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**THE MUSSEL MYTILUS:  
ECOLOGY, PHYSIOLOGY,  
GENETICS AND CULTURE**



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# THE MUSSEL MYTILUS: ECOLOGY, PHYSIOLOGY, GENETICS AND CULTURE

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## Chapter 4

### POPULATION AND COMMUNITY ECOLOGY OF MYTILUS

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#### INTRODUCTION

The Mytilidae is a family of considerable antiquity dating back to the Devonian era (Moore, 1983) and includes many important byssally attached genera such as *Choromytilus*, *Perna*, *Modiolus* and *Aulacomya*, as well as *Mytilus* itself. The development of byssal attachment threads by adult mussels, probably as a result of their neotenus retention by the byssate postlarval stages of some earlier burrowing taxa, coupled with the associated evolution of a heteromyarian wedge-shaped shell (the 'typical' mussel form) has enabled mytilid mussels to successfully exploit hard or semiconsolidated substrata (Yonge, 1976; Seed, 1990, and Chapter 2) and to dominate rocky shore habitats on all continents. Their worldwide success as dominant space occupiers, however, is perhaps most pronounced on flat or gently shelving wave-exposed shores in temperate latitudes (Lewis, 1964; Suchanek, 1985).

Mussels belonging to the genus *Mytilus* are widely distributed throughout the cooler waters of both the northern and southern hemispheres and have proved to be model organisms for various physiological, biochemical and genetic investigations (Chapters 5, 6 and 7). They are also important economically as food and fouling organisms (Chapter 10) and as biomonitors of coastal water quality (Chapters 8 and 9). In historic and prehistoric times *Mytilus* shells were used extensively for tools by native North American Indians as well as by the Pilgrim settlers (Miller, 1980). With few exceptions, in most exposed or moderately wave-exposed locations in temperate zone habitats *Mytilus* spp. form the foundation for a variety of diverse hard-shore communities. In this chapter we shall briefly examine selected aspects of the population and community ecology of mussels belonging to this successful and widely distributed genus. Despite recent changes in the taxonomy and known distribution patterns of *Mytilus* worldwide (McDonald and Koehn, 1988; McDonald et al., 1991; see also Chapters 1 and 7) we have retained the specific names as used by authors in the primary citations in order to avoid any unnecessary confusion.

## DISTRIBUTIONAL AND ZONATIONAL PATTERNS

On a worldwide basis, mussels of the family Mytilidae form the foundation (both in terms of strict percent cover, as well as organic production) for most exposed rocky shore communities within the temperate zone (Suchanek, 1985). The genus *Mytilus* is the most diverse and widely distributed of the Mytilidae, its representatives typically occupying significant space on intertidal sites on most major continents. A relatively small-sized member of the family that has received most attention, *Mytilus edulis* has the widest distributional patterns of the genus, and is typically quite eurytopic, with abilities to withstand wide fluctuations in salinity, desiccation, temperature and oxygen tension. As a result it often occupies, or has the capability of occupying, a broad variety of microhabitats. This allows it to extend its zonal range from the high intertidal to subtidal regions, its salinity range from estuaries to fully oceanic sites, and its climatic regime from mild, subtropical locations to ice-scoured and frequently frozen habitats. Other members of the genus (e.g. *Mytilus californianus* and *Mytilus galloprovincialis*), are usually more restricted to narrower bands and sites controlled by both physical and biological factors.

Although sometimes found in abundance subtidally (Newcombe, 1935; Paine, 1976b; Tursi et al., 1985), *Mytilus* species typically occur in intertidal habitats; this limited distribution appears mostly controlled by biological factors of predation and competition, rather than an inability to survive the conditions found in subtidal habitats. At Tatoosh Island, Washington, U.S.A., when given proper refuges from seastar predation by *Pisaster ochraceus*, *M. edulis* settles and survives in relatively high frequency on low intertidal and/or subtidal substrata, such as the frond crotches of brown algae (e.g. *Lessoniopsis*), with densities ranging from 5–80 mussels plant<sup>-1</sup> (Suchanek, unpublished results). *M. californianus*, a typically dominant intertidal mussel in Washington, is usually limited by *Pisaster* predation in the low intertidal (Paine 1974, 1976a), but can be found occupying vast areas subtidally to depths of nearly 30m on seamounts (Scagel, 1970; Chan, 1973; Paine 1976b; Suchanek, unpublished results). In these unique habitats, *Pisaster* is in extremely low abundance (ca. 0–0.017m<sup>-2</sup>), resulting in *M. californianus* cover from ca. 28–100% (Paine, 1976b).

