The Role of Disturbance in the Evolution of Life History Strategies in the Intertidal Mussels *Mytilus edulis* and *Mytilus californianus*

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Summary. The intertidal mussels *Mytilus edulis* and *M. californianus* compete for space on the west coast of North America. An analysis of differences in size, growth rate, age at first reproduction, life span, mode of reproduction, niche and habitats between these two species demonstrates that their life history strategies are different in several important ways. *M. californianus* is a larger, sturdier, slower growing mussel which has effective predator-deterring mechanisms and is an overall superior competitor for space in the intertidal. Its reproductive strategy is based on continually spawning at a very low level throughout a yearly cycle. *M. edulis* is a classic fugitive species which rarely attains a large size but matures early and is characterized by a single massive reproductive output each year. The differences noted in their life history strategies are very likely the result of either a) a "pre-adaptation" for coexistence, or b) a competitively-induced regional evolutionary divergence.

In Washington a band of small *M. edulis* (removed from most predation and competition) exists in a high intertidal spatial refuge, and contributes relatively little to the gene pool. Larger individuals exist in disturbed areas lower in the intertidal zone. These lower zones represent a relatively high risk, and usually only temporary, habitat for *M. edulis* because of mortality due to competition and predation. Individuals, however, colonizing these two intertidal patches contribute 43 times as much as their high intertidal counterparts in terms of reproductive fitness (calculated on a populationwide basis).

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 and Bossert 1970; Wilbur et al. 1974; Hirshfield and Tinkle 1975; reviews by Giesel 1976; Stearns 1976, 1977). The features which have received the most attention are fecundity, longevity, age at first reproduction, body size, growth rates, mode of reproduction, and niche or habitat differences. 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 life history parameters (e.g. – Tinkle 1969; Murdoch 1966; Ricklefs 1977; Snell and King 1977; Ballinger 1977), while others have tried

a more synthetic approach. Williams (1966a, b), Gadgil and 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, trophic 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 habitats (Alm 1959; Tilley 1973; McNaughton 1975), whereas Randolph (1973) compared unrelated species (of different genera) living in the same habitats. But no one has carefully considered species that are closely related, are living in the same habitats and are still competing for a common requisite thereby indentifying the mechanism for effective ecological divergence.

The most inclusive attempt to specify life history strategies was forwarded by MacArthur and 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 an predicting differences in life history phenomena (Pianka 1970, 1972, 1974; King and Anderson 1971; Roughgarden 1971; Menge 1974; McNaughton 1975; Nichols et al. 1976). Although the concept has probably 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 and Solbrig 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).[2] Sources of these disturbances include predation (Paine 1966, 1971, 1974, 1976a; Paine and Vadas 1969; Dayton and Hessler 1972; Dayton 1975), climatic disasters (Dayton et al. 1970; Loya 1972) climatic catastrophes (Heinselman 1973; Henry and Swan 1974), spatially unpredictable stochastic events such as tree falls (Richards 1952; Richards and Williamson 1975), and temporally predictable diasters such as patch formation by wave-driven logs or wave action along in the rocky intertidal (Dayton 1971; Levin and Paine 1974). Re-

2 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

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cently, 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 and 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 paper 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 that the competitively inferior species has developed very different life history and reproductive strategies by taking advantage of disturbance as a cue in order to utilize successfully a limited resource, space.

General Ecology of the *Mytilus* Species

Mytilus edulis is a relatively small (≤ 10 cm in Washington State), competitively inferior bivalve that occupies a broader geographic and intertidal range than does its congener *M. californianus* (Levinton and Suchanek 1978; Suchanek 1978). *M. edulis* is almost cosmopolitan in distribution, being abundant in the Northern, Southern, Eastern and Western Hemispheres (Soot-Ryen 1955; Seed 1976). In Washington, *M. edulis* occupies the high intertidal from 0.6 ft (2.9 m) to 10.6 ft (3.2 m) above Mean-Lowest-Low-Water (MLLW), settles in patches of open space formed in the matrix of *M. californianus* beds in the mid-intertidal and colonizes protective refugia such as kelp holdfasts, hydroid and ectoproct colonies and coralline algae in the lower intertidal and subtidal regions (Suchanek 1978). It has also been found as deep as 18–37 m (Soot-Ryen 1955).

