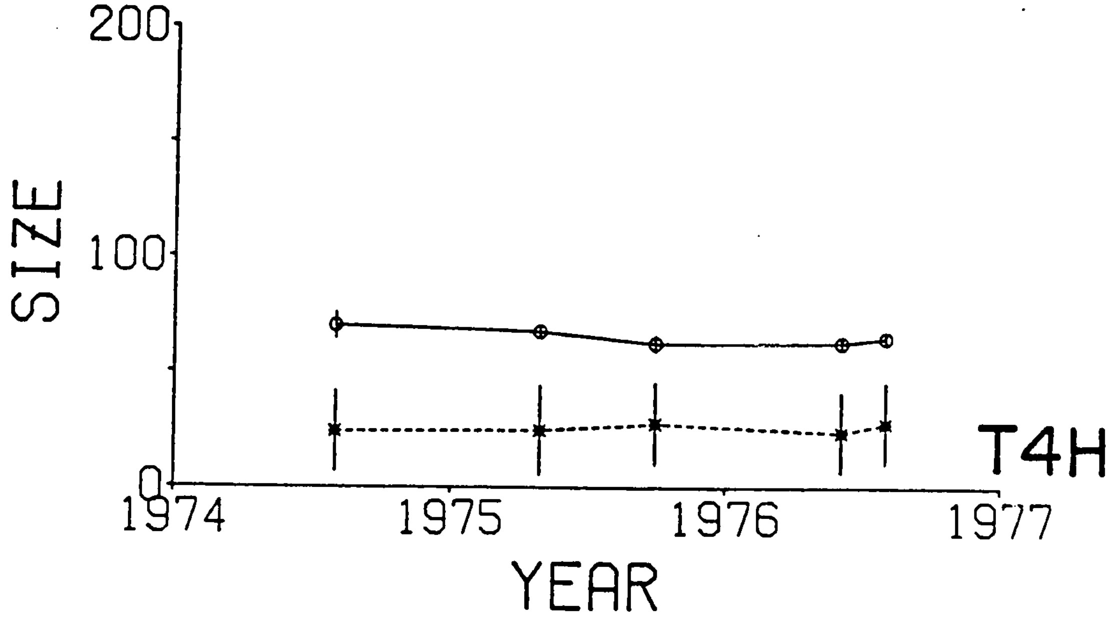

100
0
SIZE
1974
1975
1976
1977
YEAR
SIM

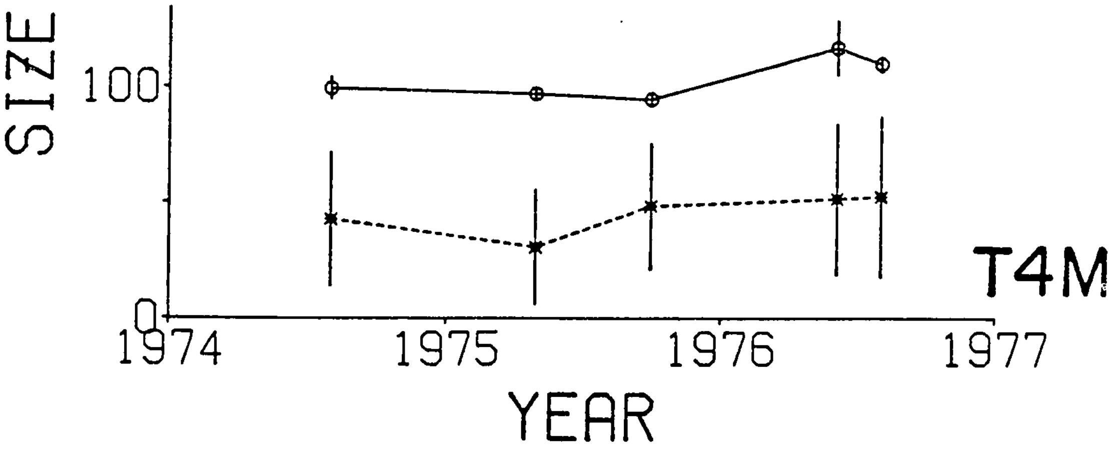

200
100
0
SIZE
1974
1975
1976
1977
YEAR
SIL

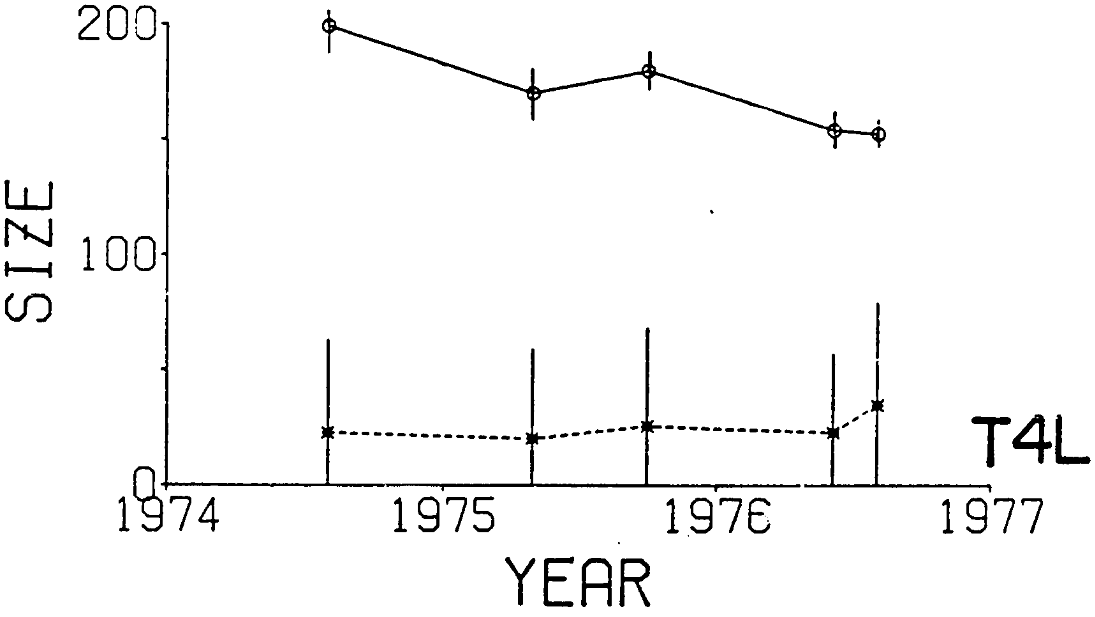

200
100
0
SIZE
1974
1975
1976
1977
YEAR
T2H

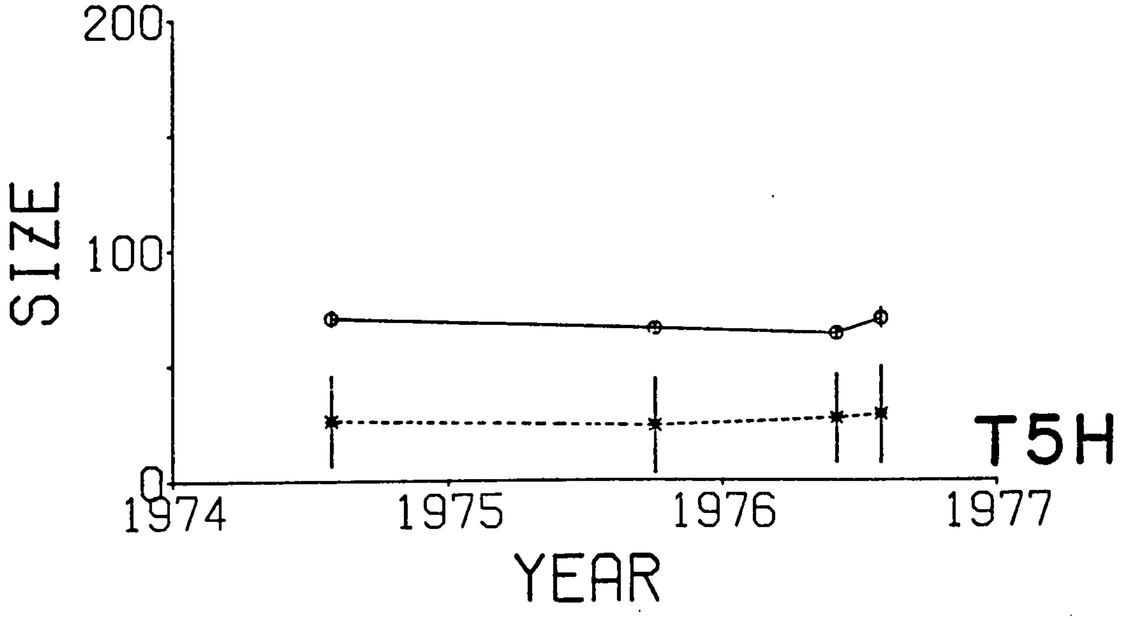

100
0
SIZE
1974
1975
1976
1977
YEAR
T2M

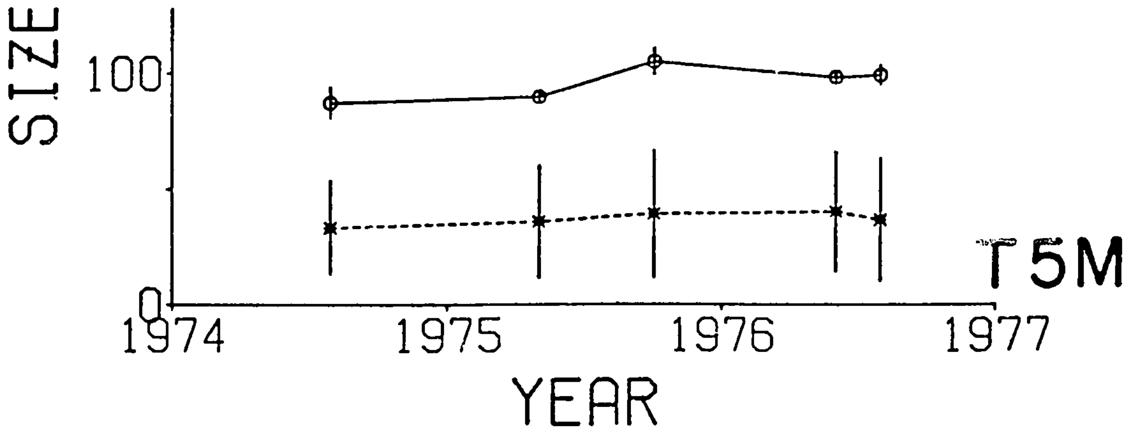

100
0
SIZE
1974
1975
1976
1977
YEAR
T2L


SIZE
200
100
0
1974
1975
1976
1977
YEAR
T4H


SIZE
100
0
1974
1975
1976
1977
YEAR
T4M


SIZE
200
100
0
1974
1975
1976
1977
YEAR
T4L


200
100
0
SIZE
1974
1975
1976
1977
YEAR
T5H


100
0
SIZE
1974
1975
1976
1977
YEAR
T5M

Appendix IV. Values for depth of bed, abundance of mussels and associates, and diversity values for associates for each sample.

SAMPLE CODE	DEPTH OF BED (cm)	ABUNDANCE OF M. CALIFORNIANUS	ABUNDANCE OF ASSOCIATES	SPP. RICHNESS OF ASSOCIATES	SHANNON-WEAVER OF ASSOCIATES	EVENNESS OF ASSOCIATES
SHI-SHI						
S1H3	5.0	222	4036	38	0.732	.463
S1H4	-	336	6246	36	0.481	.309
S1H5	6.0	457	8022	50	0.596	.351
S1H6	4.5	305	7435	36	0.449	.289
S1H7	7.0	343	6418	51	0.584	.342
S1M3	14.5	596	11085	70	0.789	.427
S1M4	-	622	6012	55	0.959	.494
S1M5	11.8	899	4340	69	1.022	.556
S1M6	13.3	1152	6254	79	1.013	.536
S1M7	14.5	980	7452	81	1.009	.529
S1L3	13.5	762	14172	86	0.699	.361
S1L4	-	399	11525	97	0.763	.384
S1L5	10.8	652	9056	99	1.173	.588
S1L6	10.5	429	15023	99	0.914	.458
S1L7	14.3	463	7623	108	1.257	.623
TATOOSH						
T2H3	5.5	760	1571	37	1.016	.648
T2H4	-	77	1398	24	0.735	.533
T2H5	3.3	45	1604	32	0.844	.561
T2H6	3.5	84	3815	43	0.948	.580
T2H7	3.3	31	5228	55	0.966	.555
T2M3	11.5	277	4257	73	0.999	.536
T2M4	-	143	2957	73	1.141	.612
T2M5	8.3	243	7366	86	1.034	.535
T2M6	12.0	329	7356	90	1.132	.579
T2M7	12.8	340	9710	105	1.153	.570
T2L3	9.0	229	13285	85	0.884	.458
T2L4	-	101	2560	82	1.154	.603
T2L5	14.5	296	11268	96	1.229	.620
T2L6	9.8	190	6829	91	0.850	.434
T2L7	9.0	179	7246	87	1.083	.558
T3H3	5.1	691	4771	54	0.961	.555
T3H4	8.0	-	-	-	-	-
T3H5	4.8	649	6310	64	0.861	.476
T3H6	5.5	539	4786	65	0.836	.461
T3H7	5.3	422	6476	66	0.841	.462
T3M3	15.0	837	2977	71	1.213	.655
T3M4	21.8	756	4132	79	1.214	.640
T3M5	19.8	829	4595	90	1.146	.602
T3M6	19.5	719	2424	61	1.196	.670
T3M7	17.3	553	8424	82	1.173	.613
T4H3	6.0	1020	667	44	1.123	.683
T4H4	-	714	653	37	1.112	.709
T4H5	6.0	591	1486	53	0.988	.573
T4H6	6.8	823	2563	64	1.216	.673
T4H7	6.3	701	1559	60	1.187	.667
T4M3	8.5	258	2478	50	0.984	.579
T4M4	-	1111	8640	79	1.105	.583
T4M5	9.5	410	4451	64	0.950	.526
T4M6	15.3	364	6760	96	1.281	.646
T4M7	12.5	237	4701	84	1.248	.649
T4L3	21.5	644	20670	124	1.124	.537
T4L4	20.5	345	6490	84	1.256	.653
T4L5	23.8	583	16523	126	1.330	.633
T4L6	17.5	664	18244	135	1.234	.579
T4L7	17.8	380	10546	105	1.256	.621

Appendix V. Condensed taxonomic representation of the associated community members for 29 major groupings providing the number of species in each group, their relative importance (as a proportion of the total number of species), the total number of individuals in each group and their relative importance (as a proportion of the total abundance of individuals).