Although suitable for the development of healthy mussel beds, many moderately exposed habitats in Europe, as well as North America, display a distinct absence of dense *M. edulis* populations, but the reasons behind this phenomenon are likely to have diverse origins. One possible explanation is provided from results of research at Lough Ine, South-west Ireland (Ebling et al., 1964), where the absence of mussels from areas of moderate exposure is apparently due to intense crab predation. In contrast, *Mytilus* in sheltered areas experience a size-refuge from predation, and the absence of crabs in exposed habitats provides a spatial refuge. Within the San Juan Archipelago,

Washington state, U.S.A., *M. edulis* is also scarce in habitats of intermediate exposure, probably because of log damage as well as dogwhelk predation (Dayton, 1971).

Subtidal populations often occur on seamounts (Paine, 1976b), dock pilings (Suchanek, 1978) and offshore oil platforms (Page and Hubbard, 1987). Typically, the unique aspects of these populations include the continuous growth and lack of predators, allowing individual *Mytilus* to attain large sizes, often in relatively short periods of time. Subtidal *Mytilus* aggregations that reach 120cm in thickness have been reported from oil platforms off the coast of California (Simpson, 1977). Growth rates for these continually submerged individuals have also been documented as some of the highest on record, yielding ca. 50mm mussels in 6–8mo (Page and Hubbard, 1987).

## Factors Limiting Upper and Lower Limits

### Upper limits

Upper distributional limits for *Mytilus* spp. are typically rather constant over long periods of time (see Suchanek, 1985 for review and data for *M. edulis* and *M. californianus*). Physiological intolerance to temperature extremes and desiccation represent the most important factors in the determination of upper limits for *Mytilus* populations in rocky intertidal sites. *M. edulis* is known to withstand extreme cold and even freezing (Williams, 1970; Aarset, 1982). The presence of nucleating agents in the haemolymph during winter probably insures that freezing (which occurs in extracellular compartments; Kanwisher, 1959, 1966) takes place at a few degrees below zero, thereby preventing intracellular freezing and subsequent injury (Aunaas, 1982; Aunaas et al., 1988). In most temperate zone habitats *M. edulis* is only subjected to lethal low temperatures periodically, if at all. However, in some locations such as the St. Lawrence Estuary, temperatures typically reach –30 to –35°C each winter (Bourget, 1983). Williams (1970) has shown that *M. edulis* can survive even after tissue temperatures declined to –10°C. Furthermore, in 24h laboratory tests using large *M. edulis* (>3cm), Bourget (1983) found that the median lethal temperature (MLT) was as low as –16°C, whereas for juveniles (<1.5cm), the MLT was considerably higher (–12.5°C). If exposed for only 16h, comparably sized *M. edulis* had minimum MLTs of –20°C and –12.5°C respectively. However, probably of more relevance to indigenous *M. edulis* populations are cyclic exposures to 'sublethal' temperatures (e.g. –8°C every 12.4h), with significant damage, which may lead to death even after three to four such cyclic exposures (Bourget, 1983).

*M. californianus* is much more stenothermal than *M. edulis* and appears unable to tolerate freezing conditions. Suchanek (1985) reported a December 1983 winter freeze

at Tatoosh Island that caused substantial mussel mortality and significantly lowered the upper distributional limit of *M. californianus*. Five years later (January 1989) another significant freeze has lowered the upper limit of the *M. californianus* zone by ca. 0.27 vertical meters, as measured at a nearby mainland site, Shi-Shi (Suchanek, unpublished data). In the upper 1.65m of this zone, *M. californianus* cover has been reduced from nearly 90% to ca. 25%, whereas in the remaining 1.31m, mussel cover has been reduced to ca. 50%. In fact, freezing is the most likely factor in preventing *M. californianus* from dominating most intertidal sites north of Sitka, Alaska, where *M. edulis* replaces it as the dominant space occupier. As a result, *M. californianus* is usually restricted to intertidal pools, crevices, or subtidal habitats from Sitka northward to the Aleutian Islands. Paine (1986) has shown that the upper distributional limits of both *M. edulis* and *M. californianus* do not appear to be affected by El Niño episodes over a 14-year period. However, Paine did find that the intensity of mussel bed matrix disruption by storm-related phenomena did show temporal correlation with El Niño periodicity, but the ultimate causes of such events are speculative (see below for other disturbance data).

