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THE ECOLOGY OF *MYTILUS EDULIS* L. IN EXPOSED ROCKY INTERTIDAL COMMUNITIES

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Abstract: Information is given to show that *Mytilus edulis* L. is an important component of exposed rocky coast communities of the Western Hemisphere. It is abundant on the exposed coast of Washington State with a potential distribution extending from + 10.6 ft (+ 3.2 m) down to at least 10 m depth: it is not continuous along this entire gradient. It dominates a band from + 10.6 ft down to +9.6 ft (+ 3.2 to + 2.9 m) tidal height where it usually intergrades with its congener *M. californianus* Conrad. Its upper limit appears to be determined by desiccation stress and the lower probably by competition and or predation.

In the mid-intertidal zone, from + 5.6 to + 9.6 ft (+ 1.7 to 2.9 m), where *M. californianus* is dominant, *M. edulis* occurs in patches of cleared space which usually form in the *M. californianus* bed matrix in winter months. Here, it acts as an opportunistic species by colonizing quickly and growing rapidly to reproductive size. It is preyed upon by *Thais* spp. which prefer it to *Mytilus californianus* and eventually is eliminated from these patches. It also occurs, sometimes abundantly, in tufts of the red alga *Endocladia muricata* (Postels & Ruprect) J. Agardh at high and mid-intertidal heights.

In low intertidal and subtidal regions, to ≈ 10 m depth, *Mytulis edulis* can be found in refuges of filamentous or intricately arranged substrata which generally offer protection from predation. These are represented by a wide variety of forms such as hydroids, bryozoans, filamentous algae, coralline algae, and kelp with convoluted holdfasts or complex stipes.

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 hemispheres (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 pillings or gravel in protected bays (hence the name 'bay mussel'), or in the extreme case at the semi-exposed mouth 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 (≈33°00′S: 71°35′W) to the Strait of Magellan (≈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.

RESULTS

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. 1 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.[1] down to the upper limit of the *Mytilus californianus* zone at

[1] 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.

+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).

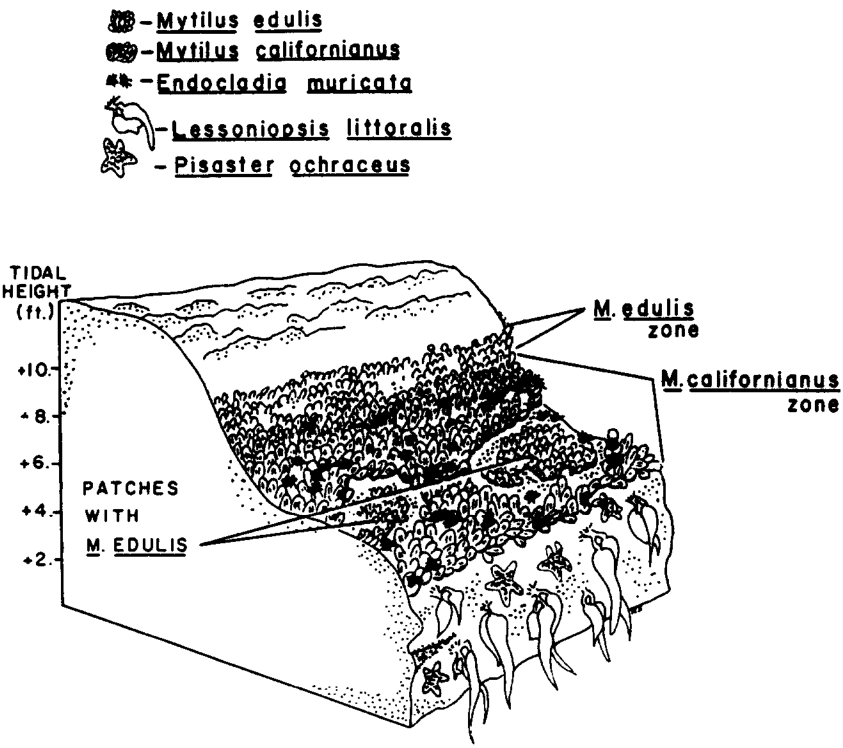

Fig. 1. Diagrammatic representation of a rocky intertidal from Tatoosh Island, Washington.