	S1H3				S1M3				S1L3			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	0	0	0	0	0	0	0	0	1	.012	5	0
PHAEOPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA	4	.015	58	.014	2	.029	2	0	1	.012	5	0
INVERTEBRATES												
PORIFERA	0	0	0	0	0	0	0	0	2	.023	30	.002
CNIDARIA												
ANTHOZOA	1	.026	2	0	0	0	0	0	2	.023	13	.001
HYDROZOA	0	0	0	0	2	.029	4	0	2	.023	118	.008
PLATYHELMINTHES	0	0	0	0	1	.014	18	.002	1	.012	13	.001
NEMERTEA	1	.026	5	.001	3	.043	19	.002	3	.035	16	.001
NEMATODA	0	0	0	0	0	0	0	0	1	.012	1	0
MOLLUSCA												
BIVALVIA	4	.105	91	.023	6	.086	435	.039	6	.070	24	.002
GASTROPODA												
(COILED SNAILS)	7	.184	331	.082	15	.214	533	.048	8	.093	196	.014
(LIMPETS, ETC.)	3	.079	141	.035	3	.043	247	.022	4	.047	520	.037
POLYPLACOPHORA	1	.026	2	0	1	.014	5	0	2	.023	9	.001
ANNELIDA												
OLIGOCHAETA	1	.026	5	.001	0	0	0	0	0	0	0	0
POLYCHAETA	3	.079	11	.003	7	.100	83	.007	10	.116	101	.007
SIPUNCULIDA	0	0	0	0	1	.014	4	0	1	.012	1	0
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.026	2	0	1	.014	6	.001	0	0	0	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.079	2892	.717	5	.071	8271	.746	5	.058	11437	.807
MALACOSTRACA												
AMPHIPODA	2	.053	373	.092	10	.143	153	.014	13	.151	425	.030
ISOPODA	4	.105	79	.020	4	.057	285	.026	6	.070	819	.058
TANAIDACEA	0	0	0	0	0	0	0	0	0	0	0	0
DECAPODA	2	.053	43	.011	0	0	0	0	6	.070	92	.006
INSECTA												
COLEOPTERA	0	0	0	0	1	.014	1	0	0	0	0	0
DIPTERA	1	.026	1	0	3	.043	8	.001	2	.023	20	.001
BRYOZOA	0	0	0	0	4	.057	664	.060	4	.046	304	.021
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.012	16	.001
ECHINOIDEA	0	0	0	0	0	0	0	0	1	.012	1	0
HOLOTHUROIDEA	0	0	0	0	1	.014	347	.031	2	.023	4	0
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	1	.012	1	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	1	.012	1	0

	S1H4				S1M4				S1L4			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	0	0	0	0	2	.021	25	.002
PHAEOPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA	3	.083	44	.007	0	0	0	0	5	.052	97	.008
INVERTEBRATES												
PORIFERA	0	0	0	0	0	0	0	0	2	.021	10	.001
CNIDARIA												
ANTHOZOA	0	0	0	0	1	.018	14	.002	3	.031	14	.001
HYDROZOA	0	0	0	0	1	.018	2	0	1	.010	43	.004
PLATYHELMINTHES	1	.028	2	0	1	.018	19	.003	1	.010	3	0
NEMERTEA	2	.056	8	.001	3	.055	63	.010	3	.031	59	.005
NEMATODA	0	0	0	0	2	.036	26	.004	2	.021	3	0
MOLLUSCA												
BIVALVIA	5	.139	103	.016	5	.091	34	.006	7	.072	291	.025
GASTROPODA												
(COILED SNAILS)	7	.194	226	.036	8	.145	244	.041	10	.103	112	.010
(LIMPETS, ETC.)	3	.083	159	.025	4	.073	207	.034	4	.041	431	.037
POLYPLACOPHORA	1	.028	1	0	0	0	0	0	3	.031	4	0
ANNELIDA												
OLIGOCHAETA	0	0	0	0	0	0	0	0	0	0	0	0
POLYCHAETA	3	.083	14	.002	9	.164	99	.016	15	.155	573	.050
SIPUNCULIDA	1	.028	1	0	1	.018	4	.001	0	0	0	0
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	1	.018	4	.001	0	0	0	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.083	5561	.890	3	.055	3998	.665	5	.052	8536	.741
MALACOSTRACA												
AMPHIPODA	3	.083	108	.017	5	.091	85	.014	8	.082	106	.009
ISOPODA	2	.056	3	0	4	.073	295	.049	7	.072	429	.037
TANAIDACEA	0	0	0	0	0	0	0	0	1	.010	1	0
DECAPODA	2	.056	16	.003	2	.036	119	.020	5	.052	36	.003
INSECTA												
COLEOPTERA	0	0	0	0	1	.018	1	0	0	0	0	0
DIPTERA	0	0	0	0	1	.018	1	0	2	.021	9	.001
BRYOZOA	0	0	0	0	2	.036	516	.086	8	.082	688	.060
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	2	.021	53	.005
ECHINOIDEA	0	0	0	0	0	0	0	0	1	.010	2	0
HOLOTHUROIDEA	0	0	0	0	1	.018	281	.047	0	0	0	0
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	S1H5				S1M5				S1L5			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	1	.020	1	0	1	.014	1	0	2	.020	26	.003
PHAEOPHYTA	1	.020	1	0	0	0	0	0	0	0	0	0
RHODOPHYTA	4	.080	54	.007	2	.029	4	.001	6	.061	76	.008
INVERTEBRATES												
PORIFERA	0	0	0	0	1	.014	12	.003	2	.020	19	.002
CNIDARIA												
ANTHOZOA	0	0	0	0	2	.029	3	.001	1	.010	3	0
HYDROZOA	0	0	0	0	2	.029	55	.013	1	.010	258	.028
PLATYHELMINTHES	0	0	0	0	1	.014	12	.003	1	.010	1	0
NEMERTEA	2	.040	6	.001	3	.043	56	.013	3	.030	42	.005
NEMATODA	0	- 0	0	0	1	.014	24	.006	1	.010	1	0
MOLLUSCA												
BIVALVIA	5	.100	138	.017	6	.087	184	.042	6	.061	365	.040
GASTROPODA												
(COILED SNAILS)	8	.160	567	.071	9	.130	314	.072	10	.101	215	.024
(LIMPETS, ETC.)	4	.080	178	.022	5	.072	168	.039	4	.040	565	.062
POLYPLACOPHORA	0	0	0	0	1	.014	3	.001	1	.010	5	.001
ANNELIDA												
OLIGOCHAETA	0	0	0	0	0	0	0	0	1	.010	5	.001
POLYCHAETA	8	.160	52	.006	7	.101	81	.019	16	.162	2183	.241
SIPUNCULIDA	0	0	0	0	1	.014	4	.001	1	.010	8	.001
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	1	.014	2	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.020	1	0	4	.058	15	.003	0	0	0	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.060	6728	.839	3	.043	1822	.420	5	.051	3488	.385
MALACOSTRACA												
AMPHIPODA	4	.080	140	.017	4	.058	33	.008	11	.111	446	.049
ISOPODA	4	.080	65	.008	3	.043	71	.016	6	.061	676	.075
TANAIDACEA	0	0	0	0	1	.014	1	0	1	.010	3	0
DECAPODA	3	.060	34	.004	2	.029	12	.003	6	.061	74	.008
INSECTA												
COLEOPTERA	0	0	0	0	3	.043	11	.003	0	0	0	0
DIPTERA	1	.020	1	0	3	.043	15	.003	4	.040	20	.002
BRYOZOA	1	.020	56	.007	2	.029	612	.141	5	.051	519	.057
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	2	.020	53	.006
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.014	825	.190	2	.020	2	0
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	1	.010	3	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	S1H6				S1M6				S1L6			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	0	0	0	0	1	.013	3	0	1	.010	1	0
PHAEOPHYTA	0	0	0	0	0	0	0	0	1	.010	1	0
RHODOPHYTA	3	.083	44	.006	0	0	0	0	5	.051	83	.006
INVERTEBRATES												
PORIFERA	0	0	0	0	0	0	0	0	2	.020	21	.001
CNIDARIA												
ANTHOZOA	1	.028	5	.001	1	.013	2	0	2	.020	12	.001
HYDROZOA	0	0	0	0	3	.038	12	.002	3	.030	273	.018
PLATYHELMINTHES	0	0	0	0	1	.013	6	.001	1	.010	4	0
NEMERTEA	0	0	0	0	3	.038	41	.007	3	.030	34	.002
NEMATODA	0	0	0	0	1	.013	3	0	0	0	0	0
MOLLUSCA												
BIVALVIA	5	.139	87	.012	7	.089	102	.016	6	.061	133	.009
GASTROPODA												
(COILED SNAILS)	8	.222	395	.053	12	.152	550	.088	12	.121	351	.023
(LIMPETS,ETC.)	4	.111	171	.023	5	.063	270	.043	4	.040	970	.065
POLYPLACOPHORA	1	.028	1	0	1	.013	12	.002	1	.010	15	.001
ANNELIDA												
OLIGOCHAETA	0	0	0	0	1	.013	1	0	0	0	0	0
POLYCHAETA	3	.083	10	.001	10	.123	153	.024	20	.202	2161	.144
SIPUNCULIDA	0	0	0	0	1	.013	1	0	1	.010	5	0
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	1	.013	1	0	1	.010	1	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	1	.013	1	0	0	0	0	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.083	6627	.891	4	.051	3144	.503	5	.051	8853	.590
MALACOSTRACA												
AMPHIPODA	2	.056	42	.006	6	.076	77	.012	10	.101	199	.013
ISOPODA	2	.056	4	.001	5	.063	359	.057	5	.051	793	.053
TANAIDACEA	0	0	0	0	1	.013	1	0	0	0	0	0
DECAPODA	2	.056	17	.002	4	.051	268	.043	4	.040	53	.004
INSECTA												
COLEOPTERA	0	0	0	0	0	0	0	0	0	0	0	0
DIPTERA	0	0	0	0	1	.013	1	0	2	.020	9	.001
BRYOZOA	2	.056	32	.004	7	.089	773	.124	8	.081	951	.063
ECHINODERMATA												
ASTERIODEA	0	0	0	0	1	.013	1	0	1	.010	99	.007
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.013	472	.075	0	0	0	0
OPHIUROIDEA	0	0	0	0	0	0	0	0	1	.010	1	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	S1H7				S1M7				S1L7			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	0	0	0	0	2	.019	8	.001
PHAEOPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA	5	.098	50	.008	3	.037	8	.001	5	.046	151	.020
INVERTEBRATES												
PORIFERA	0	0	0	0	0	0	0	0	2	.019	24	.003
CNIDARIA												
ANTHOZOA	1	.020	3	0	1	.012	3	0	2	.019	13	.002
HYDROZOA	0	0	0	0	1	.012	44	.006	2	.019	317	.042
PLATYHELMINTHES	0	0	0	0	1	.012	20	.003	1	.009	1	0
NEMERTEA	1	.020	6	.001	3	.037	51	.007	3	.028	15	.002
NEMATODA	2	.039	2	0	2	.025	11	.001	1	.009	1	0
MOLLUSCA												
BIVALVIA	7	.137	194	.030	5	.062	66	.008	6	.056	185	.024
GASTROPODA												
(COILED SNAILS)	9	.176	329	.051	10	.123	251	.034	8	.074	414	.054
(LIMPETS, ETC.)	4	.078	204	.032	5	.062	303	.041	4	.037	511	.067
POLYPLACOPHORA	0	0	0	0	1	.012	4	.001	3	.028	16	.002
ANNELIDA												
OLIGOCHAETA	1	.020	1	0	1	.012	1	0	0	0	0	0
POLYCHAETA	8	.157	29	.005	13	.160	130	.017	27	.250	2146	.282
SIPUNCULIDA	0	0	0	0	1	.012	21	.003	1	.009	4	.001
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	2	.025	2	0	1	.009	1	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.059	5347	.833	5	.062	4400	.590	6	.056	2155	.283
MALACOSTRACA												
AMPHIPODA	2	.039	112	.017	8	.099	42	.006	7	.065	309	.041
ISOPODA	3	.059	9	.001	5	.062	357	.038	7	.065	535	.070
TANAIDACEA	1	.020	1	0	0	0	0	0	1	.009	1	0
DECAPODA	3	.059	44	.007	4	.050	246	.033	5	.046	111	.015
INSECTA												
COLEOPTERA	0	0	0	0	3	.037	5	.001	0	0	0	0
DIPTERA	0	0	0	0	2	.025	2	0	3	.028	4	.001
BRYOZOA	1	.020	87	.014	3	.037	941	.126	6	.056	640	.084
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	2	.019	55	.007
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.012	543	.073	2	.019	5	.001
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.012	1	0	1	.009	1	0

	T2H3				T2M3				T2L3			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
PHAEOPHYTA	0	0	0	0	0	0	0	0	2	.024	3	0
RHODOPHYTA	2	.054	115	.073	4	.055	37	.009	6	.071	195	.015
INVERTEBRATES												
PORIFERA	0	0	0	0	1	.014	68	.016	2	.024	109	.008
CNIDARIA												
ANTHOZOA	1	.027	1	.001	1	.014	14	.003	1	.012	4	0
HYDROZOA	0	0	0	0	1	.014	65	.015	1	.012	211	.016
PLATYHELMINTHES	0	0	0	0	1	.014	3	.001	0	0	0	0
NEMERTEA	1	.027	1	.001	1	.014	7	.002	2	.024	7	.001
NEMATODA	0	0	0	0	1	.014	3	.001	1	.012	1	0
MOLLUSCA												
BIVALVIA	8	.216	678	.431	8	.110	249	.058	8	.094	198	.015
GASTROPODA												
(COILED SNAILS)	7	.189	287	.183	13	.178	1198	.281	14	.165	8167	.615
(LIMPETS, ETC.)	6	.162	98	.062	6	.082	136	.032	7	.082	196	.015
POLYPLACOPHORA	1	.027	7	.004	2	.027	10	.002	2	.024	12	.001
ANNELIDA												
OLIGOCHAETA	0	0	0	0	0	0	0	0	0	0	0	0
POLYCHAETA	0	0	0	0	5	.068	14	.003	6	.071	34	.003
SIPUNCULIDA	1	.027	3	.002	1	.014	6	.001	1	.012	21	.002
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	1	.014	7	.002	1	.012	3	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.081	200	.127	4	.055	66	.016	5	.059	1203	.091
MALACOSTRACA												
AMPHIPODA	1	.027	36	.023	6	.082	34	.008	7	.082	176	.013
ISOPODA	3	.081	22	.014	4	.055	143	.034	7	.082	760	.057
TANAIDACEA	1	.027	3	.002	1	.014	4	.001	1	.012	2	0
DECAPODA	0	0	0	0	2	.027	30	.007	3	.035	11	.001
INSECTA												
COLEOPTERA	0	0	0	0	2	.027	24	.006	1	.012	5	0
DIPTERA	1	.027	1	.001	1	.014	5	.001	1	.012	4	0
BRYOZOA	1	.027	119	.076	5	.068	858	.202	3	.035	780	.059
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.012	14	.001
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.014	1276	.300	1	.012	1167	.088
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.014	1	0	1	.012	2	0