Mytilus californianus is a larger, competitively dominant species restricted to the west coast of North America. Although the range of *M. californianus* extends from the Aleutian Islands to Isla Socorro, Mexico (Soot-Ryen 1955), this species only occupies major areas of intertidal space from British Columbia south. This is where the most intense competition for space with *M. edulis* can be observed. 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 (Suchanek 1978), although it can be found as deep as 100 ft (30 m) (Paine 1976b). In this intertidal range, it also supports an extremely diverse assemblage of associated organisms (over 300 species) living within the intersticies of the beds (Suchanek 1980).

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, they co-exist. In bays, where *M. edulis* is favored by the environmental conditions, *M. californianus* becomes covered with silt and subsequently is 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, both species are quite capable of occupying areas of even the most severe wave action (Suchanek 1978). 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 more substantial shell of its congener indicating a mechanism for such competitive exclusion.

In Washington, *M. edulis* occurs in the *M. californianus* zone (usually only in patches of cleared space) and is subject to intense predation by the carnivorous gastropods *Thais canaliculata* and *T. emarginata* which inevitably eliminate it from these temporal refugia (Suchanek 1978).

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°17′N:124°41′W) or at Tatoosh Island (48°24′N:124°44′W). See Dayton (1971) for maps and descriptions of these sites. Other field observations and comparative samples were taken from Torch Bay, Alaska (58°20′N:136°48′W), an exposed locality, and upper Glacier Bay, Alaska (58°47′N:136°29′W), a more protected site.

There are a number of inherent problems in the analysis of factors influencing different life history strategies between these mussels. Because qualitative and quantitative data on spawning from natural field populations of mussels is difficult to obtain, gametic output must be inferred. Gonad weights were used as the most reasonable indicator of potential gametic output. Larvae are even more difficult to follow because they are planktonic, and I have no information about larval dispersal or mortality. Data on growth rates, age at potential first reproduction, and mode of reproduction of settled individuals were directly obtainable from field observations.

Life span must be inferred from growth ring analyses (a poor indicator in the Washington intertidal) 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.

To obtain relative shell weight data for the two species, twenty-five individuals of each species were collected from the zone where both species overlap at Strawberry Island, Tatoosh (tidal height=2.9 m). 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.

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

In order to estimate quantitatively the reproductive status of these populations at various times during the yearly cycle, I used a GONAD INDEX (G.I.) which is a function of gonad weight and body length:

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

Because the weight of mussel tissue (both somatic and gonadal) increases as a cubic function of the length (Fig. 1), 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. 1 is 4.99 and is described by the fitted exponential curve of *gonad weight*, with the formula $W = 0.5 e^{0.51}$ (coefficient of determination, $r^2 = 0.89$), where W = weight (g) and l = length (mm). Final G.I. values for each sample date in the Results section consist of an average for all sizes. A check on the accuracy of this
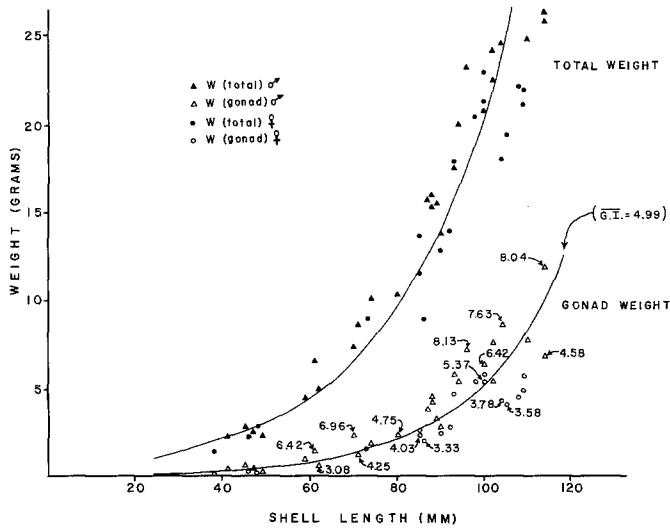
Fig. 1. Relationship between total body weight and gonad weight versus shell length in *M. californianus* for a typical sample from the low intertidal on 10 August 1976. The numbers on the Gonad Weight curve represent calculated *Gonad Index* values using the formula derived in the text. The mathematically fitted exponential curves represent the mean total body weight and mean gonad weight for each respective shell length
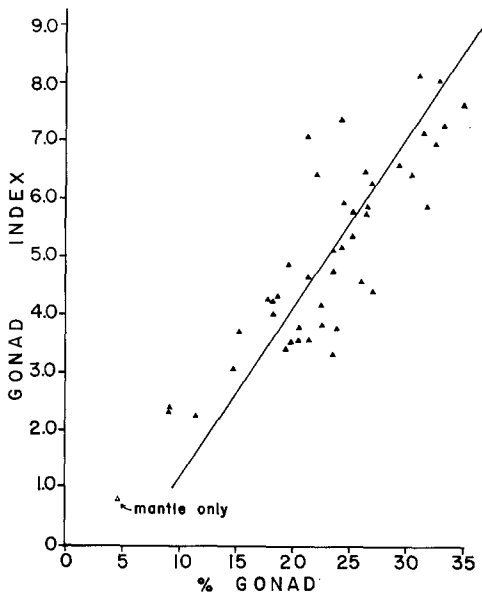