The detrimental effects of extreme high temperatures on setting upper limits for *Mytilus* spp. has also been well-documented. For nearly all mytilid species studied so far, high temperatures usually interact additively or synergistically with desiccation to control upper zonal limits. Occasional, sudden and massive mortalities at the upper limit of intertidal mussel bands are often correlated with prolonged periods of unusually high temperatures and associated desiccation stress (Suchanek, 1978, 1985; Tsuchiya, 1983). For instance, in northern Japan an extreme period of hot days (air temperature ca. 34°C, resulting in mussel tissue temperatures >40°C) caused mortality for about 50% of intertidal *M. edulis* within one hour, with mortality occurring over approximately the upper 75% of the intertidal range for *M. edulis* (Tsuchiya, 1983). Interestingly, another mussel, *Septifer (Mytilisepta) virgatus*, living at the same site above the *M. edulis* zone, suffered only limited (16.8%) mortality.

In consistently warmer climates, behavioural activities probably modify the abilities of some *Mytilus* species to circumvent the effects of desiccation and/or high temperature. British *M. edulis* have an upper sustained thermal tolerance limit of about 29°C (Read and Cumming, 1967; Almada-Villela et al., 1982), but can probably withstand somewhat higher temperatures for short periods of time (Cawthorne, 1979). European *M. edulis* very likely never experience temperatures greater than about 25°C, but the Indian mussel, *Perna* (formerly *Mytilus*) *viridis*, is predictably exposed to annual mean temperatures of ca. 27.3°C year-round, with deviations of only about 1.4°C (Davenport, 1983). Both species close their valves in response to aerial exposure (as well as to lowered salinity), but *P. viridis* also first takes a bubble of air into the mantle cavity, which probably increases its tolerance to desiccation in such high temperature environments, especially in high intertidal sites (Davenport, 1983). If

similar behavioural differences exist between *Mytilus* and *Septifer* (see above), this may also help to explain their significant differences in survivability at high temperatures.

Finally, recruitment or movement into cracks, crevices or pools obviously affords much better protection from the physical effects of both temperature and desiccation, although those habitats can also protect mussels from the influence of storm waves and wave-driven logs. Observations on the effect of such microhabitats in increasing survival in mussel populations have been reviewed in Suchanek (1985).

In some cases, competition with other fauna or flora can also influence upper distributional patterns for *Mytilus* spp. For example, in very exposed rocky intertidal sites along the U.S. west coast, individuals of *M. californianus*, at the upper limit of their intertidal distribution, appear to be negatively affected by the sea palm *Postelsia palmaeformis*. During a typical growth season at Bodega Bay, California, about 5% or more of the *Postelsia* population is overgrowing *Mytilus* at the upper tidal range (Suchanek, unpublished results). Although the mechanisms involved are not completely clear, *Postelsia* could adversely affect *M. californianus* by several potential mechanisms: (1) overgrowth of valves and feeding apertures by sea palm holdfasts, with subsequent reduction of food intake for *Mytilus*, resulting in elimination of the mussels, (2) overgrowth of the mussels by holdfasts with subsequent dislodgement during storms, again resulting in elimination of the mussels or (3), proprietary settlement by *Postelsia* in high disturbance gaps, preventing *Mytilus* from attaining space in those intertidal sites (Suchanek, unpublished results), although Paine (1979, 1984) states that mussels eventually reclaim this lost space.

#### Lower limits

Lower zonal limits for many sessile fauna, including mussels, have been shown to be under strong influence from biological factors, especially predators (Connell, 1972; Paine, 1974). For over five decades seastars have been recognized as the most important predators establishing *Mytilus* lower limits (Newcombe, 1935; Kitching et al., 1959; Paris, 1960; Ebling et al., 1964; Kitching and Ebling, 1967; Paine, 1974; Menge, 1983; and see review by Suchanek, 1985). On the east coast of England predatory seastars (*Asterias rubens*) and dogwhelks (*Nucella lapillus*) control the lower limits of *M. edulis* beds, essentially eliminating these mussels from the lower intertidal zone (Seed, 1969b). In Ireland, crabs (*Carcinus* and *Liocarcinus*), dogwhelks (*Nucella*) and seastars (*Marthasterias*) most likely control mussel zonation (Kitching and Ebling, 1967). Along New England shores strong evidence shows that the lower limit of *M. edulis* is controlled by a suite of consumers: *Nucella*, two seastars of the genus *Asterias*, and three crabs (*Carcinus* sp. and *Cancer* spp.) (Menge, 1983 and see Suchanek, 1985). At Shi-Shi in Washington state, U.S.A. *M. edulis* settles