	T2H4				T2M4				T2L4			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	0	0	0	0	1	.012	14	.005
PHAEOPHYTA	0	0	0	0	0	0	0	0	1	.012	1	0
RHODOPHYTA	0	0	0	0	3	.041	7	.002	4	.049	55	.021
INVERTEBRATES												
PORIFERA	0	0	0	0	1	.014	32	.011	2	.244	52	.020
CNIDARIA												
ANTHOZOA	0	0	0	0	1	.014	12	.004	0	0	0	0
HYDROZOA	0	0	0	0	0	0	0	0	1	.012	35	.014
PLATYHELMINTHES	0	0	0	0	1	.014	41	.014	1	.012	1	0
NEMERTEA	0	0	0	0	2	.027	12	.004	1	.012	1	0
NEMATODA	1	.042	1	.001	2	.027	36	.012	1	.012	2	.001
MOLLUSCA												
BIVALVIA	4	.167	1035	.740	7	.096	476	.160	8	.098	24	.009
GASTROPODA												
(COILED SNAILS)	3	.125	67	.048	18	.247	1006	.340	12	.146	1029	.402
(LIMPETS,ETC.)	3	.125	9	.006	6	.082	112	.038	4	.049	33	.013
POLYPLACOPHORA	1	.042	13	.009	1	.014	11	.004	2	.024	7	.003
ANNELIDA												
OLIGOCHAETA	0	0	0	0	1	.014	1	0	0	0	0	0
POLYCHAETA	0	0	0	0	8	.110	53	.018	6	.073	304	.119
SIPUNCULIDA	1	.042	4	.003	0	0	0	0	1	.012	13	.005
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	2	.024	2	.001
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	1	.014	11	.004	1	.012	6	.002
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	2	.083	7	.005	3	.041	115	.039	5	.061	121	.047
MALACOSTRACA												
AMPHIPODA	2	.083	69	.049	6	.082	47	.016	11	.134	124	.048
ISOPODA	4	.167	176	.126	4	.055	50	.017	5	.061	367	.143
TANAIDACEA	1	.042	12	.009	1	.014	21	.007	1	.012	1	0
DECAPODA	0	0	0	0	1	.014	2	.001	5	.061	25	.010
INSECTA												
COLEOPTERA	0	0	0	0	2	.027	24	.008	0	0	0	0
DIPTERA	1	.042	2	.001	1	.014	3	.001	1	.012	4	.002
BRYOZOA	1	.042	3	.002	2	.027	261	.088	4	.049	308	.120
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.012	15	.006
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.014	624	.211	1	.012	16	.006
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	T2H5				T2M5				T2L5			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	1	.012	2	0	2	.021	11	.001
PHAEOPHYTA	0	0	0	0	1	.012	4	.001	4	.042	20	.002
RHODOPHYTA	1	.031	5	.003	6	.070	136	.018	9	.096	326	.029
INVERTEBRATES												
PORIFERA	1	.031	8	.005	2	.023	79	.011	2	.021	235	.021
CNIDARIA												
ANTHOZOA	0	0	0	0	1	.012	13	.002	0	0	0	0
HYDROZOA	0	0	0	0	1	.012	18	.002	2	.021	642	.057
PLATYHELMINTHES	0	0	0	0	1	.012	33	.004	0	0	0	0
NEMERTEA	0	0	0	0	2	.023	34	.005	1	.010	2	0
NEMATODA	2	.063	31	.019	2	.023	102	.014	1	.010	1	0
MOLLUSCA												
BIVALVIA	3	.094	952	.594	8	.093	1305	.177	7	.073	104	.009
GASTROPODA												
(COILED SNAILS)	4	.125	53	.033	12	.140	1820	.247	12	.125	1946	.173
(LIMPETS, ETC.)	3	.094	17	.011	6	.070	227	.031	5	.052	46	.004
POLYPLACOPHORA	1	.031	46	.029	1	.012	35	.005	1	.010	11	.001
ANNELIDA												
OLIGOCHAETA	1	.031	5	.003	1	.012	4	.001	0	0	0	0
POLYCHAETA	1	.031	1	.001	7	.081	60	.008	7	.073	1468	.130
SIPUNCULIDA	1	.031	7	.004	0	0	0	0	1	.010	30	.003
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	2	.023	3	0	2	.021	2	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.031	1	.001	2	.023	10	.001	4	.042	9	.001
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.094	45	.028	3	.035	70	.010	5	.052	397	.035
MALACOSTRACA												
AMPHIPODA	3	.094	22	.014	8	.093	130	.018	8	.083	3495	.310
ISOPODA	3	.094	351	.219	5	.058	172	.023	6	.063	1013	.090
TANAIDACEA	1	.031	49	.031	1	.012	107	.015	1	.010	2	0
DECAPODA	0	0	0	0	1	.012	2	0	5	.052	123	.011
INSECTA												
COLEOPTERA	1	.031	2	.001	3	.035	27	.004	3	.031	9	.001
DIPTERA	1	.031	1	.001	5	.058	7	.001	2	.021	2	0
BRYOZOA	1	.031	8	.005	3	.035	790	.107	4	.042	1044	.093
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.010	15	.001
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.012	2176	.295	1	.010	315	.028
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	T2H6				T2M6				T2L6			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	1	.011	1	0	0	0	0	0
PHAEOPHYTA	0	0	0	0	1	.011	4	.001	2	.022	4	.001
RHODOPHYTA	6	.140	224	.059	6	.067	101	.014	1	.011	56	.008
INVERTEBRATES												
PORIFERA	1	.023	32	.008	2	.022	151	.021	2	.022	437	.064
CNIDARIA												
ANTHOZOA	0	0	0	0	1	.011	63	.009	1	.011	1	0
HYDROZOA	0	0	0	0	1	.011	47	.006	3	.033	46	.007
PLATYHELMINTHES	0	0	0	0	1	.011	3	0	1	.011	4	0
NEMERTEA	2	.047	8	.002	2	.022	22	.003	3	.033	6	.001
NEMATODA	2	.047	3	.001	2	.022	93	.013	1	.011	3	0
MOLLUSCA												
BIVALVIA	4	.093	2284	.599	7	.078	1329	.181	9	.099	245	.036
GASTROPODA												
(COILED SNAILS)	9	.209	280	.073	17	.189	2631	.358	16	.176	4291	.628
(LIMPETS, ETC.)	4	.093	61	.016	6	.067	225	.031	5	.055	59	.009
POLYPLACOPHORA	1	.023	65	.017	2	.022	46	.006	2	.022	11	.002
ANNELIDA												
OLIGOCHAETA	1	.023	10	.003	1	.011	5	.001	0	0	0	0
POLYCHAETA	0	0	0	0	6	.067	46	.006	12	.132	54	.009
SIPUNCULIDA	1	.023	35	.009	0	0	0	0	1	.011	6	.001
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	1	.011	1	0	1	.011	1	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	3	.033	7	.001	1	.011	4	.001
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	2	.047	32	.008	5	.056	88	.012	4	.044	237	.035
MALACOSTRACA												
AMPHIPODA	2	.047	33	.009	7	.078	133	.018	7	.077	81	.012
ISOPODA	3	.070	508	.133	4	.044	539	.073	4	.044	220	.032
TANAIDACEA	1	.023	96	.025	1	.011	59	.008	1	.011	17	.002
DECAPODA	0	0	0	0	3	.033	23	.003	4	.044	23	.003
INSECTA												
COLEOPTERA	2	.047	4	.001	3	.033	63	.009	1	.011	1	0
DIPTERA	1	.023	11	.003	3	.033	5	.001	1	.011	1	0
BRYOZOA	1	.023	129	.034	2	.022	754	1.025	5	.055	803	.118
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.011	10	.002
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	0	0	0	0	1	.011	916	.125	1	.011	207	.030
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.011	1	0	1	.011	1	0

	T2H7				T2M7				T2L7			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	1	.010	6	.001	0	0	0	0
PHAEOPHYTA	0	0	0	0	1	.010	2	0	1	.011	1	0
RHODOPHYTA	5	.091	136	.027	8	.076	156	.016	3	.034	55	.008
INVERTEBRATES												
PORIFERA	0	0	0	0	2	.019	151	.016	2	.023	214	.030
CNIDARIA												
ANTHOZOA	0	0	0	0	1	.010	33	.003	0	0	0	0
HYDROZOA	0	0	0	0	2	.019	111	.011	1	.011	26	.004
PLATYHELMINTHES	1	.018	16	.003	1	.010	23	.002	0	0	0	0
NEMERTEA	1	.018	2	0	3	.029	44	.005	3	.034	18	.002
NEMATODA	2	.036	19	.004	2	.019	102	.011	2	.022	13	.002
MOLLUSCA												
BIVALVIA	4	.073	3028	.579	7	.067	450	.046	9	.103	340	.047
GASTROPODA												
(COILED SNAILS)	6	.109	602	.115	19	.181	3254	.335	11	.126	2570	.355
(LIMPETS, ETC.)	5	.091	56	.011	7	.067	292	.030	6	.069	93	.013
POLYPLACOPHORA	1	.018	29	.006	1	.010	28	.003	1	.011	13	.002
ANNELIDA												
OLIGOCHAETA	1	.018	464	.089	1	.010	1	0	0	0	0	0
POLYCHAETA	5	.091	53	.010	12	.114	51	.005	13	.149	47	.006
SIPUNCULIDA	1	.018	27	.005	1	.010	1	0	1	.011	17	.002
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	1	.010	1	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.018	2	0	2	.019	7	.001	1	.011	3	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.055	68	.013	5	.048	834	.086	5	.057	1179	.163
MALACOSTRACA												
AMPHIPODA	3	.055	25	.005	8	.076	354	.036	9	.103	180	.025
ISOPODA	4	.073	466	.089	4	.038	667	.069	4	.046	461	.064
TANAIDACEA	1	.018	127	.024	1	.010	38	.004	1	.011	47	.006
DECAPODA	0	0	0	0	2	.019	60	.006	3	.034	12	.002
INSECTA												
COLEOPTERA	4	.073	7	.001	4	.038	54	.005	3	.034	5	.001
DIPTERA	5	.091	9	.002	4	.038	8	.001	3	.034	5	.001
BRYOZOA	1	.018	90	.017	4	.038	816	.084	3	.034	466	.064
ECHINODERMATA												
ASTERIODEA	0	0	0	0	0	0	0	0	1	.011	4	.001
ECHINOIDEA	0	0	0	0	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	1	.018	2	0	1	.010	2168	.223	1	.011	1477	.204
OPHIUROIDEA	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	T4H3				T4M3				T4L3			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA....................	0	0	0	0	0	0	0	0	1	.008	1	0
PHAEOPHYTA.....................	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA.....................	1	.023	70	.105	4	.080	7	.003	9	.073	204	.010
INVERTEBRATES												
PORIFERA.......................	1	.023	7	.010	1	.020	6	.002	1	.008	6	0
CNIDARIA												
ANTHOZOA.................	2	.045	7	.010	1	.020	71	.029	0	0	0	0
HYDROZOA.................	0	0	0	0	1	.020	16	.006	2	.016	663	.032
PLATYHELMINTHES................	0	0	0	0	1	.020	1	0	1	.008	2	0
NEMERTEA.......................	0	0	0	0	1	.020	3	.001	3	.024	60	.003
NEMATODA.......................	0	0	0	0	1	.020	2	.001	2	.016	22	.001
MOLLUSCA												
BIVALVIA.................	6	.136	101	.151	4	.080	192	.077	8	.065	69	.003
GASTROPODA												
(COILED SNAILS)........	7	.159	23	.034	8	.160	754	.304	12	.097	497	.024
(LIMPETS, ETC.).........	5	.114	50	.075	5	.100	98	.040	7	.056	37	.002
POLYPLACOPHORA...........	1	.023	1	.001	1	.020	29	.012	2	.016	7	0
ANNELIDA												
OLIGOCHAETA..............	0	0	0	0	0	0	0	0	0	0	0	0
POLYCHAETA...............	6	.136	13	.019	2	.040	6	.002	17	.137	8373	.405
SIPUNCULIDA....................	1	.023	12	.018	1	.020	101	.041	1	.008	16	.001
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA..............	0	0	0	0	1	.020	1	0	1	.008	1	0
ARACHNIDA												
PSEUDOSCORPIONIDA..	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA............	0	0	0	0	0	0	0	0	3	.024	5	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA...........	3	.068	30	.045	5	.100	45	.018	5	.040	1098	.053
MALACOSTRACA												
AMPHIPODA..........	3	.068	55	.082	4	.080	34	.014	13	.105	3378	.163
ISOPODA............	3	.068	30	.045	4	.080	72	.029	8	.065	3753	.182
TANAIDACEA.........	1	.023	4	.006	1	.020	4	.002	2	.016	4	0
DECAPODA...........	0	0	0	0	1	.020	2	.001	7	.056	273	.013
INSECTA												
COLEOPTERA.........	0	0	0	0	0	0	0	0	0	0	0	0
DIPTERA............	2	.045	8	.012	0	0	0	0	2	.016	288	.014
BRYOZOA........................	1	.023	234	.351	2	.040	416	.168	8	.065	1834	.089
ECHINODERMATA												
ASTERIODEA...............	0	0	0	0	0	0	0	0	2	.016	29	.001
ECHINOIDEA...............	0	0	0	0	0	0	0	0	2	.016	8	0
HOLOTHUROIDEA............	1	.023	22	.033	1	.020	618	.249	3	.024	22	.001
OPHIUROIDEA..............	0	0	0	0	0	0	0	0	1	.008	18	.001
CHORDATA												
UROCHORDATA..................	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES.............	0	0	0	0	0	0	0	0	1	.008	2	0

	T4B4				T4M4				T4L4			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	0	0	0	0	0	0	0	0	1	.012	19	.003
PHAEOPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA	3	.081	11	.017	4	.051	45	.005	6	.071	188	.029
INVERTEBRATES												
PORIFERA	1	.027	9	.014	1	.013	29	.003	1	.012	34	.005
CNIDARIA												
ANTHOZOA	1	.027	8	.012	1	.013	116	.013	1	.012	1	0
HYDROZOA	0	0	0	0	2	.025	16	.002	2	.024	307	.047
PLATYHELMINTHES	0	0	0	0	1	.013	7	.001	0	0	0	0
NEMERTEA	0	0	0	0	2	.025	9	.001	2	.024	10	.002
NEMATODA	0	0	0	0	2	.025	510	.059	2	.024	4	.001
MOLLUSCA												
BIVALVIA	7	.189	125	.191	6	.076	2255	.261	5	.060	56	.009
GASTROPODA												
(COILED SNAILS)	5	.135	13	.020	11	.139	1531	.177	10	.119	693	.107
(LIMPETS, ETC.)	5	.135	26	.040	5	.063	330	.038	3	.036	62	.010
POLYPLACOPHORA	1	.027	3	.005	2	.025	110	.013	2	.024	9	.001
ANNELIDA												
OLIGOCHAETA	0	0	0	0	1	.013	2	0	0	0	0	0
POLYCHAETA	1	.027	2	.003	10	.127	58	.007	8	.095	1247	.192
SIPUNCULIDA	0	0	0	0	1	.013	104	.012	1	.012	1	0
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	2	.025	5	.001	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	3	.038	7	.001	1	.012	1	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	2	.054	91	.139	5	.063	196	.023	6	.071	1191	.184
MALACOSTRACA												
AMPHIPODA	2	.054	61	.093	6	.076	61	.008	10	.119	1039	.160
ISOPODA	4	.108	101	.155	4	.051	211	.024	5	.060	639	.099
TANAIDACEA	1	.027	2	.003	2	.025	519	.060	1	.012	1	0
DECAPODA	0	0	0	0	0	0	0	0	5	.060	98	.015
INSECTA												
COLEOPTERA	0	0	0	0	2	.025	34	.004	0	0	0	0
DIPTERA	1	.027	1	.002	3	.038	3	0	1	.012	20	.003
BRYOZOA	1	.027	187	.286	1	.013	1205	.139	6	.071	833	.129
ECHINODERMATA												
ASTEROIDEA	1	.027	1	.002	1	.013	3	0	1	.012	16	.002
ECHINOIDEA	0	0	0	0	0	0	0	0	1	.012	1	0
HOLOTHUROIDEA	1	.027	12	.018	1	.013	1264	.146	2	.024	7	.001
OPHIUROIDEA	0	0	0	0	0	0	0	0	1	.012	3	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	0	0	0	0	0	0	0	0