Fig. 2. Comparison of actual gonad tissue (as a percentage of total body weight) with the calculated Gonad Index derived in the text. $r = 0.86$. Data taken from Fig. 1

Gonad Index as an estimator of the proportion of body tissue invested into reproduction was done on the data in Fig. 1. The comparison is presented graphically in Fig. 2 and shows a close relationship between the calculated G.I. and the renal percentage of gonad material 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* (Gabbott and Bayne 1973; Thompson et al. 1974; Gabbott 1976). However, Elvin (1974) has shown these reserves to be minimal in *M. californanus*, mainly because it lives in such
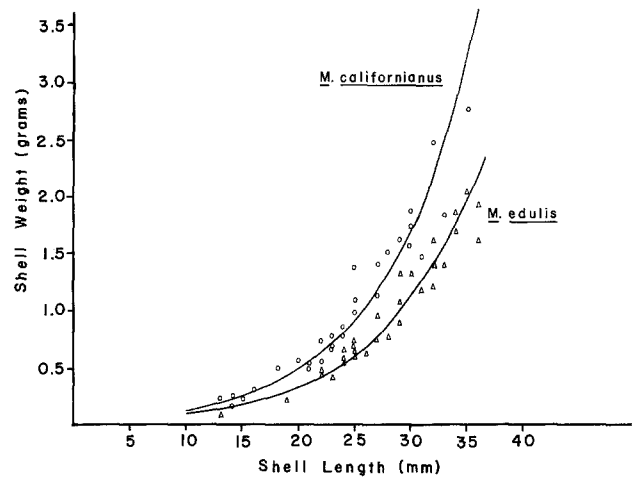

Fig. 3. Shell weight versus length for *M. edulis* and *M. californianus* from the high intertidal at Tatoosh Island, Washington. Curves are fit mathematically. ANCOVA shows a significant difference between the two species at $p < 0.001$ ($F = 70$, $df = 1,46$)

a productive environment. I am assuming the same to be true for *M. edulis* on the Washington coast.

Results

The major factors influencing life history strategies were analyzed for the two mussels, *Mytilus edulis* and *Mytilus californianus*. The following parameters were considered.

1) Size
2) Growth Rate
3) Age at First Reproduction
4) Life Span
5) Mode of Reproduction
6) Niche and Habitat Differences

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 and 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 (Suchanek 1978). Although subtidal *M. californianus* may reach 250 mm (Paine 1976b), they are smaller in the intertidal and may only attain a length of about 200 mm.

Shell thickness and durability may also give *M. californianus* a competitive and/or anti-predatory edge over *M. edulis*. Figure 3 shows that shells of *M. californianus* are on the average significantly heavier than those of comparable sized *M. edulis*. Analysis of co-variance on log-log transformed variables yields a significant difference at $p < 0.001$. Harger (1967) reported similar results from California and 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 (Suchanek 1979; also Figs. 3
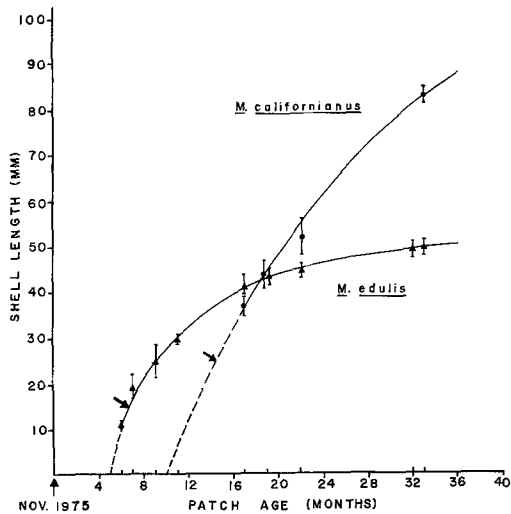
Fig. 4. Growth rates of *M. edulis* and *M. californianus* in a patch (ca. 50 m²) from the low to mid intertidal on Strawberry Island (Tatoosh), Washington. Data points represent shell lengths of the ten largest individuals found in the patch on each sampling date (±S.E.). Curves were fitted by eye. Dashed lines to the abscissa indicate estimated times of settlement and initial growth in the patch. Arrows indicate the first potential reproductive maturation size (and age) for each species (i.e. – first visible storage of gametic products in the mantle tissue). Data on size at first reproduction obtained by direct observation of gametes – see section on Age at First Reproduction