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 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*

The *M. californianus* zone extends downward from +9.6 ft (+2.9 m) to a lower limit of +5.6 ft (+1.7 m) resulting in a zone 4.0 ft (1.2 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 or 80% of the available primary or secondary space[1] 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,

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 italics.

	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)*

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 of 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.

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

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 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 & 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* occurs 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* 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 food 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 ≈ 140 mm (J. Standing, pers. comm.).

TABLE III

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

	Tidal height (ft)	Size (mm)
High (in *M. edulis* zone)	+10.5	19.50 (3.69)
Mid (in patches in *M. californianus* zone)	+ 8.5	28.28 (2.78)
Low (in patches in *M. californianus* zone)	+ 6.5	40.37 (10.26)
Low intertidal to subtidal (on holdfasts and stipes of kelp)	+ 5.5 to −30.0	21.30 (2.91)

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, 1969) 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 (Suchanek, in prep.).

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 & 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 (*Larus glaucescens* Naumann) nesting on the island, and subsequently fed to nestlings. This massive summer mortality occurred in the three consecutive summers, 1974–1976. Fig. 2 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.

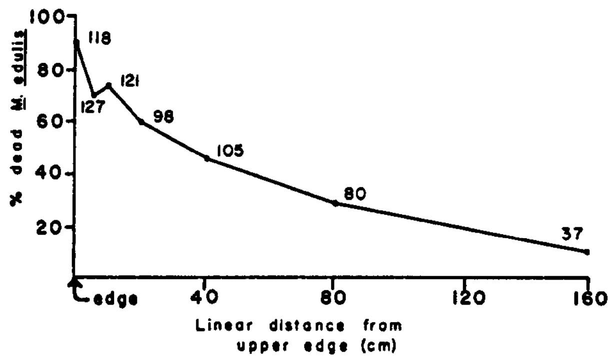

Fig. 2. Percentage dead *Mytilus edulis* measured along a line down from the upper edge of the mussel bed showing the effect of desiccation (10.vi.75).

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. 3). In general, there is a distinct 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. 3 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*