	T4HS				T4MS				T4LS			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE												
CHLOROPHYTA	2	.038	50	.034	0	0	0	0	2	.016	4	0
PHAEOPHYTA	1	.019	1	.001	0	0	0	0	1	.008	5	0
RHODOPHYTA	3	.057	12	.008	2	.031	14	.003	6	.048	79	.005
INVERTEBRATES												
PORIFERA	1	.019	13	.009	1	.016	7	.002	1	.008	39	.002
CNIDARIA												
ANTHOZOA	1	.019	9	.006	1	.016	13	.003	3	.024	18	.001
HYDROZOA	0	0	0	0	1	.016	14	.003	2	.016	532	.032
PLATYHELMINTHES	1	.019	9	.006	0	0	0	0	0	0	0	0
NEMERTEA	3	.057	10	.007	1	.016	2	0	3	.023	33	.002
NEMATODA	2	.038	28	.019	1	.016	142	.032	1	.008	6	0
MOLLUSCA												
BIVALVIA	5	.094	147	.099	6	.094	72	.016	10	.079	321	.019
GASTROPODA												
(COILED SNAILS)	5	.094	35	.024	12	.188	1244	.279	13	.103	3283	.199
(LIMPETS,ETC.)	5	.094	425	.286	5	.078	117	.026	5	.040	108	.007
POLYPLACOPHORA	1	.019	27	.018	2	.031	69	.016	2	.016	54	.003
ANNELIDA												
OLIGOCHAETA	1	.019	7	.005	1	.016	9	.002	0	0	0	0
POLYCHAETA	5	.094	24	.016	8	.125	19	.004	18	.143	2967	.180
SIPUNCULIDA	1	.019	4	.003	1	.016	83	.017	1	.008	55	.003
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	1	.016	2	0	2	.016	2	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	0	0	0	0	2	.031	2	0	0	0	0	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.057	121	.081	4	.063	128	.029	6	.048	1483	.090
MALACOSTRACA												
AMPHIPODA	4	.075	7	.005	6	.094	66	.015	14	.111	3573	.216
ISOPODA	3	.057	14	.009	3	.048	254	.057	8	.063	1807	.109
TANAIDACEA	1	.019	6	.004	1	.016	1	0	2	.016	7	0
DECAPODA	0	0	0	0	0	0	0	0	6	.058	174	.011
INSECTA												
COLEOPTERA	1	.019	3	.002	0	0	0	0	0	0	0	0
DIPTERA	2	.038	5	.003	1	.016	1	0	2	.016	83	.005
BRYOZOA	1	.019	524	.353	1	.016	881	.198	8	.063	1818	.110
ECHINODERMATA												
ASTERIODEA	0	0	0	0	1	.016	6	.001	3	.024	36	.002
ECHINOIDEA	0	0	0	0	0	0	0	0	2	.016	3	0
HOLOTHUROIDEA	1	.019	5	.003	1	.016	1304	.293	3	.024	11	.001
OPHIUROIDEA	0	0	0	0	0	0	0	0	1	.008	21	.001
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.016	1	0	1	.008	1	0

	T4H6				T4M6				T4L6			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	1	.016	11	.004	1	.010	2	0	2	.015	49	.002
PHAEOPHYTA	0	0	0	0	1	.010	3	0	2	.015	25	.001
RHODOPHYTA	7	.109	87	.032	3	.031	16	.002	9	.067	472	.026
INVERTEBRATES												
PORIFERA	1	.016	34	.013	2	.021	242	.036	2	.015	53	.003
CNIDARIA												
ANTHOZOA	1	.016	3	.001	1	.010	213	.032	1	.007	5	0
HYDROZOA	0	0	0	0	2	.021	237	.035	2	.015	639	.035
PLATYHELMINTHES	0	0	0	0	0	0	0	0	1	.007	1	0
NEMERTEA	2	.031	7	.003	3	.031	11	.002	2	.015	12	.001
NEMATODA	2	.031	102	.038	2	.021	148	.022	2	.015	38	.002
MOLLUSCA												
BIVALVIA	6	.094	592	.222	8	.083	177	.026	10	.074	146	.008
GASTROPODA												
(COILED SNAILS)	11	.172	61	.023	14	.146	1775	.263	15	.111	4824	.264
(LIMPETS,ETC.)	5	.078	256	.096	6	.063	161	.024	6	.044	61	.003
POLYPLACOPHORA	2	.031	11	.004	2	.021	40	.006	3	.022	10	.001
ANNELIDA												
OLIGOCHAETA	1	.016	2	.001	1	.010	3	0	0	0	0	0
POLYCHAETA	2	.031	5	.002	14	.146	189	.028	20	.148	2876	.158
SIPUNCULIDA	1	.016	6	.002	1	.010	376	.056	1	.007	72	.004
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	0	0	0	0	0	0	0	0	1	.007	1	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.016	1	0	2	.021	2	0	2	.015	3	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	2	.031	220	.083	6	.063	273	.040	6	.044	801	.044
MALACOSTRACA												
AMPHIPODA	7	.109	148	.056	7	.073	.55	.023	14	.104	3142	.172
ISOPODA	5	.078	330	.124	4	.042	1176	.174	9	.067	2167	.119
TANAIDACEA	1	.016	12	.005	1	.010	8	.001	3	.022	3	0
DECAPODA	1	.016	1	0	5	.052	73	.011	6	.044	205	.011
INSECTA												
COLEOPTERA	3	.047	7	.003	1	.010	5	.001	0	0	0	0
DIPTERA	1	.016	32	.012	1	.010	1	0	1	.007	3	0
BRYOZOA	1	.016	735	.276	4	.042	894	.132	7	.052	2581	.141
ECHINODERMATA												
ASTERIODEA	0	0	0	0	1	.010	5	.001	2	.015	16	.001
ECHINOIDEA	0	0	0	0	0	0	0	0	1	.007	1	0
HOLOTHUROIDEA	0	0	0	0	1	.010	572	.085	2	.015	4	0
OPHIUROIDEA	0	0	0	0	1	.010	1	0	1	.007	39	.002
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.010	2	0	2	.015	4	0

	T4H7				T4M7				T4L7			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	1	.017	1	.001	0	0	0	0	1	.010	3	0
PHAEOPHYTA	0	0	0	0	0	0	0	0	0	0	0	0
RHODOPHYTA	5	.083	57	.037	2	.024	13	.003	4	.038	88	.008
INVERTEBRATES												
PORIFERA	1	.017	33	.021	2	.024	47	.010	2	.019	17	.002
CNIDARIA												
ANTHOZOA	1	.017	39	.025	1	.012	131	.028	3	.029	20	.002
HYDROZOA	1	.017	3	.002	2	.024	94	.020	3	.029	550	.052
PLATYHELMINTHES	0	0	0	0	1	.012	2	0	1	.010	2	0
NEMERTEA	2	.033	2	.001	3	.036	71	.015	3	.029	11	.001
NEMATODA	2	.033	91	.058	2	.024	262	.056	2	.019	11	.001
MOLLUSCA												
BIVALVIA	6	.100	136	.087	8	.095	96	.020	6	.057	58	.005
GASTROPODA												
(COILED SNAILS)	6	.100	37	.024	12	.143	1016	.216	11	.105	1599	.152
(LIMPETS, ETC.)	6	.100	181	.116	6	.071	124	.026	4	.038	79	.007
POLYPLACOPHORA	1	.017	16	.010	1	.012	47	.010	0	0	0	0
ANNELIDA												
OLIGOCHAETA	0	0	0	0	1	.012	3	.001	0	0	0	0
POLYCHAETA	6	.100	10	.006	8	.095	83	.018	17	.162	1198	.114
SIPUNCULIDA	1	.017	9	.006	1	.012	200	.043	1	.010	13	.001
ARTHROPODA												
CHELICERATA												
PYCNOGONIDA	1	.017	1	.001	1	.012	1	0	0	0	0	0
ARACHNIDA												
PSEUDOSCORPIONIDA	0	0	0	0	0	0	0	0	0	0	0	0
ACARINA	1	.017	1	.001	3	.036	7	.001	1	.010	4	0
MANDIBULATA												
CRUSTACEA												
CIRRIPEDIA	3	.050	168	.108	4	.048	206	.044	6	.057	2645	.251
MALACOSTRACA												
AMPHIPODA	6	.100	23	.015	6	.071	169	.036	13	.124	1172	.111
ISOPODA	2	.033	69	.044	4	.048	248	.053	6	.057	1255	.119
TANAIDACEA	1	.017	6	.004	1	.012	3	.001	2	.019	6	.001
DECAPODA	0	0	0	0	2	.024	26	.006	4	.038	106	.010
INSECTA												
COLEOPTERA	1	.017	1	.001	4	.048	11	.002	0	0	0	0
DIPTERA	2	.033	7	.004	1	.012	3	.001	2	.019	82	.008
BRYOZOA	3	.050	576	.369	5	.060	678	.144	5	.048	1593	.151
ECHINODERMATA												
ASTERIODEA	0	0	0	0	1	.012	4	.001	3	.029	21	.002
ECHINOIDEA	0	0	0	0	0	0	0	0	1	.010	2	0
HOLOTHUROIDEA	1	.017	92	.059	1	.012	1154	.245	2	.019	5	0
OPHIUROIDEA	0	0	0	0	0	0	0	0	1	.010	4	0
CHORDATA												
UROCHORDATA	0	0	0	0	0	0	0	0	0	0	0	0
VERTEBRATA												
OSTEICHTHYES	0	0	0	0	1	.012	2	0	1	.010	2	0

	T5H3				T5M3			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE								
CHLOROPHYTA	0	0	0	0	0	0	0	0
PHAEOPHYTA	0	0	0	0	0	0	0	0
RHODOPHYTA	4	.074	71	.015	4	.056	10	.003
INVERTEBRATES								
PORIFERA	1	.019	11	.002	1	.014	88	.030
CNIDARIA								
ANTHOZOA	1	.019	2	0	1	.014	50	.017
HYDROZOA	0	0	0	0	1	.014	15	.005
PLATYHELMINTHES	0	0	0	0	1	.014	13	.004
NEMERTEA	1	.019	5	.001	2	.028	8	.003
NEMATODA	2	.037	358	.075	1	.014	3	.001
MOLLUSCA								
BIVALVIA	6	.111	1974	.414	9	.127	288	.097
GASTROPODA								
(COILED SNAILS)	7	.130	316	.066	14	.197	797	.268
(LIMPETS, ETC.)	5	.093	134	.028	5	.070	121	.041
POLYPLACOPHORA	1	.019	40	.008	1	.014	24	.008
ANNELIDA								
OLIGOCHAETA	1	.019	16	.003	0	0	0	0
POLYCHAETA	6	.111	48	.010	4	.056	9	.003
SIPUNCULIDA	1	.019	2	0	1	.014	2	.001
ARTHROPODA								
CHELICERATA								
PYCNOGONIDA	0	0	0	0	0	0	0	0
ARACHNIDA								
PSEUDOSCORPIONIDA	2	.037	4	.001	0	0	0	0
ACARINA	0	0	0	0	1	.014	6	.002
MANDIBULATA								
CRUSTACEA								
CIRRIPEDIA	3	.056	26	.005	4	.056	298	.100
MALACOSTRACA								
AMPHIPODA	2	.037	33	.007	8	.113	180	.060
ISOPODA	4	.074	69	.014	4	.056	82	.028
TANAIDACEA	1	.019	1077	.226	1	.014	1	0
DECAPODA	0	0	0	0	0	0	0	0
INSECTA								
COLEOPTERA	3	.056	9	.002	3	.042	5	.002
DIPTERA	1	.019	6	.001	1	.014	1	0
BRYOZOA	1	.019	562	.118	3	.042	856	.288
ECHINODERMATA								
ASTERIODEA	0	0	0	0	0	0	0	0
ECHINOIDEA	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	1	.019	8	.002	1	.014	120	.040
OPHIUROIDEA	0	0	0	0	0	0	0	0
CHORDATA								
UROCHORDATA	0	0	0	0	0	0	0	0
VERTEBRATA								
OSTEICHTHYES	0	0	0	0	0	0	0	0

	T5M4			
	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
ALGAE				
CHLOROPHYTA....................	0	0	0	0
PHAEOPHYTA.....................	0	0	0	0
RHODOPHYTA.....................	4	.051	36	.009
INVERTEBRATES				
PORIFERA.......................	2	.025	263	.064
CNIDARIA				
ANTHOZOA.................	1	.013	12	.003
HYDROZOA.................	2	.025	26	.006
PLATYHELMINTHES................	1	.013	11	.003
NEMERTEA.......................	2	.025	6	.001
NEMATODA.......................	1	.013	1	0
MOLLUSCA				
BIVALVIA.................	8	.101	150	.036
GASTROPODA				
(COILED SNAILS)........	12	.152	992	.240
(LIMPETS, ETC.).........	5	.063	174	.042
POLYPLACOPHORA...........	1	.013	52	.013
ANNELIDA				
OLIGOCHAETA..............	0	0	0	0
POLYCHAETA...............	7	.089	26	.006
SIPUNCULIDA....................	1	.013	1	0
ARTHROPODA				
CHELICERATA				
PYCNOGONIDA..............	1	.013	1	0
ARACHNIDA				
PSEUDOSCORPIONIDA..	0	0	0	0
ACARINA............	2	.025	10	.002
MANDIBULATA				
CRUSTACEA				
CIRRIPEDIA...........	4	.051	1234	.300
MALACOSTRACA				
AMPHIPODA..........	6	.076	191	.046
ISOPODA............	4	.051	[illegible]	.120
TANAIDACEA.........	1	.013	[illegible]	.003
DECAPODA...........	2	.025	[illegible]	.002
INSECTA				
COLEOPTERA.........	2	.025	16	.004
DIPTERA............	0	0	0	0
BRYOZOA........................	7	.089	396	.096
ECHINODERMATA				
ASTERIODEA...............	1	.013	1	0
ECHINOIDEA...............	0	0	0	0
HOLOTHUROIDEA............	1	.013	16	.004
OPHIUROIDEA..............	0	0	0	0
CHORDATA				
UROCHORDATA.................	0	0	0	0
VERTEBRATA				
OSTEICHTHYES.............	1	.013	1	0

	T5H5				T5M5			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	0	0	0	0	1	.013	136	.030
PHAEOPHYTA	2	.031	6	.001	0	0	0	0
RHODOPHYTA	5	.078	231	.036	5	.063	84	.018
INVERTEBRATES								
PORIFERA	0	0	0	0	2	.025	72	.016
CNIDARIA								
ANTHOZOA	2	.031	53	.008	2	.025	109	.024
HYDROZOA	0	0	0	0	1	.013	11	.002
PLATYHELMINTHES	1	.016	2	0	1	.013	1	0
NEMERTEA	3	.047	22	.003	2	.025	12	.003
NEMATODA	2	.031	275	.044	1	.013	2	0
MOLLUSCA								
BIVALVIA	7	.109	3829	.607	9	.113	209	.045
GASTROPODA								
(COILED SNAILS)	10	.156	537	.085	12	.150	1026	.223
(LIMPETS, ETC.)	5	.078	185	.029	5	.063	199	.043
POLYPLACOPHORA	2	.031	28	.004	1	.013	64	.014
ANNELIDA								
OLIGOCHAETA	1	.016	24	.004	0	0	0	0
POLYCHAETA	6	.094	71	.011	7	.088	17	.004
SIPUNCULIDA	0	0	0	0	1	.013	6	.001
ARTHROPODA								
CHELICERATA								
PYCNOGONIDA	0	0	0	0	1	.013	2	0
ARACHNIDA								
PSEUDOSCORPIONIDA	2	.031	9	.001	0	0	0	0
ACARINA	2	.031	4	.001	3	.038	9	.002
MANDIBULATA								
CRUSTACEA								
CIRRIPEDIA	3	.047	22	.003	4	.050	299	.065
MALACOSTRACA								
AMPHIPODA	2	.031	3	0	5	.063	98	.021
ISOPODA	1	.016	7	.001	3	.038	62	.014
TANAIDACEA	1	.016	420	.067	1	.013	24	.005
DECAPODA	0	0	0	0	3	.038	17	.004
INSECTA								
COLEOPTERA	2	.031	5	.001	3	.038	23	.005
DIPTERA	3	.047	22	.003	2	.025	2	0
BRYOZOA	1	.016	546	.087	3	.038	1213	.264
ECHINODERMATA								
ASTERIODEA	0	0	0	0	1	.013	2	0
ECHINOIDEA	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	1	.016	9	.001	1	.013	896	.195
OPHIUROIDEA	0	0	0	0	0	0	0	0
CHORDATA								
UROCHORDATA	0	0	0	0	0	0	0	0
VERTEBRATA								
OSTEICHTHYES	0	0	0	0	0	0	0	0