and 4) and strength may be an important factor in its dominance over *M. edulis,* especially if *M. californianus* can crush its congener. However, the shell of *M. californianus* may play another important role as an anti-predatory mechanism against drilling gastropods of the genus *Thais.* The preference of *Thais* spp. *M. edulis* over *M. californianus* has been documented (Harger 1972b; Suchanek 1978) and will be discussed further under the section Niche and Habitat Differences.

Growth Rates

Growth rates for these two mytilids are dependent on tidal height and on the amount of available food (Coe and Fox 1942; Rao 1953, 1954; Dehnel 1956), but differ between the two species. Under continual submersion, *M. edulis* has the potential to exceed 80 mm within 9 months (an average growth rate of 9 mm/mo.; Reish 1964).

The relative growth rates of the two *Mytilus* species are shown in Fig. 4. These data were taken from a large patch in the mid-to-low 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 back to the abscissa represent estimated times of settlement for both species. No *M. californianus* were identified in situ on 21 October 1976 for if they were present, they were virtually indistinguishable from *M. edulis* at that size (4–5 mm) in such a mixed species group.

In the low intertidal at Tatoosh Island, the growth rate of *M. edulis* is initially rapid (ranging from 8–12 mm/mo.), but then decreases as its length approaches 55–60 mm (Fig. 4), agreeing with rates published by Graham and Gay (1945) and Stubbings (1954). At 40 mm, *M. edulis* is surpassed in growth rate and age-specific size by its congener. These findings are consistent with the projected growth curves of Harger (1970a).

M. californianus usually settles later (in cleared intertidal patches) and grows continuously but more slowly (maximum

growth rate 2–5 mm/mo., Coe and 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. 4 is initially ca 5.0 mm/mo. (extrapolated) and at the end of 33 months declines to ca 2.0 mm/mo. These figures are consistent with Coe and 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

The age at first potential reproduction was determined by direct measurement of gonadal weights for various sized mussels (see methods) and inference of mussel age from a) their occurrence in known-age patches, and b) tidal-height-specific lengths. Figure 4 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, in the low intertidal zone, 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 which has been used on bivalve species and which measures differences in the relative proportions of organic material (conchiolin) and calcium carbonate (aragonite or calcite) may not reflect yearly marks or may yield spurious results (Barker 1970; Craig and Hallam 1963; Pannella and 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 or 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, 1964; Craig and Hallam 1963; Barker 1970) or may be abraded beyond recognition (Seed 1973).

The most important aspect 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 have been 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 (Suchanek 1978), 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.). Towards the southern extent of its range, where again *M. califor-*
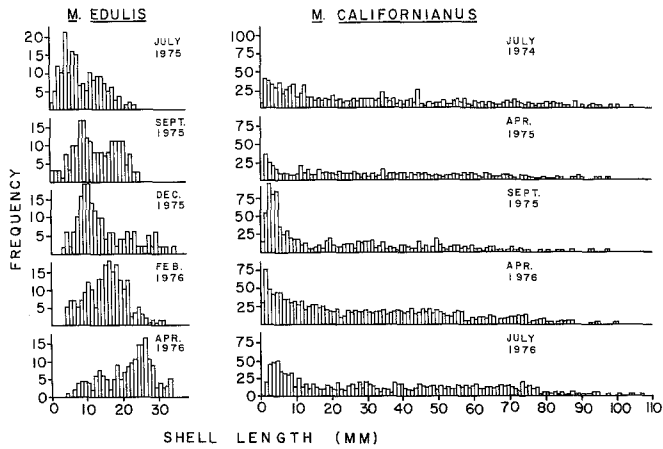
The actual life span of *M. californianus* is considerably longer than that of *M. edulis*. *M. californianus* outcompetes its congener in the long run, usually persisting up to 7–20 years minimum in the intertidal (data based on recovery rates for disturbed mussel beds of known age and extrapolated growth rate data), very possibly reaching 50–100 years of age in some very low intertidal or deep subtidal regions which receive less disturbance.