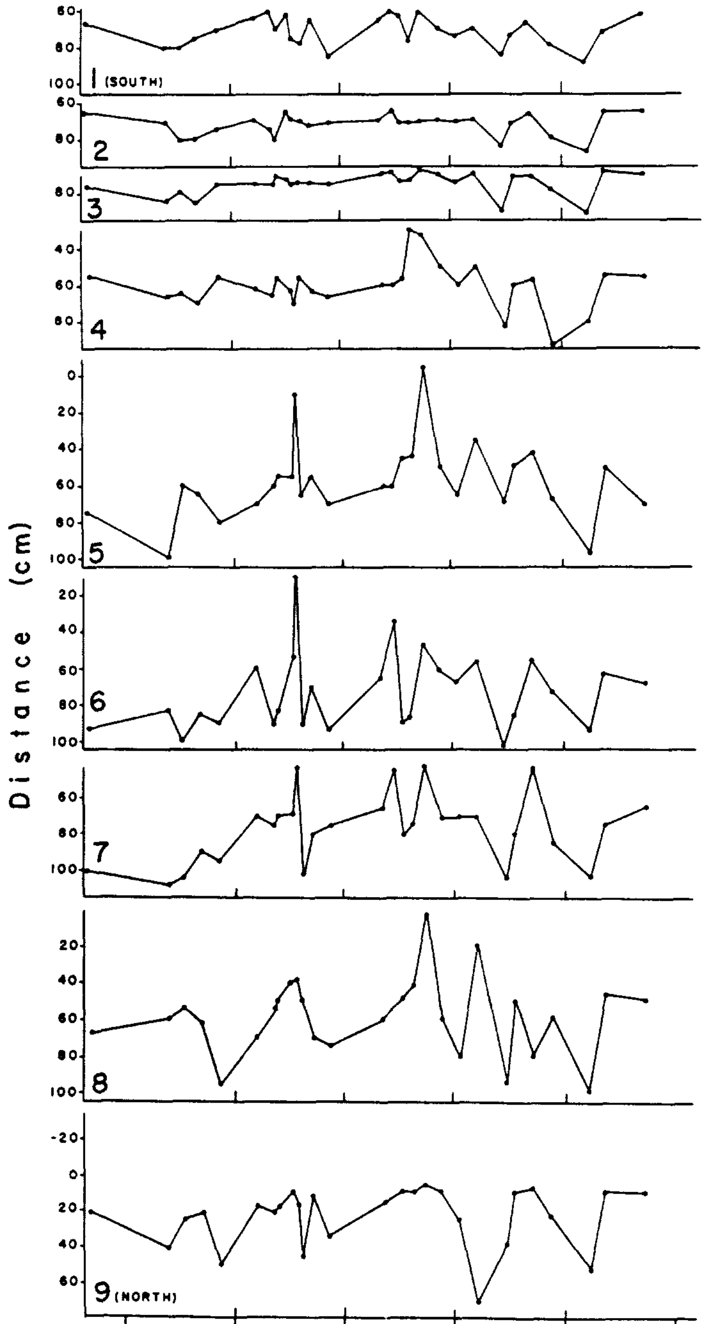

Fig. 3. Absolute distances from permanent markers (Nos 1–9), ≈3 m apart, along a rocky shore at Tatoosh Island, Washington to the upper edge of the *Mytilus edulis* bed to show seasonal fluctuation in the upper edge of the bed: a rise in the graphs indicates a rise in the position of the upper edge of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

populations of Paine (1974, his Table I) which were measured from the same markers.

Competition and predation

A majority of the intertidal zone from +5.6 to +9.6 ft (+1.7 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 1 & 4). 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 (Suchanek, in prep.).

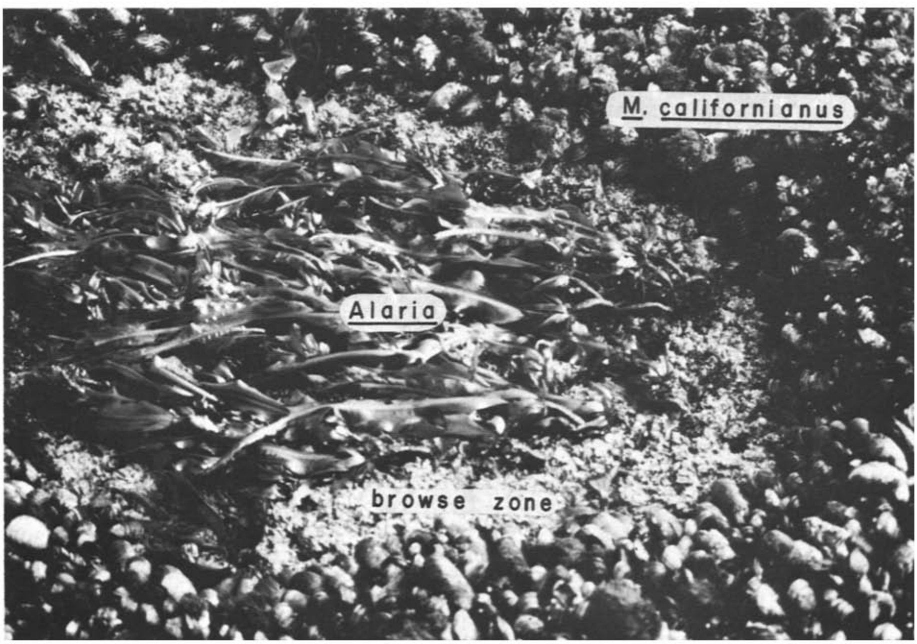

Fig. 4. Natural patch in *Mytilus californianus* bed showing a distinct browse zone (≈20 cm) and macroalgae (*Alaria*) growing in the central area of the patch: *M. edulis* (not evident in the Fig.) have also settled and occupy primary and secondary space under the cover of macroalgae.

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

TABLE IV

Average no. animals per 0.10 m^2 from two natural patches in the mid-intertidal zone at 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.iii. 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	–

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. 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 occasionally 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 21st 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 ($\leqslant$1.50 cm) *M. californianus* (Paine, 1974, his Table IV) are almost certainly a mixture of the two *Mytilus* species. It is often impossible to distinguish conclusively small ($\leqslant$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, 1976). 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 $+17.3 \pm 14.62$ 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.

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