	T5H6				T5M6			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	0	0	0	0	0	0	0	0
PHAEOPHYTA	2	.031	5	.001	0	0	0	0
RHODOPHYTA	3	.046	110	.023	4	.066	14	.006
INVERTEBRATES								
PORIFERA	1	.015	4	.001	1	.016	144	.059
CNIDARIA								
ANTHOZOA	2	.031	76	.016	3	.049	67	.028
HYDROZOA	0	0	0	0	1	.016	14	.006
PLATYHELMINTHES	1	.015	9	.002	1	.016	1	0
NEMERTEA	2	.031	10	.002	1	.016	4	.002
NEMATODA	2	.031	130	.027	0	0	0	0
MOLLUSCA								
BIVALVIA	7	.108	2954	.617	8	.131	82	.034
GASTROPODA								
(COILED SNAILS)	12	.185	384	.080	12	.197	408	.168
(LIMPETS, ETC.)	4	.062	128	.027	5	.082	96	.040
POLYPLACOPHORA	1	.015	32	.007	1	.016	23	.009
ANNELIDA								
OLIGOCHAETA	1	.015	5	.001	0	0	0	0
POLYCHAETA	5	.077	13	.003	2	.033	2	.001
SIPUNCULIDA	0	0	0	0	0	0	0	0
ARTHROPODA								
CHELICERATA								
PYCNOGONIDA	1	.015	1	0	1	.016	2	.001
ARACHNIDA								
PSEUDOSCORPIONIDA	1	.015	10	.002	0	0	0	0
ACARINA	2	.031	5	.001	0	0	0	0
MANDIBULATA								
CRUSTACEA								
CIRRIPEDIA	3	.046	57	.012	4	.066	218	.090
MALACOSTRACA								
AMPHIPODA	3	.046	18	.004	3	.049	91	.038
ISOPODA	3	.046	68	.014	3	.049	390	.161
TANAIDACEA	1	.015	51	.011	1	.016	7	.003
DECAPODA	0	0	0	0	3	.049	51	.021
INSECTA								
COLEOPTERA	3	.046	29	.006	1	.016	1	0
DIPTERA	2	.031	3	.001	0	0	0	0
BRYOZOA	2	.031	651	.136	4	.066	644	.266
ECHINODERMATA								
ASTERIODEA	0	0	0	0	0	0	0	0
ECHINOIDEA	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	1	.015	33	.007	1	.016	164	.068
OPHIUROIDEA	0	0	0	0	1	.016	1	0
CHORDATA								
UROCHORDATA	0	0	0	0	0	0	0	0
VERTEBRATA								
OSTEICHTHYES	0	0	0	0	0	0	0	0

	T5H7				T5M7			
ALGAE	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.	TOTAL SPP.	PROP. BY SPP.	TOTAL ABUND.	PROP. BY ABUND.
CHLOROPHYTA	1	.015	1	0	1	.012	1	0
PHAEOPHYTA	0	0	0	0	0	0	0	0
RHODOPHYTA	4	.061	234	.036	4	.049	42	.005
INVERTEBRATES								
PORIFERA	1	.015	9	.001	2	.024	145	.017
CNIDARIA								
ANTHOZOA	1	.015	48	.007	1	.012	138	.016
HYDROZOA	0	0	0	0	1	.012	73	.009
PLATYHELMINTHES	1	.015	4	.001	1	.012	21	.002
NEMERTEA	2	.030	9	.001	3	.037	31	.004
NEMATODA	2	.030	405	.063	1	.012	3	0
MOLLUSCA								
BIVALVIA	9	.136	3958	.611	10	.122	200	.024
GASTROPODA								
(COILED SNAILS)	13	.197	550	.085	14	.171	2480	.294
(LIMPETS, ETC.)	6	.091	181	.028	5	.061	158	.019
POLYPLACOPHORA	1	.015	18	.003	1	.012	28	.003
ANNELIDA								
OLIGOCHAETA	1	.015	9	.001	1	.012	2	0
POLYCHAETA	5	.076	29	.004	7	.085	30	.004
SIPUNCULIDA	0	0	0	0	1	.012	3	0
ARTHROPODA								
CHELICERATA								
PYCNOGONIDA	0	0	0	0	1	.012	5	.001
ARACHNIDA								
PSEUDOSCORPIONIDA	2	.030	12	.002	0	0	0	0
ACARINA	1	.015	1	0	1	.012	7	.001
MANDIBULATA								
CRUSTACEA								
CIRRIPEDIA	3	.045	124	.019	5	.061	1403	.167
MALACOSTRACA								
AMPHIPODA	2	.030	11	.002	6	.073	406	.048
ISOPODA	3	.045	77	.012	3	.037	721	.086
TANAIDACEA	1	.015	129	.020	1	.012	18	.002
DECAPODA	0	0	0	0	2	.024	74	.009
INSECTA								
COLEOPTERA	3	.045	22	.003	4	.049	8	.001
DIPTERA	1	.015	12	.002	1	.012	1	0
BRYOZOA	2	.030	543	.083	4	.049	899	.107
ECHINODERMATA								
ASTERIODEA	0	0	0	0	0	0	0	0
ECHINOIDEA	0	0	0	0	0	0	0	0
HOLOTHUROIDEA	1	.015	90	.014	1	.012	1527	.181
OPHIUROIDEA	0	0	0	0	0	0	0	0
CHORDATA								
UROCHORDATA	0	0	0	0	0	0	0	0
VERTEBRATA								
OSTEICHTHYES	0	0	0	0	0	0	0	0

Appendix VI. Raw data list: Counts of individual organisms in each of the 303 taxa for all samples.

	S1H3	S1H4	S1H5	S1H6	S1H7	S1M3	S1M4	S1M5	S1M6	S1M7	S1L3	S1L4	S1L5	S1L6	S1L7
ALGAE															
Cladophora spp.															
ulvoids			1								5	14	3	1	5
Urospora sp.									3			11	23		3
Alaria marginata															
Analipus japonica															
Fucus distichus			1												
Haedophyllum sessile															
Laminaria spp.														1	
Pelvetiopsis limitata															
Ralfsia pacifica															
Callophyllus spp.															
corallines			3		9	1		2		5	5	79	55	76	108
Endocladia muricata	10	28	41	12	20	1				2			2	2	3
Gigartina sp. A															
Gigartina sp. B	42	12	6	22	17					1			3	1	
Halosaccion glandiforme															
Hildenbrandia sp.	1	4	4												
Iridaea cornucopiae															
Iridaea sp.												3			
Microcladia borealis												2	3		
Petrocelis spp.	5			10	3							2	5	3	6
Polysiphonia spp.													9		20
Porphyra sp. A															
Porphyra sp. B					1							11			
Schizymenia spp.														1	14
PROTOZOA															
Eponides columbiensis															
PORIFERA															
Cliona celata															
Halichondria panicea								12			28	3	11	8	3
Haliclona permollis											2	7	8	13	21
CNIDARIA															
Abietinaria abietina								1	2					12	2
Abietinaria amphora															
Abietinaria anguina															
Aglaophenia sp.						2			2		3			2	
Campanularia sp.															
Clytia hesperia															
Garveia groenlandica															
Sertularella fusiformis						2	2	54	8	44	115	43	258	259	315
Stylantheca porphyra												1			
Anthopleura elegantissima	2			5	3		14	2	2	3	3	4		7	3
Anthopleura xanthogrammica								1			10	9	3	5	10
Diadumene sp.															
PLATYHELMINTHES															
Notoplana (?inquieta)		2				18*	19*	12*	6*	20*	13	3	1	4	1
NEMERTEA															
Amphiporus (?formidabilis)	5	7			6	10	35	10	26	41	8	18	2	11	11
Emplectonema gracile			5			7	20	43	14	5	7	37	36	22	2
Paranemertes peregrina		1	1			2	8	3	1	5	1	4	4	1	2
NEMATODA															
Unidentified sp. A					1		25	24	3	9	1	1			1
Unidentified sp. B					1		1			2		2	1		
MOLLUSCA															
Cyanoplax dentiens	2	1		1		3		3	12	4	1	1			2
Katharina tunicata															1
Mopalia ciliata											8	2	5	15	13
Mopalia muscosa												1			
Acmaea mitra															
Calliostoma ligatum						1			1			1			
Collisella digitalis	7	20	34	10	23	82	56	80	94	99	96	55	90	35	23
Collisella pelta		3	70	22	34	23	8	10	29	57	104	198	94	412	189
Collisella strigatella	133	136	75	118	146	142	142	71	141	145	306	161	370	516	288
Diodora aspera	1						1								
Homalopoma lacunatum		2		1		3						1	4	13	
Homalopoma luridum					1										
Lirularia lirulata															
Lirularia succincta	3		1		2	11			3	1	3			1	
Littorina scutulata	284	207	544	367	288	15	4	2	3	20		7	3		
Littorina sitkana						2	45	20	9	1	7	8	5	1	1
Notoacmea scutum			8	1	1			3	5	1	14	17	11		11
Tegula funebralis	76	2	2	2	15	26	22	6	26	25					
Alvinia carpenteri														1	
Alvinia compacta															
Alvinia dinora															

	S1H3	S1H4	S1H5	S1H6	S1H7	S1M3	S1M4	S1M5	S1M6	S1M7	S1L3	S1L4	S1L5	S1L6	S1L7
Balcis sp.															
Barleeia sanjuanensis		3		2	3	403	116	236	410	118	149	54	115	231	302
Bittium eschrichtii			1												
Cerithiopsis stejnegeri						1		1	1				16	4	4
Crepidula adunca															
Crepidula convexa															
Crepidula fornicata															
Crepidula plana									1						
Crepipatella lingulata															
Lacuna vincta	4		3	3	2	11	12	16	10	1	1	1		1	1
Opalia chacei															
Trichotropis cancellata															
Velutina velutina	1														
Alia (=Mitrella) carinata		1	3	2	1	5		3	6	1	5	10	32	16	11
Amphissa columbiana					2		1	2	1		11	7	13	42	76
Ceratostoma foliatum															
Granulina margaritula															
Mitrella tuberosa															
Nassarius mendicus															
Ocenebra lurida						1									
Searlesia dira	1														
Thais canaliculata				1		7				3*	14*	16*	27*	36	17*
Thais emarginata	32	9	12	17	15	46	43*	28	79	80*	6	13	1	4	
Odostomia (Evalea) deliciosa						1	1		1	1			1		2
Onchidella borealis								4		1				2	
Siphonaria thersites															
Adula californiensis	7	10	15	11	4	11	2	4	4	5	2		15	10	17
Modiolus sp.			6		1			1					2	7	
Musculus taylori (?=M. pygmaeus)		1			1	82		2	3	1	2	1			1
Mytilus californianus	221	337	454	309	345	887	619	920	1168	966	806	410	653	446	481
Mytilus edulis	59	56	100	49	79	326	25	161	82	46	9	259	299	106	151
Chlamys sp.															
Pododesmus cepio															
Kellia laperousii												7			
Lasaea rubida															
Lasaea subviridis	1	3	9	13	4	4	1	15	1			3	2		1
Macoma inquinata													1		
Mysella tumida				1											
Petricola carditoides															
Protothaca staminea	24	43	8	13	103	11	5		9	12	2	8		1	4
Saxidomus giganteus															
Hiatella arctica					2	1	1	1	1	2	6	11	46	5	11
Mya arenaria															
Entodesma saxicola											1	2		4	
ANNELIDA															
Oligochaeta spp.	5				1				1	1			5		
Naineris dendritica							18								
Polydora (=Boccardia) proboscidea		1	1						6	1					
Cirratulus cirratus															
Tharyx multifilis							1			2					
Armandia brevis					1							7			
Travisia sp.															1
Eulalia levicornuta													1	1	1
Eulalia viridis															
Arctonoe vittata												1		11	
Eunoe senta															1
Halosydna brevisetosa							1				4	3	1	6	13
Harmothoe extenuata										1					
Harmothoe lunulata															
Harmothoe multisetosa															
Hesperone (?adventor)															
Lepidasthenia longicirrata															
Lepidonotus squamatus											5	4	15	14	
Polyeunoa tuta															
Pholoe minuta	2		1		3	1		1	4	1			3	1	
Paleanotus bellis														1	5
Paleanotus (=Chrysopetalum) occidentale															
Micropodarke dubia															
Syllis adamantea adamantea (=Typosyllis adamanteus)			18	2	6	10	7	28	20	22	30	21	36	59	6
Syllis alternata															
Syllis armillaris									1			1	1	1	2
Syllis elongata										1		3			
Syllis gracilis															
Syllis harti				1										1	
Syllis heterochaeta			1						1			1			
Syllis pulchra			6		1		1	9	1	1	14	5	2	2	3
Syllis stewarti		1			7	33	32	36	100	56	5	20	2	46	11
Syllis variegata															
Syllis spp.			6		2	1		4	2	1	11	2	6	21	10
Cheilonereis cyclurus															

	S1H3	S1H4	S1H5	S1H6	S1H7	S1M3	S1M4	S1M5	S1M6	S1M7	S1L3	S1L4	S1L5	S1L6	S1L7
Nereis limnicola						1				5					
Nereis vexillosa	8	12	16	7	8	28	8	2	13	18	23	17	7	35	30
Nereis sp. A															
Nereis sp. B													2		
Sphaerodoridae sp. A															1
Lumbrineris zonata														1	
Arabella iricolor	1		3			9	27	1	3	19	4				1
Arabella semimaculata															1
Idanthyrsus armatus											2	1	3	1	
Sabellaria cementarium													1	1	
Pectinaria californiensis															1
Pectinaria (=Cistenides) granulata															
Pectinaria (=Amphictene) moorei															1
Ampharetidae sp. A															1
Eupolymnia (?heterobranchia)					1					1	3				
Laphania boecki															1
Streblosoma bairdi															
Demonax (=Sabella) medius															2
Distylia rugosa															2
Eudistylia polymorpha															
Eudistylia vancouveri													1	1	6
Laonome Kroyeri															1
Myxicola infundibulum															3
Potamilla (=Pseudopotamilla) intermedia															4
Potamilla (=Pseudopotamilla) myriope															1
Potamilla neglecta															
Schizobranchia insignis													4	1	13
Serpula vermicularis														3	
Serpulidae sp. A															
Spirorbidae sp. A															
Spirorbidae sp. B							4					483	2098	1453	2019
SIPUNCULIDA															
Phascolosoma agassizii		1				4	4	4	1	21	1		8	5	4
ARTHROPODA															
Achelia latifrons									1					1	
Nymphopsis spinosissima															
Phoxichilidium femoratum								2							
Pycnogonum stearnsi															
Halobisium occidentale															
Pseudoscorpionida sp. A															
Acari sp. A			1			6	4	7		1					
Acari sp. B															
Acari sp. C															
Acari sp. D															
Acari sp. E	2							4		1					1
Acari sp. F								3							
Acari sp. G								1							
Acari sp. H															
Acari sp. I															
Acari sp. J															
Balanus cariosus	7	13	81	53	54	128	34	21	17	480	466	219	384	416	703
Balanus crenatus						8				11	50	23	22	8	53
Balanus glandula	1043	1382	1885	1181	1070	3277	1191	671	1063	1667	1875	773	793	949	820
Balanus nubilus															4
Chthamalus dalli	1842	4166	4762	5393	4228	4857	2773	1130	2063	2239	9020	7438	2181	7438	497
Pollicipes (=Mitella) polymerus						1			1	3	26	83	108	42	78
Anatanais normani															
Leptochelia dubia															1
Pancolus californiensis					1			1	1			1	3		
Synapseudes intumescens															
Cirolana harfordi			1			188	265	1	315	307	374	108	313	533	125
Dynamenella dilit[illegible]												2	1		
Dynamenella sheareri	1	1	21	2	5	51	6	7	4	37	199	172	246	167	119
Edotea sublittoralis															
Exosphaeroma amplicauda															1
Exosphaeroma octoncum											2				
Exosphaeroma rhomburum															
Gnorimosphaeroma oregonensis	76														
Ianiropsis analoga										126					
Ianiropsis (=Janiropsis) kincaidi			1			26	19		4	2	188	18	91	44	68
Idotea (=Pentidotea) schmitti										3					
Idotea wosnesenskii	1			2	2				29		1	1	7	31	4
Jaeropsis dubia															
Jaeropsis (?lobata)															
Munna chromatocephala	1	2	40		2	20	5	63	7	8	55	2	18	18	17
Synidotea bicuspida															1
Ampithoe simulans											1		1		
Aoroides columbiae															
Caprella angusta															
Caprella greenleyi											1				
Corophium brevis	8	4		2	2					1	1	1		2	