Mode of Reproduction

Figure 5 shows a comparison of size-frequency distributions over time for both species from the Washington outer coast. 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 continuous, rather even size-frequency distribution further implying a slow, but continuous, recruitment of individuals over time. These samples were purposefully collected from an apparently monospecific stand for each species and it was assumed that the difficult-to-identify individuals (< 5 mm) belonged to that species comprising the stand. These data support other accounts of size-frequency distributions of the two mussel species (for *M. edulis*, Craig and Hallam 1963; Seed 1973; for *M. californianus*, Ackerman 1971), but differ from those of Harger (1967) who found a bimodal size distribution for the former species and Paine (1976a) who found a bimodal distribution for the latter. Paine suggested that for *M. californianus* this could be caused by the limited period of establishment of the original matrix of 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. 6. Plankton-
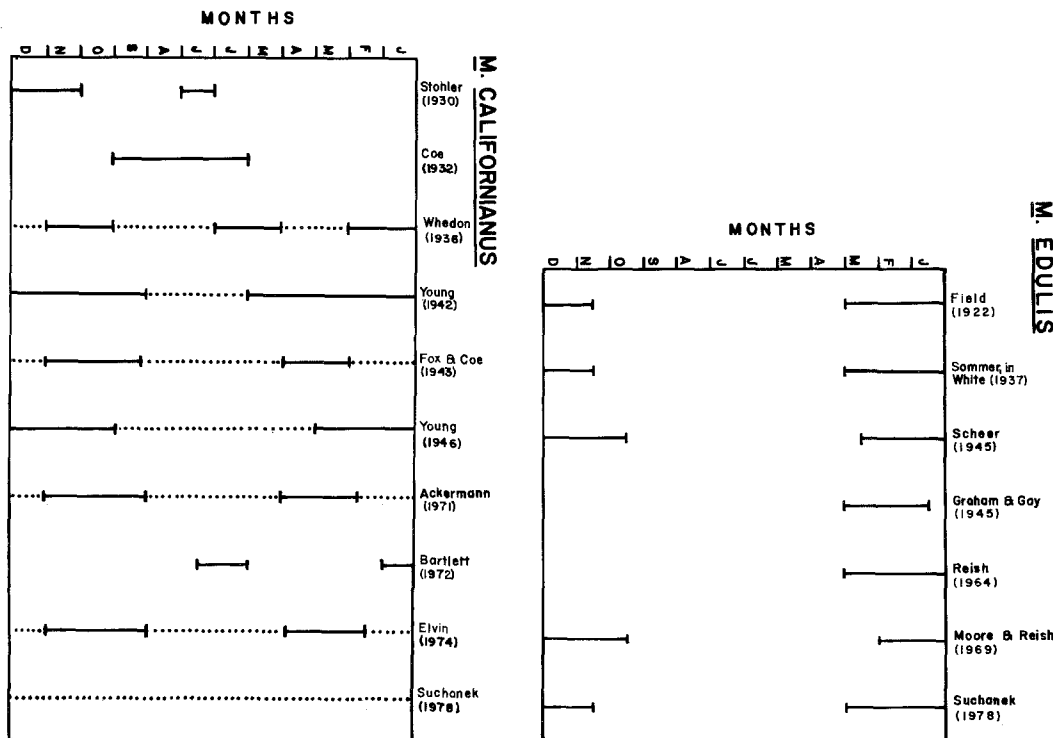

Fig. 5. Changes in size-frequency distributions for monospecific stands of *M. edulis* (mid-intertidal zone, Shi-Shi) and *M. californianus* (mid-intertidal zone, Tatoosh) over time. Samples were collected destructively for each species, each within a 10 m² area. Note different scales on ordinate axes

nianus does not compete for space (on the exposed outer coast of southern Chile), intertidal *M. edulis* reach 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; here it 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).