Fig. 4.1. Photograph from Shi-Shi, Washington state, North America, illustrating *Pisaster* predation on *Mytilus* beds. Central core bed is composed of *Mytilus californianus* (central left and fouled with light coloured barnacles, mostly *Semibalanus cariosus*), surrounded by a dense ring of *Mytilus edulis*. After locating these recently recruited *M. edulis*, the *Pisaster* herd at the perimeter consumed over 90% of the bed within one week. The central *M. californianus* core is relatively protected from such predation by virtue of its location on the highest portion of an intertidal mound.

unpredictably in patches of open space, typically just below the intertidal distribution of *M. californianus* (Suchanek, unpublished results). These individuals grow quickly to reproductive size but are soon 'discovered' and consumed by 'herds' of roaming *Pisaster ochraceus* seastars, which can eliminate large beds of *M. edulis* within a few days (Fig. 4.1). Physiological intolerance to desiccation is believed to be the most likely factor that limits the upshore extension of most predators controlling the lower limits of *Mytilus* beds. As such, the upper intertidal zones represent an effective refuge for *Mytilus*, although this incurs costs of lowered fitness for these mussels in terms of reduced reproductive output (see Suchanek, 1981).

The lower limits of other *Mytilus* species appear to be controlled in much the same way as that of *M. edulis*. In an elegant removal experiment, Paine (1974) showed causality by systematically removing the predatory seastar *Pisaster* from a stretch of Tatoosh Island shoreline in Washington state, which resulted in a downward vertical extension of the *M. californianus* band by an average of 0.84m. In other experimental removals, Paine (1971) working with the seastar *Stichaster* in New Zealand, and Paine et al. (1985) working with the seastar *Heliaster* in Chile, showed similar trends in altering the lower limits of the indigenous mussels *Perna* and *Perumytilus* respectively. Typically, when seastar predators are then allowed to re-enter the

system, the lower limit returns to the previous state. However, if the mussels are able to grow beyond the size which seastars are capable of consuming (Paine, 1976a; Paine et al., 1985; and see p.128–132 on size-limited predation), an altered state in which mussels exist below their typical lower limit may persist for up to 10 to 30 years for *Mytilus* and *Perna* respectively. A removal of *Pisaster* over a six and a half year period from a region in central California, where sea otters occur, did not result in the predicted lowering of the mussel zone, and in some transects resulted in an upward movement of the mussel zone (VanBlaricom, 1988), although other factors such as variable recruitment may be responsible for these inconsistent results.

Physical factors also occasionally fix lower limits to mussel zonation patterns. In California (Cimberg, 1975; Littler et al., 1983) sand burial periodically can limit the lower distribution of *M. californianus*, and Daly and Mathieson (1977) report similar results for *M. edulis* populations in New Hampshire, U.S.A.

Competition from mussels or other sessile organisms clearly sets the lower limits for *Mytilus* in at least some sites. Along the west coast of North America, *M. californianus* dominates *M. edulis* in most exposed rocky intertidal habitats (Suchanek, 1978, 1981). Whether this effect is mediated by the 'brute force' of crushing its congener (as suggested by Harger, 1972), or some other mechanism, is still unclear. *M. edulis* can certainly withstand the rigours of extremely wave-battered shores, including the maintenance of byssal thread attachments under the most high-energy conditions, since it occupies a predictable band above the *M. californianus* zone (Suchanek, 1978). In addition, it temporarily occupies disturbance gaps within the *M. californianus* zone, and is commonly found in the holdfasts and stipe crotches of the brown alga *Lessoniopsis*, well below the *M. californianus* zone. In Washington, as disturbance gaps heal, *M. edulis* is eventually replaced by *M. californianus*. In Alaska, however, where *M. californianus* is eliminated from most intertidal sites by freezing, *M. edulis* is free to dominate the majority of intertidal space at tidal heights more typical of *M. californianus* from more southerly locations. The lower limits of *M. edulis* in Alaska are also determined by dogwhelk and seastar predation (see above), but where predators are eliminated (e.g. sites near glacial melt waters, where salinity is extremely low as in Glacier Bay, Alaska), *M. edulis* dominates intertidal and subtidal space, with a vertical extent of 5.5m or more (Suchanek, unpublished results).