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	S1H3	S1H4	S1H5	S1H6	S1H7	S1M3	S1M4	S1M5	S1M6	S1M7	S1L3	S1L4	S1L5	S1L6	S1L7
Dsetella (?californica)															
Hyale anceps			3			62	19	25	21	12	213	68	264	78	177
Hyale frequens						1					12	7	90	80	51
Hyale grandicornis californica			3			2					1		1		
Hyale plumulosa	365	103	130	40	110	5	2		22	1					
Ischyrocerus anguipes															
Ischyrocerus serratus															
Jassa falcata						17	1	1	2	4	150	19	42	6	19
Melita californica															
Melita desdichada															
Metopa cistella															
Najna (?=consiliorum)															
Oligochinus lighti						17	1	6	9	17	9	1	2		
Orchestia sp.															
Orchomene sp. A															
Orchomene sp. B												3	1		
Parallorchestes ochotensis						1					2		12	7	1
Paramoera cf. mohri		1	4			44	62	1	22	6					
Paramoera sp.															
Paraphoxus cf. obtusidens											2				
Parapleustes den											10	1	5	9	14
Parapleustes natilus						4			1	1			1	7	3
Parapleustes pugettensis											22	6	27	8	44
Photis sp.														1	
Pontogeneia intermedia											1			1	
Stenothoides burbanki															
Cancer branneri															
Fabia subquadrata										3	3		3	4	2
Hemigrapsus nudus	41	15	23	15	7			2	9	1					
Oedignathus inermis									2		9	5	17	25	26
Pachycheles rudis											7	6	15		14
Pagurus spp.	2		9	2	18	6	10		5	11	4	2			
Petrolisthes cinctipes		1	2		9	96	109	10	252	231	64	20	32	7	39
Petrolisthes eriomeris															
Pugettia gracilis													1		
Pugettia richii											5	3	6	17	30
Coelopa sp.						3		3		1					
Oedoparena glauca			1					8		1	9		4	8	
Paraclunio alaskensis	1					4	1				11	9	11	1	2
Paraphorosyllus nigripennis						1		4	1				5		2
Diptera sp. A															
Diptera sp. B															
Diptera sp. C															
Diaulota densissima								2		1					
Liparocephalus brevipennis						1		9		4					
Coleoptera sp. A							1								
BRYOZOA															
Alcyonidium polyoum						11		3	2	59	3	68	73	35	107
Flustrella corniculata									2					2	
Crisia occidentalis									3			5			
Crisia pugeti														2	
Tubulipora pacifica															
Bugula pugeti												2			
Callopora horrida						2			3			8	8	16	21
Cellaria mandibulata															
Dendrobeania curvirostrata									1						
Dendrobeania (?laxa)												15			
Hippodiplosia insculpta												5			3
Hippothoa hyalina			56	30	87	1049	512	609	760	879	293	396	395	811	412
Microporella californica															
Microporella (?marsupiata)															
Schizoporella linearis inarmata													3	6	11
Smittina retifrons							4			3	7	189	37	50	86
Tricellaria ternata				2		2			2		1			29	
ECHINODERMATA															
Henricia leviuscula												2	1		1
Leptasterias hexactis											16	51	52	99	54
Pisaster ochraceus															
Strongylocentrotus droebachiensis															
Strongylocentrotus franciscanus															
Strongylocentrotus purpuratus											1	2			
Cucumaria pseudocurata						347	281	825	472	543	2		1		3
Cucumaria miniata															
Eupentacta quinquesemita											2		1		2
Ophiopholis aculeata														1	
CHORDATA															
Pyura haustor											1		1		
Clinocottus embryum															
Phytichthys chirus										1	1				1
Xiphister atropurpureus															

	T2H3	T2H4	T2H5	T2H6	T2H7	T2M3	T2M4	T2M5	T2M6	T2M7	T2L3	T2L4	T2L5	T2L6	T2L7
ALGAE															
Cladophora spp.													2		
ulvoids								2	1	6			9		
Urospora sp.												14			
Alaria marginata											2		12	1	
Analipus japonica													5		
Fucus distichus															
Hedophyllum sessile											1	1	2	3	1
Laminaria spp.													1		
Pelvetiopsis limitata															
Ralfsia pacifica								4	4	2					
Callophyllis spp.													3		
corallines						2		5	9	6	178	43	228	56	52
Endocladia muricata	4		5	196	95	24	4	86	58	95	8		9		1
Gigartina sp. A				7	2	10		19	19	28	4		15		2
Gigartina sp. B															
Halosaccion glandiforme				3	4					12			9		
Hildenbrandia sp.											2				
Iridaea cornucopiae				9	34					4					
Iridaea sp.													3		
Microcladia borealis				3				1		3	1	1	40		
Petrocelis spp.					1	1	2		11	1	2		12		
Polysiphonia spp.	111			6											
Porphyra sp. A									2	7		5			
Porphyra sp. B															
Schizymenia spp.								3				6	7		
PROTOZOA															
Eponides columbiensis															
PORIFERA															
Cliona celata															
Halichondria panicea			8	32		68	32	78	144	148	44	28	107	367	192
Haliclona permollis								1	6	6	65	24	128	70	22
CNIDARIA															
Abietinaria abietina													182	2	
Abietinaria amphora															
Abietinaria anguina															
Aglaophenia sp.															
Campanularia sp.															
Clytia hesperia															
Garveia groenlandica														4	
Sertularella fusiformis						64		18	47	109	211	35	460	40	26
Stylantheca porphyra															
Anthopleura elegantissima	1					14	12	13	63	33	4			1	
Anthopleura xanthogrammica															
Diadumene sp.															
PLATYHELMINTHES															
Notoplana (?*inquieta*)					16*	3	41*	33*	3	23*		1		4	
NEMERTEA															
Amphiporus (?*formidabilis*)				5		7	6	21	18	32	6			3	4
Emplectonema gracile	1			3	2					1	1	1	2	1	1
Paranemertes peregrina							6	13	4	11				2	13
NEMATODA															
Unidentified sp. A		1	2	1	2	3	34	52	57	87	1	2	1	3	11
Unidentified sp. B			29	2	17		2	50	36	15					2
MOLLUSCA															
Cyanoplax dentiens	7	13	46	65	29	9	11	35	41	28	10	1	11	6	13
Katharina tunicata												6		5	
Mopalia ciliata						1			5		2				
Mopalia muscosa															
Acmaea mitra															
Calliostoma ligatum						1	1	5	6	3	59	8	2	5	
Collisella digitalis	22	6	3	13	12	56	30	61	51	102	18	8	1	1	2
Collisella pelta	7	1		14	7	6	23	14	13	28	108	17	16	26	31
Collisella strigatella	31	2	12	29	32	21	6	12	33	15	45	7	16	26	27
Diodora aspera															
Homalopoma lacunatum	65			1	1	208	121	178	278	439	325	40	282	308	150
Homalopoma luridum							2			1	1				
Lirularia lirulata															
Lirularia succincta				1			10		9	6	1	1	15	21	1
Littorina scutulata				7	7	1	2		6				4		
Littorina sitkana	66	61	44	256	585	7	42	13	30	34	13		7	4	97
Notoacmea scutum	4					2	5	13	10	5	7	1	8	4	1
Tegula funebralis															
Alvinia carpenteri											1		26		
Alvinia compacta												1	15	20	
Alvinia dinora													3		4

	T2H3	T2H4	T2H5	T2H6	T2H7	T2M3	T2M4	T2M5	T2M6	T2M7	T2L3	T2L4	T2L5	T2L6	T2L7
Balcis sp.							1								1
Barleeia sanjuanensis	144	5	4	8	7	935	753	1569	2208	2655.	7020	905	1502	3812	2171
Bittium eschrichtii										1					
Cerithiopsis stejnegeri	12	1		3		27	31	24	50	60	18	39	52	91	134
Crepidula adunca											1				1
Crepidula convexa															
Crepidula fornicata															
Crepidula plana										2	1				
Crepipatella lingulata															
Lacuna vincta			2				2	1		2		1			
Opalia chacei	3						2	1							
Trichotropis cancellata									1						
Velutina velutina									1	1					
Alia (=Mitrella) carinata						7	8		1	10	288	8	44	1	
Amphissa columbiana				1	7	2	7	1	6	6	322	13	20	8	5
Ceratostoma foliatum	4					1	5	2	2	1	37	4		3	1
Granulina margaritula						1	2			1				1	1
Mitrella tuberosa										1					
Nassarius mendicus												1		1	
Ocenebra lurida										2					
Searlesia dira															
Thais canaliculata				2		1	10	8	9	5	49		2	5	7
Thais emarginata	13	3		1	1	6	3	17	13*	17	2	1	2	3	2
Odostomia (Evalea) deliciosa						1	4	1	7	4	31	8	14	1	
Onchidella borealis	26		2		1	46	43	723*	111	133*	16		5	2	31
Siphonaria thersites	8			5	4	5	5		7	7					
Adula californiensis	8	1		7	4		2	1	8		1	2	11	12	23
Modiolus sp.	4					49	27	33	38	33	8	7	17	18	30
Musculus taylori (?=M. pygmaeus)	8	400	45	702	1490	28	12	142	110	99	6	2	8	34	86
Mytilus californianus	755	80	52	92	54	276	143	262	331	341	229	100	300	187	178
Mytilus edulis	596	599	792	1316	1098	18		29	18	51	11	4	18	5	26
Chlamys sp.															
Pododesmus cepio															
Kellia laperousii							1			1					1
Lasaea rubida						1									
Lasaea subviridis	45	35	85	259	436	145	402	1075	1096	177	18		27	15	21
Macoma inquinata															
Mysella tumida															
Petricola carditoides															
Protothaca staminea	14					6	30	22	52	84	109	2	12	143	123
Saxidomus giganteus	2													4	
Hiatella arctica	1					2	2	2	7	5	40	4	11	13	29
Mya arenaria															
Entodesma saxicola											3	2		1	1
ANNELIDA															
Oligochaeta spp.			5	10	464		1	4	5	1					
Nainereis dendritica															2
Polydora (=Boccardia) proboscidea															
Cirratulus cirratus														1	
Tharyx multifilis															
Armandia brevis															
Travisia sp.															
Eulalia levicornuta											1			1	
Eulalia viridis															
Arctonoe vittata															
Eunoe senta															
Halosyndna brevisetosa												1	1		
Harmothoe extenuata															
Harmothoe lunulata															1
Harmothoe multisetosa															
Hesperone (?adventor)															
Lepidasthenia longicirrata															
Lepidonotus squamatus															
Polyeunoa tuta															
Pholoe minuta							9	17	18	9			1	1	5
Paleanotus bellis															
Paleanotus (=Chrysopetalum) occidentale													1		
Micropodarke dubia															1
Syllis adamantea adamantea (=Typosyllis adamanteus)					12	2			3	2	2		1		
Syllis alternata			1		13			1		3		1			1
Syllis armillaris							1		1	1				1	2
Syllis elongata															1
Syllis gracilis															
Syllis harti					5										
Syllis heterochaeta							2	2		4					
Syllis pulchra						5	1	3		1	1			1	
Syllis stewarti					2	5	35	34	16	17	5	2	1	4	21
Syllis variegata															
Syllis spp.					21	1	1	1		5				5	2
Cheilonereis cyclurus															

	T2H3	T2H4	T2H5	T2H6	T2H7	T2M3	T2M4	T2M5	T2M6	T2M7	T2L3	T2L4	T2L5	T2L6	T2L7
Nereis limnicola															
Nereis vexillosa						1	1	2	5	6	15	4	8	9	4
Nereis sp. A														1	
Nereis sp. B															
Sphaerodoridae sp. A															
Lumbrineris zonata															
Arabella iricolor							3			1					1
Arabella semimaculata															
Idanthyrsus armatus															
Sabellaria cementarium															
Pectinaria californiensis															
Pectinaria (=Cistenides) granulata															
Pectinaria (=Amphictene) moorei															
Ampharetidae sp. A															
Eupolymnia (?heterobranchia)												3		1	1
Laphania boecki															
Streblosoma bairdi															
Demonax (=Sabella) medius														1	
Distylia rugosa															
Eudistylia polymorpha															
Eudistylia vancouveri															
Laonome Kroyeri															
Myxicola infundibulum															
Potamilla (=Pseudopotamilla) intermedia															
Potamilla (=Pseudopotamilla) myriops															
Potamilla neglecta															
Schizobranchia insignis															
Serpula vermicularis															
Serpulidae sp. A															
Spirorbidae sp. A															
Spirorbidae sp. B											10	293	1455	28	5
SIPUNCULIDA															
Phascolosoma agassizii	3	4	7	35	27	6				1	21	13	30	6	17
ARTHROPODA															
Achelia latifrons								1	1	1			1		
Nymphopsis spinosissima												1			
Phoxichilidium femoratum								2				1	1	1	
Pycnogonum stearnsi															
Halobisium occidentale															
Pseudoscorpionida sp. A															
Acari sp. A						7	11	8		6			1	4	3
Acari sp. B															
Acari sp. C															
Acari sp. D			1												
Acari sp. E					2			2			3	6	6		
Acari sp. F										1			1		
Acari sp. G															
Acari sp. H															
Acari sp. I													1		
Acari sp. J															
Balanus cariosus	3	1	2	3	19	50	53	61	58	691	1017	79	335	180	963
Balanus crenatus													11	1	
Balanus glandula	183	6	42	29	48	12	22	2	14	81	141	4	8	2	50
Balanus nubilus									1	1	1	1	6		2
Chthamalus dalli	114		1		1	3	40	7	14	59	39	36	37	54	60
Pollicipes (=Mitella) polymerus						1				2	5	1			104
Anatanais normani															
Leptochelia dubia															
Pancolus californiensis	3	12	49	96	127	4	21	107	59	38	2	1	2	17	47
Synapseudes intumescens															
Cirolana harfordi		1		4	3	24	11	30	363	330	221	189	451	184	281
Dynamenella dilitata											1	7	2		
Dynamenella sheareri	20	138	232	488	461	114	34	118	166	312	516	107	212	17	153
Edotea sublittoralis															
Exosphaeroma amplicauda															
Exosphaeroma octoncum															
Exosphaeroma rhomburum											1				
Gnorimosphaeroma oregonensis															
Ianiropsis analoga															
Ianiropsis (=Janiropsis) kincaidi	1	20	96		1			3		10	12	37	157	10	10
Idotea (=Pentidotea) schmitti															
Idotea wosnesenskii	1					1		1	1		4		4		
Jaeropsis dubia															
Jaeropsis (?lobata)															
Munna chromatocephala		17	23	16	1	4	4	20	9	15	5	27	187	9	17
Synidotea bicuspida							1								
Ampithoe simulans				4						1	4			1	4
Aoroides columbiae															
Caprella angusta															
Caprella greenleyi												2		2	
Corophium brevis															