Fig. 6. Review of literature on spawning dates for *M. edulis* and *M. californianus*. Solid lines indicate major spawns. Dotted lines indicate sporadic or low level continuous spawning

ic existence for veliger larvae was assumed to be 2–4 weeks (Bayne 1964; Seed 1969a, 1976), and the original data for Fig. 6 were 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 *M. edulis*, which depends on seasonally available settling sites, spawns primarily in the winter months. This allows larvae to settle into newly created patches of cleared space in the *M. californianus* zone in late winter and early spring (Suchanek 1978). 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 to Washington in patchy disturbance features. These lavae which have settled in winter patches then have the potential to provide colonizers for any patches being formed in late spring or even summer, but it is more likely that the majority of plantigrades are derived from those larger *M. edulis* which have survived at least one year in the low intertidal and are stimulated to spawn the following winter.

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 by local selection pressures such as disturbance of the physical environment, predation, or optimal conditions for planktonic larval survival. 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*.

Selection pressures on spawning periods operative on the exposed outer coast of Washington most likely influence only those populations actually located on the coast and have little influence on the "inner" waters (i.e. – the Strait of Juan de Fuca and especially Puget Sound and Washington Sound). Because there is a net outflow of surface waters (i.e. – in the upper 64 m of the water column) from Puget Sound out through the Strait of Juan de Fuca (Barnes and 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 two months duration (reaching the maximum period of larval life for *M. edulis*). Therefore, even if some larvae from the inner Sound region were to travel in this water mass, dispersion would be so great that they would make a very 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 accomplish further larval dispersal in subsequent years.

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 (Suchanek 1978). This evidence suggests that, for both species, available settling sites may be a strong selective force in determining spawning periods and intensity.

M. edulis clearly shows 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. 7A demonstrates the yearly fluctuations of a different gonad index for *M. edulis* (redrawn from Seed, 1975) over a three
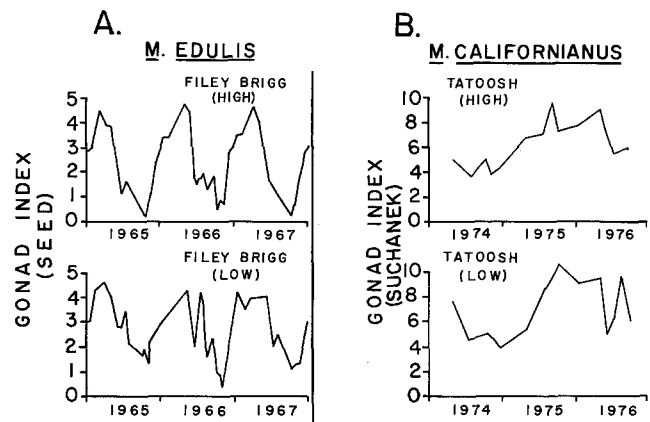

Fig. 7. Comparison of gonad development in *M. edulis* (taken from Seed, 1975 in England: see text for Seed's index) and *M. californianus* from Tatoosh Island, from high and low intertidal sites over three year periods

year period of Filey Brigg, England. Seed's index represents a visual determination of the state of gonad development and gametogenesis from 0 (a reproductively inactive or "spawned out" mussel) to 5 (a mussel with fully ripe gonads). It shows the distinct seasonal nature of gonad development, and that gametic products of this species are nearly or completely spent at the end of a spawning season, only to build up and crash again the following season. Although there are obvious inherent problems associated with comparing Seed's results (from a distant location) with events happening in Washington, the data of Fig. 6 indicate strongly that a similar type of seasonal cycle exists for *M. edulis* on the west coast of North America.

In contrast, gonad development in *M. californianus* is not predictable. Fig. 7B shows the yearly cycle of gonad development in *M. californianus* from Tatoosh Is. as calculated by the gonad index derived above (see Fig. 1). No consistent seasonal trends can be discerned. Ackerman (1971), working in California, and Elvin (1974), in Oregon, also found a relatively high, constant gonad index but with some noticeable peaks in spring and autumn. This is also consistent with the cumulative data of Fig. 6, 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.

Niche and Habitat Differences

M. edulis is well-known as a very tolerant species, capable of withstanding severe heat, cold, low salinity and desiccation (Seed 1976). In Washington, its upper intertidal limit is physiologically controlled by heat and desiccation stress during summer months (Suchanek 1978) and exceeds the limit of *M. californianus*. *M. edulis'* lower limit is set primarily by competitive exclusion by *M. californianus* except in patches of cleared space in the *M. californianus* zone where it gains a temporary reprieve. I have found no evidence of *M. edulis* being crushed by *M. californianus* (e.g. Harger 1967) nor have I found *M. edulis* present or settling into the matrix of *M. californianus* beds, except in the zone of overlap between the two species (Suchanek 1978). As the proportion of *M. californianus* increases in natural patches, the settlement of *M. edulis* appears to decline dramatically. Competitive exclusion seems to occur but the mechanism is unclear. It is possible that juvenile *M. edulis* have a greater susceptibility

to predation or that *M. californianus* produces an allelo-chemical defense against settling *M. edulis*, but neither hypothesis has been tested. In any case, within the zone of sympatry, *M. edulis* is clearly a competitively inferior fugitive species which rarely attains a large size, produces a relatively thin shell (which is more easily drilled by predators), and spawns out completely each season.

Nearly throughout its range, *M. californianus* is the dominant competitor for intertidal space; it attains a larger size and has better predator defenses than *M. edulis*. It avoids predation in two ways. First, by producing an extra inner shell layer, *M. californianus* develops a more robust shell than *M. edulis* and is consequently a less preferred prey item for predatory gastropods (Suchanek 1978). Second, *M. californianus'* size is considerably larger than *M. edulis,* enabling it to exceed the predatory capabilities of the sea star *Pisaster ochraceus* (Paine 1976a).

While it is clear that *M. edulis* is the inferior competitor, in those areas in which *M. californianus* does not occur (for physiological or other reasons), *M. edulis* becomes the dominant space occupier, apparently growing much older and 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* over 15.6 feet (4.8 m) of vertical height including intertidal and subtidal areas. In the southern hemisphere, on the exposed shores of Chiloe in southern Chile, and in Inner Puget Sound waters where *M. californianus* does not exist similar extensions occur (pers. obs.).

Features of this replacement phenomenon by a dominant competitor seem to occur on other continents as well. In Chile, the purple mussel, *Perumytilus purpuratus* (Lamarck) exists in sympatry with *M. edulis. P. purpuratus* is a heavily ribbed mytilid with a nearly complementary range along the coast of South America to that of *M. californianus* (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 in New Zealand. Here, *M. edulis* is again small, scarce, and insignificant (Stephenson and Stephenson 1972), and the larger competitive dominant, *Perna canaliculus* occupies a lower, broader intertidal band (Paine 1971; 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 and Levins 1964, 1967). These two species of mussels have apportioned bare rock substrata in the rocky intertidal on both a spatial and a temporal basis, and exhibit widely different life history and reproductive strategies thereby facilitating coexistence. These differences 1) may have developed as the result of an evolutionary divergence by *M. edulis* away from the strategies of its superior competitor (*M. californianus*), 2) could be "pre-adapted" traits fostering coexistence, or 3) may be a direct response to regional environmental factors, irrespective of a sympatric competitor. No in-depth studies were performed on differences in the genetics or annual reproductive cycles of *M. edulis* in Washington (the zone of sympatry with *M. californianus*) and Alaska (relative to this discussion, an effective zone of allopatry). Substantial differences, however, do occur in size, life span, and habitats between these two species in and out of sympatry, suggesting that these differences may either be "pre-

adapted" or be the result of an evolutionary divergence. It seems impossible at this time to distinguish between these two possibilities.

In Washington, 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 size and lower production of gametes. 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 inter-specific 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. 7), 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 intertidal 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 $= 40.4 \pm 1.0$ 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 $8,132 \pm 2,072/m^2$, whereas those in the lower intertidal patches only reach $3,872 \pm 980/m^2$. 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 the lower refuge populations contribute considerably more toward maintaining overall population levels than the thin zone of small sized individuals found in the upper intertidal.

In the lower intertidal 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 and Paine 1974). The timing of reproduction in *M. edulis* along western North America appears to be cued to this predictable disturbance, and 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 and habitat differences for *M. edulis* seem to be 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.

Williams (1966a, b) has claimed that a high per-season reproductive effort should characterize small, short-lived 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 ef-

fort 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 mechanism in favor of rapid growth to reproductive size and a substantial early reproductive effort. *M. californianus* lies at the opposite end of this spectrum.

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