	T2B3	T2B4	T2B5	T2B6	T2B7	T2M3	T2M4	T2M5	T2M6	T2M7	T2L3	T2L4	T2L5	T2L6	T2L7
Dnetella (?californica)															
Hyale anceps			1	29	15	15	8	88	53	225	127	42	525	44	94
Hyale frequens							1				1	11	2552		
Hyale grandicornis californica	36	59			13	1									
Hyale plumulosa															
Ischyrocerus anguipes												1			
Ischyrocerus serratus															
Jassa falcata							1	2	2	11	11	33	186	8	15
Melita californica												2			
Melita desdichada															
Metopa cistella															
Najna (?=consiliorum)												1			
Oligochinus lighti					2	6	6	28	7	54	6	5			18
Orchestia sp.															
Orchomene sp. A															
Orchomene sp. B															
Parallorchestes ochotensis									1		3		27		1
Paramoera cf. mohri			1			11	31	9	69	57				1	3
Paramoera sp.															
Paraphoxus cf. obtusidens															
Parapleustes den												1	12		
Parapleustes natilus						1		1	1	5	24	15	114	24	42
Parapleustes pugettensis												11	20		2
Photis sp.															
Pontogeneia intermedia													39		
Stenothoides burbanki															
Cancer branneri												1			
Fabia subquadrata						28	2		21	20	3	5	50	3	3
Hemigrapsus nudus															
Oedignathus inermis									1		7	13	62	13	8
Pachycheles rudis														1	
Pagurus spp.												1			
Petrolisthes cinctipes						2		2		41	1		7		
Petrolisthes eriomeris													1		
Pugettia gracilis															
Pugettia richii									1			5	3	6	1
Coelopa sp.					3			2		3					1
Oedoparena glauca					1					1					
Paraclunio alaskensis	1	2		11	2	5		3	1	1	4	4	1	1	3
Paraphorosyllus nigripennis			1		3		3	1	4				1		1
Diptera sp. A															
Diptera sp. B															
Diptera sp. C															
Diaulota densissima				1	5		3	16	6	12			3		1
Liparocephalus brevipennis			2	3	2	24	21	11	57	38	5		6	1	4
Coleoptera sp. A															
BRYOZOA															
Alcyonidium polyoum						5		2		7		10		4	
Flustrella corniculata													2		2
Crisia occidentalis															
Crisia pugeti										5					
Tubulipora pacifica															
Bugula pugeti															
Callopora horrida												3	15	18	
Cellaria mandibulata						1	1		1	1					
Dendrobeania curvirostrata															
Dendrobeania (?laxa)															
Hippodiplosia insculpta											6				
Hippothoa hyalina	118	3	8	129	90	821	260	785	753	803	770	289	1021	779	560
Microporella californica															
Microporella (?marsupiata)															
Schizoporella linearis inarmata						25		3							
Smittina retifrons						6						6	6	1	
Tricellaria ternata											4			1	
ECHINODERMATA															
Henricia leviuscula															
Leptasterias hexactis											14	15	15	10	4
Pisaster ochraceus															
Strongylocentrotus droebachiensis															
Strongylocentrotus franciscanus															
Strongylocentrotus purpuratus															
Cucumaria pseudocurata					2	1276	629	2176	916	2168	1167	17	315	207	1477
Cucumaria miniata															
Eupentacta quinquesemita															
Ophiopholis aculeata															
CHORDATA															
Pyura haustor															
Clinocottus embryum															
Phytichthys chirus									1		2			1	
Xiphister atropurpureus						1									

ALGAE	T4H3	T4H4	T4H5	T4H6	T4H7	T4M3	T4M4	T4M5	T4M6	T4M7	T4L3	T4L4	T4L5	T4L6	T4L7
Cladophora spp.															
ulvoide			4	11							1		2	1	
Urospora sp.			46						2			19	2	39	3
Alaria marginata															
Analipus japonica													5	13	
Fucus distichus															
Haedophyllum sessile								1						12	
Laminaria spp.															
Pelvitiopsis limitata															
Ralfsia pacifica			1												
Callophyllus spp.														2	
corallines		1	8	5	5	3	6		1		142	148	31	320	68
Endocladia muricata		1		15	1	1	29	12	13	10	4	10	15		
Gigartina sp. A															
Gigartina sp. B			3	5		1	6	2		1	8		21	1	
Halosaccion glandiforme											3		2		
Hildenbrandia sp.													1		
Iridaea cornucopiae														3	
Iridaea sp.											2			14	
Microcladia borealis				6	6						2	12		70	
Petrocelis spp.			1			2	4				40	9	9		3
Polysiphonia spp.	70	9		34	31							5		2	
Porphyra sp. A															
Porphyra sp. B				21	14				2		1			25	3
Schizymenia spp.				1							2	4		15	14
PROTOZOA															
Eponides columbiensis															
PORIFERA															
Cliona celata															
Halichondria panicea	7	9	13	34	33	6	29	7	236	36	6		39	44	11
Haliclona permollis									6	11		34		9	6
CNIDARIA															
Abietinaria abietina							4		32	4	266	40	172	152	31
Abietinaria amphora															
Abietinaria anguina															
Aglaophenia sp.															
Campanularia sp.															
Clytia hesperia															
Garveia groenlandica															17
Sertularella fusiformis					3	16	12	14	205	90	397	267	210	487	502
Stylantheca porphyra													5	5	3
Anthopleura elegantissima	5	8	9	3	39	71	116	13	211	131			4		8
Anthopleura xanthogrammica												1	9		9
Diadumene sp.	2														
PLATYHELMINTHES															
Notoplana (?inquieta)			9*		*	1	7	*		2	2*		*	1	2
NEMERTEA															
Amphiporus (?formidabilis)			4	3	1	3	6	2	8	59	24	3	18	11	8
Emplectonema gracile			2	4	1		3		2	4	32	7	12		1
Paranemertes peregrina			4						1	8	4		3	1	2
NEMATODA															
Unidentified sp. A			5	3	1	2	506	142	142	261	14	1	6	23	7
Unidentified sp. B			23	99	90		4		6	1	8	3		15	4
MOLLUSCA															
Cyanoplax dentiens	1	3	27	10	16	29	109	107	38	47	2	3	42	6	
Katharina tunicata				1			1	2	2					1	
Mopalia ciliata											5	6	12	3	
Mopalia muscosa															
Acmaea mitra															1
Calliostoma ligatum								1	1			1	28	6	
Collisella digitalis	9	6	11	37	37	24	132	53	33	21	1		7	2	2
Collisella pelta	2	2	1	4	26	17	22	15	38	12	24	24	68	24	48
Collisella strigatella	35	15	10	27	35	47	77	31	57	33	6	30	26	30	18
Diodora aspera											1			1	
Homalopoma lacunatum	7	1	3	24	10	43	65	170	345	250	14	5	161	146	90
Homalopoma luridum														1	
Lirularia lirulata															
Lirularia succincta		1					4		8		2	3	75	11	15
Littorina scutulata	1		9	2	3		31								
Littorina sitkana	10	2	6	7	13	2	10		13		2		18	2	1
Notoacmea scutum	2	1			6	3	9	5	10	15	1	8	6	3	11
Tegula funebralis															
Alvinia carpenteri											2				
Alvinia compacta													1		
Alvinia dinora												1			

	T4H3	T4H4	T4H5	T4H6	T4H7	T4M3	T4M4	T4M5	T4M6	T4M7	T4L3	T4L4	T4L5	T4L6	T4L7
Balcis sp.														1	
Barleeia sanjuanensis	1	8	15	14	7	684	1364	1038	1184	723	444	636	2773	4617	1385
Bittium eschrichtii															
Cerithiopsis stejnegeri	1		4	1	3	12	24	17	162	32	1	2	27	41	2
Crepidula adunca															
Crepidula convexa											1				
Crepidula fornicata															
Crepidula plana					1				2		1		1	1	
Crepipatella lingulata															
Lacuna vincta							1								
Opalia chacei															
Trichotropis cancellata															
Velutina velutina				1											
Alia (=Mitrella) carinata						3	4	2	13	1	5	21	128	13	64
Amphissa columbiana				2				2	17	1	15	6	10	103	26
Ceratostoma foliatum				1			2	2	4	1	3	3	6	7	5
Granulina margaritula				2					1				6	1	
Mitrella tuberosa														1	
Nassarius mendicus					1										
Ocenebra lurida						1		1	1		1		4	1	
Searlesia dira															
Thais canaliculata	1			6		8	1	5	5	1	4	12	23	39	7
Thais emarginata	2		*			1	25	3	10	3					1
Odostomia (Evalea) deliciosa		1						2	13	3	4	2	26	33	3
Onchidella borealis	2	2	400*	187*	76*	7	90*	13	21	38*					
Siphonaria thersites															
Adula californiensis	17	21		13	11			1	2	2	7	8	44	21	10
Modiolus sp.	7	4	5	130	2	25	26	31	26	30	6	1	4	1	
Musculus taylori (?=M. pygmaeus)		5	10	7			213	2		2		1	2	1	1
Mytilus californianus	1020	705	589	824	724	260	1115	359	378	239	646	228	563	655	381
Mytilus edulis	62	84	68	278	62		18		13	13	30	41	44	24	19
Chlamys sp.													1		
Pododesmus cepio															
Kellia laperousii		1			1				17		1		13	1	
Lasaea rubida													1		
Lasaea subviridis	10	9	63	162	55	150	1985	21	60	33	1		5	6	1
Macoma inquinata											3				
Mysella tumida														1	
Petricola carditoides															
Protothaca staminea	4				5	6	4	10	38	10	7		191	55	10
Saxidomus giganteus									1						
Hiatella arctica	1	1				11	9	7	20	3	14	6	16	35	17
Mya arenaria															
Entodesma saxicola															
ANNELIDA															
Oligochaeta spp.			7	2			2	9	3	3					
Naineris dendritica															
Polydora (=Boccardia) proboscidea															
Cirratulus cirratus															
Tharyx multifilis															1
Armandia brevis															
Travisia sp.															
Eulalia levicornuta															2
Eulalia viridis			1												
Arctonoe vittata									1	3				1	6
Eunoe senta															
Halosyndna brevisetosa					2		1		3		69	32	90	38	13
Harmothoe extenuata									1						
Harmothoe lunulata															
Harmothoe multisetosa	1														
Hesperone (?adventor)														4	
Lepidasthenia longicirrata														3	
Lepidonotus squamatus									2		2		2	10	3
Polyeunoa tuta														3	
Pholoe minuta			1		1		15	2	6	2			1	2	1
Paleanotus bellis											1			2	
Paleanotus (=Chrysopetalum) occidentale															
Micropodarke dubia															
Syllis adamantea adamantea (=Typosyllis adamanteus)			1					2	2	2	19	8	17	1	
Syllis alternata			18						2		5				
Syllis armillaris									1		9		2	2	3
Syllis elongata									2		2		2		4
Syllis gracilis								1						1	
Syllis harti											1				
Syllis heterochaeta								1					1		
Syllis pulchra				1			4		1	9			4		
Syllis stewarti	2		3	5	3	4	25	10	9	3	25	9	9	3	2
Syllis variegata															
Syllis spp.					1		1				2	1	9	1	6
Cheilonereis cyclurus															

	T4H3	T4H4	T4H5	T4M6	T4H7	T4M3	T4M4	T4M5	T4M6	T4M7	T4L3	T4L4	T4L5	T4L6	T4L7
Nereis limnicola								1				1			
Nereis vexillosa	1					2	3	1	5	3	4	4	7	11	3
Nereis sp. A													1	1	
Nereis sp. B															
Sphaerodoridae sp. A															
Lumbrineris zonata															
Arabella iricolor											1		5	1	1
Arabella semimaculata															
Idanthyrsus armatus							2								
Sabellaria cementarium															
Pectinaria californiensis													2		
Pectinaria (=Cistenides) granulata														1	
Pectinaria (=Amphictene) moorei															
Ampharetidae sp. A													1		
Eupolymnia (?heterobranchia)											9		5	1	1
Laphania boecki															
Streblosoma bairdi											2				
Demonax (=Sabella) medius															
Distylia rugosa															
Eudistylia polymorpha					2										
Eudistylia vancouveri							1								
Laonome kroyeri															1
Myxicola infundibulum															
Potamilla (=Pseudopotamilla) intermedia										1					
Potamilla (=Pseudopotamilla) myriops	1														2
Potamilla neglecta											1				
Schizobranchia insignis	1				1		1	1	1						1
Serpula vermicularis							5				6		112		
Serpulidae sp. A															
Spirorbidae sp. A	7	2							153	60	8215	1191	2697	2789	1146
Spirorbidae sp. B															
SIPUNCULIDA															
Phascolosoma agassizii	12		4	6	9	101	104	83	376	200	16	1	55	72	13
ARTHROPODA															
Achelia latifrons							1								
Nymphopsis spinosissima															
Phoxichilidium femoratum							4	2		1	1		1	1	
Pycnogonum stearnsi					1	1							1		
Halobisium occidentale															
Pseudoscorpionida sp. A															
Acari sp. A							5	1	1	4					
Acari sp. B											2				
Acari sp. C											1				
Acari sp. D										1					
Acari sp. E				1	1		1	1			2	1		2	4
Acari sp. F							1		1	2					
Acari sp. G															
Acari sp. H															
Acari sp. I															
Acari sp. J														1	
Balanus cariosus	1		5		1	16	16	53	74	65	657	180	206	307	1736
Balanus crenatus									1		31	7	7	18	3
Balanus glandula	17	35	24	73	30	6	12	8	21	36	22	13	15	7	111
Balanus nubilus						1	1		1			10	20	13	3
Chthamalus dalli	12	56	92	147	123	19	106	43	167	53	362	953	1232	421	772
Pollicipes (=Mitella) polymerus						3	60	24	9	53	26	28	2	35	20
Anatanais normani											3	1	6	1	5
Leptochelia dubia															
Pancolus californiensis	4	2	6	12	6	4	518	1	8	3	1		1	1	1
Synapseudes intumescens							1							1	
Cirolana harfordi	3	16		24		57	141	240	1085	157	1836	232	164	1704	684
Dynamenella dilitata											118	32	80	116	10
Dynamenella sheareri	24	51	7	250	42	13	55	13	76	60	288	240	373	33	25
Edotea sublittoralis															
Exosphaeroma amplicauda															
Exosphaeroma octoncum													5		
Exosphaeroma rhomburum															
Gnorimosphaeroma oregonensis															
Ianiropsis analoga											3			5	
Ianiropsis (=Janiropsis) kincaidi	3	33	6	37	27	1	5	1	12	24	1274	116	566	244	513
Idotea (=Pentidotea) schmitti				1										2	
Idotea wosnesenskii											1		1		1
Jaeropsis dubia											6		1	4	
Jaeropsis (?lobata)															
Munna chromatocephala		1	1	18		1	10		3	7	227	19	106	58	22
Synidotea bicuspida														1	
Ampithoe simulans	5	3		58	5					2					
Aoroides columbiae													4		1
Caprella angusta											1		2		
Caprella greenleyi											2	2		23	2
Corophium brevis															

	T4H3	T4H4	T4H5	T4H6	T4H7	T4M3	T4M4	T4M5	T4M6	T4M7	T4L3	T4L4	T4L5	T4L6	T4L7
Duetella (?californica)											2				
Hyale anceps			4	56	10	24	51	54	122	104	40	12	249	27	23
Hyale frequens									1		400	201	1332	346	479
Hyale grandicornis californica	47	58	1	5	4			2							
Hyale plumulosa															
Ischyrocerus anguipes											71	4	29	67	28
Ischyrocerus serratus											108		6	5	5
Jassa falcata						1	3	1	10	2	1011	718	1558	1857	321
Melita californica											981	20	243	306	36
Melita desdichada				2											
Metopa cistella											24	6	7	63	
Najna (?=consiliorum)														4	
Oligochinus lighti			1		2		2		3	14					
Orchestia sp.															
Orchomene sp. A															1
Orchomene sp. B															
Parallorchestes ochotensis								1					2	20	1
Paramoera cf. mohri					1	7	11	3	7	23			2		
Paramoera sp.	3		1	15	1										
Paraphoxus cf. obtusidens															
Parapleustes den											39	2	18	56	13
Parapleustes natilus				10		2	4	5	12	24		70		1	
Parapleustes pugettensis											484		120	353	215
Photis sp.															
Pontogeneia intermedia											12	4		16	47
Stenothoides burbanki													1		
Cancer branneri				1					1		6		6	1	
Fabia subquadrata										1	10	6	12	10	7
Hemigrapsus nudus													1		
Oedignathus inermis									5		147	64	95	135	63
Pachycheles rudis									3		99	20	39	27	18
Pagurus spp.											4	1			
Petrolisthes cinctipes						2			62	25				14	
Petrolisthes eriomeris											4				
Pugettia gracilis															
Pugettia richii									2		3	7	21	18	18
Coelopa sp.	3		4		1										
Oedoparena glauca															
Paraclunio alaskensis	5	1		32	6		2			3	287	20	83	3	82
Paraphorosyllus nigripennis			1				1	1	1						
Diptera sp. A															
Diptera sp. B															
Diptera sp. C															
Diaulota densissima			3	2	1		8			2					
Liparocephalus brevipennis				4			26		8	9					
Coleoptera sp. A															
BRYOZOA															
Alcyonidium polyoum					1					10	122	4	43	39	20
Flustrella corniculata														2	
Crisia occidentalis											17		2		
Crisia pugeti									6			23	15	30	
Tubulipora pacifica															
Bugula pugeti											42				
Callopora horrida					25					9	135	48	242	392	160
Cellaria mandibulata															
Dendrobeania curvirostrata															
Dendrobeania (?laxa)															
Hippodiplosia insculpta															
Hippothoa hyalina	234	187	524	535	550	414	1205	881	784	647	722	484	751	1378	1123
Microporella californica															
Microporella (?marsupiata)															
Schizoporella linearis inarmata											6		2		
Smittina retifrons						2			94	12	686	226	749	420	210
Tricellaria ternata									10		104	48	15	270	80
ECHINODERMATA															
Henricia leviuscula											2		2	3	2
Leptasterias hexactis		1					3	6	5	4	27	16	32	13	18
Pisaster ochraceus													2		1
Strongylocentrotus droebachiensis											6		2	1	2
Strongylocentrotus franciscanus															
Strongylocentrotus purpuratus											2	1	1		
Cucumaria pseudocurata	22	12	5		92	618	1264	1304	572	1154	1		2	1	
Cucumaria miniata											8	1	2		3
Eupentacta quinquesemita											13	6	4	3	3
Ophiopholis aculeata									1		18	3	21	39	4
CHORDATA															
Pyura haustor															
Clinocottus embryum															
Phytichthys chirus									2	2	2		1	3	2
Xiphister atropurpureus														1	

	T5H3	T5H4	T5H5	T5H6	T5H7	T5M3	T5M4	T5M5	T5M6	T5M7
ALGAE										
Cladophora spp.										
ulvoids					1					1
Urospora sp.								136		
Alaria marginata										
Analipus japonica										
Fucus distichus										
Haedophyllum sessile										
Laminaria spp.										
Pelvetiopsis limitata			4	1						
Ralfsia pacifica			2	4						
Callophyllus spp.										
corallines			2	3	5		4	1		14
Endocladia muricata	44		184	100	201	4	27	77	11	25
Gigartina sp. A	18		37	7	26	2	4	2	1	1
Gigartina sp. B										
Halosaccion glandiforme										
Hildenbrandia sp.								1		
Iridaea cornucopiae										
Iridaea sp.						2				
Microcladia borealis										
Petrocelis spp.	8		7		2	2	1	3	1	2
Polysiphonia spp.										
Porphyra sp. A			1					1		
Porphyra sp. B										
Schizymenia spp.										
PROTOZOA										
Eponides columbiensis										
PORIFERA										
Cliona celata										
Halichondria panicea	11			4	9	88	226	54	144	118
Haliclona permollis							37	18		27
CNIDARIA										
Abietinaria abietina							6			
Abietinaria amphora										
Abietinaria anguina										
Aglaophenia sp.										
Campanularia sp.										
Clytia hesperia										
Garveia groenlandica										
Sertularella fusiformis						15	20	11	16	73
Stylantheca porphyra			2							
Anthopleura elegantissima	2		51	74	48	50	12	108	65	138
Anthopleura xanthogrammica									1	
Diadumene sp.				2				1	1	
PLATYHELMINTHES										
Notoplana (?*inquieta*)	*		2*	9*	4*	13*	11*	1*	1*	21*
NEMERTEA										
Amphiporus (?*formidabilis*)	5		14	9	6	4	5	9		18
Emplectonema gracile			7	1	3					6
Paranemertes peregrina			1			4	1	3	6	9
NEMATODA										
Unidentified sp. A	135		266	125	391	3	1	2		3
Unidentified sp. B	23		9	5	14					
MOLLUSCA										
Cyanoplax dentiens	40		27	32	18	24	32	64	23	28
Katharina tunicata										
Mopalia ciliata			1							
Mopalia muscosa										
Acmaea mitra										
Calliostoma ligatum						1	1			2
Collisella digitalis	80		76	48	61	62	49	51	34	64
Collisella pelta	6		4	1	3	21	14	15	3	8
Collisella strigatella	29		12	23	6	21	52	39	11	34
Diodora aspera										
Homalopoma lacunatum	17		47	80	109	99	74	148	67	291
Homalopoma luridum			1		1		1			
Lirularia lirulata										
Lirularia succincta			1	3	2	9	12	13	20	83
Littorina scutulata	9		25	1	1	5		4	1	
Littorina sitkana	52		173	24	31	71	18	118	6	241
Notoacmea scutum	3		3		1	1	19	14	6	11
Tegula funebralis										1
Alvinia carpenteri				1						
Alvinia compacta										
Alvinia dimora										

	T5H3	T5H4	T5H5	T5H6	T5H7	T5M3	T5M4	T5M5	T5M6	T5M7
Balcis sp.										
Barleeia sanjuanensis	228		271	257	379	531	733	683	298	1782
Bittium eschrichtii										
Caritchiopsis steinegeri	2		7	7	6	53	138	27	5	49
Crepidula adunca										
Crepidula convexa										
Crepidula fornicata										
Crepidula plana										
Crepipatella lingulata										
Lacuna vincta					6					
Opalia chacei										
Trichotropis cancellata							1			
Velutina velutina										
Alia (=Mitrella) carinata	1			1		3	6	3	2	
Amphissa columbiana				2	2	1	3	1	2	3
Ceratostoma foliatum								1		3
Granulina margaritula					1				1	2
Mitrella tuberosa										
Nassarius mendicus										
Ocenebra lurida				1					2	2
Searlesia dira										
Thais canaliculata			3	2	1	3		3		5
Thais emarginata	7		7	9	84	16	4	4	3	14
Odostomia (Evalea) deliciosa			2		3	3	1	1	1	2
Onchidella borealis	164		909	56	1094	164	40	80	42	61
Siphonaria thersites					1					
Adula californiensis	6				1	2	1	6	2	2
Modiolus sp.	4		2	6	2	9	1	10	6	4
Musculus taylori (?=M. pygmaeus)	234		393	287	280	31	12	13	8	21
Mytilus californianus	686		650	540	421	825	753	766	693	616
Mytilus edulis	83		78	52	57	22	12	35	17	36
Chlamys sp.										
Pododesmus cepio										
Kellia laperousii						1	1	3	1	4
Lasaea rubida				1	3	6				10
Lasaea subviridis	1616		3344	2601	3607	182	113	109	28	104
Macoma inquinata										
Mysella tumida										
Petricola carditoides										
Protothaca staminea	33		11	1	7	32	6	21	16	8
Saxidomus giganteus										
Hiatella arctica			1	2	1	3	4	11	4	5
Mya arenaria										
Entodesma saxicola										
ANNELIDA										
Oligochaeta spp.	16		24	5	9					2
Naineris dendritica										
Polydora (=Boccardia) proboscidea										
Cirratulus cirratus										
Tharyx multifilis										
Armandia brevis										
Travisia sp.										
Eulalia levicornuta										
Eulalia viridis										
Arctonoe vittata										
Eunoe senta										
Halosyndna brevisetosa							2	2		
Harmothoe extenuata										
Harmothoe lunulata										
Harmothoe multisetosa										
Hesperone (?adventor)										
Lepidasthenia longicirrata										
Lepidonotus squamatus										
Polyeunoa tuta										
Pholoe minuta	27		1	2	3		1	2		5
Paleanotus bellis										
Paleanotus (=Chrysopetalum) occidentale										
Micropodarke dubia										
Syllis adamantea adamantea (=Typosyllis adamanteus)	4		3			3	4		1	4
Syllis alternata	7		40	1						
Syllis armillaris							1			1
Syllis elongata										
Syllis gracilis								1		
Syllis harti			7							
Syllis heterochaeta	1				3		1			1
Syllis pulchra					2	1		6		
Syllis stewarti	8		6	5	17	2	5	2		15
Syllis variegata										
Syllis spp.			14	6	6			1	2	3
Cheilonereis cyclurus										

	T5H3	T5H4	T5H5	T5H6	T5H7	T5M3	T5M4	T5M5	T5M6	T5M7
Nereis limnicola										
Nereis vexillosa	1					3				1
Nereis sp. A										
Nereis sp. B										
Sphaerodoridae sp. A										
Lumbrineris zonata										
Arabella tricolor										
Arabella semimaculata										
Idanthyrsus armatus										
Sabellaria cementarium										
Pectinaria californiensis										
Pectinaria (=Cistenides) granulata										
Pectinaria (=Amphictene) moorei										
Ampharetidae sp. A										
Eupolymnia (?heterobranchia)										
Laphania boecki										
Streblosoma bairdi										
Demonax (=Sabella) medius										
Distylia rugosa										
Eudistylia polymorpha										
Eudistylia vancouveri										
Laonome Kroyeri										
Myxicola infundibulum										
Potamilla (=Pseudopotamilla) intermedia										
Potamilla (=Pseudopotamilla) myriops										
Potamilla neglecta										
Schizobranchia insignis										
Serpula vermicularis								1		
Serpulidae sp. A										
Spirorbidae sp. A							12			
Spirorbidae sp. B										
SIPUNCULIDA										
Phascolosoma agassizii	2					2	1	6		3
ARTHROPODA										
Achelia latifrons										
Nymphopsis spinosissima										
Phoxichilidium femoratum				1			1	2	2	5
Pycnogonum stearnsi										
Halobisium occidentale	3		8	10	9					
Pseudoscorpionida sp. A	1		1		1					
Acari sp. A				1		6	9	5		7
Acari sp. B										
Acari sp. C							1			
Acari sp. D										
Acari sp. E			1	2				1		
Acari sp. F								1		
Acari sp. G										
Acari sp. H			1		1					
Acari sp. I										
Acari sp. J										
Balanus cariosus	3		4	5	24	265	927	280	86	1173
Balanus crenatus										3
Balanus glandula	13		5	8	17	18	15	9	42	115
Balanus nubilus										
Chthamalus dalli	10		13	44	83	13	27	1	80	95
Pollicipes (=Mitella) polymerus						2	265	9	10	17
Anatanais normani										
Leptochelia dubia										
Pancolus californiensis	1077		420	51	129	1	13	24	7	18
Synapseudes intumescens										
Cirolana harfordi	1			4	3	10	309	35	148	165
Dynamenella dilitata					69					
Dynamenella sheareri	34		7	50		52	181	17	36	319
Edotea sublittoralis										
Exosphaeroma amplicauda										
Exosphaeroma octoncum										
Exosphaeroma rhomburum										
Gnorimosphaeroma oregonensis										
Ianiropsis analoga										
Ianiropsis (=Janiropsis) kincaidi	2					1	1			
Idotea (=Pentidotea) schmitti										
Idotea wosnesenskii										
Jaeropsis dubia										
Jaeropsis (?lobata)										
Munna chromatocephala	32			14	5	19	4	10	6	17
Synidotea bicuspida										
Ampithoe simulans										3
Aoroides columbiae										
Caprella angusta										
Caprella greenleyi										
Corophium brevis										

	T5H3	T5H4	T5H5	T5H6	T5H7	T5M3	T5M4	T5M5	T5M6	T5M7
Duetella (?californica)										
Hyale anceps	15		2	8	6	57	123	17	40	238
Hyale frequens						1				
Hyale grandicornis californica						1				
Hyale plumulosa										
Ischyrocerus anguipes										
Ischyrocerus serratus										
Jassa falcata						5	7	7		10
Melita californica						1				
Melita desdichada										
Metopa cistella										
Najna (?=consiliorum)										
Oligochinus lighti				2		8	3	8		17
Orchestia sp.										
Orchomene sp. A										
Orchomene sp. B										
Parallorchestes ochotensis										
Paramoera cf. mohri	18		1	8	5	60	28	66	51	137
Paramoera sp.						47	26			
Paraphoxus cf. obtusidens										
Parapleustes den										
Parapleustes natilus							4			1
Parapleustes pugettensis										
Photis sp.										
Pontogeneia intermedia										
Stenothoides burbanki										
Cancer branneri										
Fabia subquadrata						1		1	3	12
Hemigrapsus nudus										
Oedignathus inermis										
Pachycheles rudis						2				
Pagurus spp.							1	2	2	
Petrolisthes cinctipes							7	14	46	62
Petrolisthes eriomeris										
Pugettia gracilis										
Pugettia richii										
Coelopa sp.	6		19	2	12			1		
Oedoparena glauca			1			1				
Paraclunio alaskensis								1		
Paraphorosyllus nigripennis			2	1			2			
Diptera sp. A										
Diptera sp. B										
Diptera sp. C										
Diaulota densissima	6		5	11	18	4	1	6	2	
Liparocephalus brevipennis	3			18	4	1	15	17	1	6
Coleoptera sp. A										
BRYOZOA										
Alcyonidium polyoum						2	10		7	14
Flustrella corniculata							2			
Crisia occidentalis										
Crisia pugeti							4			
Tubulipora pacifica										
Bugula pugeti										
Callopora horrida						60	7	9	21	
Cellaria mandibulata						1				
Dendrobeania curvirostrata										
Dendrobeania (?laxa)										
Hippodiplosia insculpta										
Hippothoa hyalina	562		546	648	540	785	368	202	615	882
Microporella californica										
Microporella (?marsupiata)										
Schizoporella linearis inarmata										
Smittina retifrons				1	1		4	2	1	2
Tricellaria ternata							1			1
ECHINODERMATA										
Henricia leviuscula										
Leptasterias hexactis							1	2		
Pisaster ochraceus										
Strongylocentrotus droebachiensis										
Strongylocentrotus franciscanus										
Strongylocentrotus purpuratus										
Cucumaria pseudocurata	8		9	33	90	120	16	896	164	1527
Cucumaria miniata										
Eupentacta quinquesemita										
Ophiopholis aculeata										
CHORDATA										
Pyura haustor										
Clinocottus embryum							1			
Phytichthys chirus										
Xiphister atropurpureus										

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