It should be noted that in all of the studies discussed above on similarities and differences in competitive abilities, physiological adaptations, and distributions of '*M. edulis*' at various geographic locations along the west coast of North America, the assumption is that the small blue or blue-black *M. edulis*-looking morphotype, identified in the field by previous investigators, is indeed *M. edulis*. New information on the systematics of *Mytilus* (McDonald et al., 1991; see also Chapters 1 and 7) may be especially critical in understanding unusual differences in both distribution and competitive abilities between mussels from different geographic sites.

For instance, Harger (1972) reports that *M. edulis* is a species adapted to calm waters and protected embayments and is not found on the exposed outer coast of California, where the larger *M. californianus* is dominant. Suchanek (1978, 1985), however, reported that *M. edulis* maintains a predictably discrete and dominant zone in extremely wave-exposed rocky shores in the high intertidal zone in Washington, and usually in the mid to high intertidal zone in Alaska. Are these contradictory reports indicative of different ecological niches involving habitat preferences, physiological tolerances and/or competitive abilities for two or more species of *Mytilus*? Considerably more ecological, physiological and genetic data are needed before we can answer these questions.

How or whether we must now alter our current interpretations of species-species interactions involving a universal '*M. edulis*' from these locations along the Pacific coast of North America is uncertain. More understanding of the identity of the *M. edulis* morphotypes and genotypes is needed before we can truly be confident that the similarities or differences we report are real and meaningful characteristics attributed to a single species. See Chapters 1 and 7 for a more detailed discussion.

## REPRODUCTION

Most marine organisms have a geographical range over which they survive and a narrower range over which they breed successfully. Investigations of natural reproductive cycles are therefore central, not only to studies of population dynamics, but also to our understanding of biogeography and speciation. In the case of commercial bivalves such as *Mytilus*, which are known to exhibit a significant loss of condition following spawning, they will also indicate when the population can be harvested most effectively. Studies of natural reproductive cycles are most valuable when carried out over several years since the onset and duration of both gametogenesis and spawning in *Mytilus* can exhibit considerable temporal and spatial variation. The reproductive cycle comprises the entire sequence of events from activation of the gonad, through gametogenesis to the release of ripe gametes (= spawning), and the subsequent recession of the gonad. Typically, it can be broadly divided into a reproductive period which starts with the initiation of gametogenesis and culminates in the emission of gametes, and a reproductively quiescent period in which the energy stores required to fuel gametogenesis are accumulated (see Gabbott, 1983). The reproductive period is characterized by one or more gametogenic cycles each of which is followed by the release of gametes when the reproductive follicles become partially or completely emptied. Like many temperate water bivalves, most *Mytilus* populations exhibit a seasonal pattern of reproduction. In some populations, however, mussels may slowly dribble gametes more or less continuously over an

extended part of the year, a pattern more typically associated with populations in less cyclical environments.

## Anatomy and Histology of the Gonad

Apart from a few hermaphrodites the sexes in *Mytilus* are separate and most populations contain approximately equal numbers of males and females (Seed, 1976; Sunila, 1981; Kautsky, 1982a; Brousseau, 1983; Sprung, 1983), although these cannot be distinguished on external characters. The colour of the reproductive tissue of *M. edulis* varies considerably, but typically females are orange coloured while males are creamy-white; the mantle tissues of recently spent mussels are thin and transparent, often with reddish-brown blotches. A simple and convenient colorimetric method for determining the sex of *M. edulis* has recently been described by Jabbar and Davies (1987).

*M. edulis* can become sexually mature in its first year but the size at which this occurs depends largely on local growth rates (Seed, 1976; Sprung, 1983 and references therein). Most gametes are generated within the extensive mantle folds, though small amounts of the reproductive tissue also extend into the visceral mass and mesosoma. Paired gonoducts, which discharge into the mantle cavity on papillae situated between the mesosoma and the inner gill lamellae, lead into five major canals with convoluted walls forming longitudinal ciliated ridges. These lead in turn into a series of smaller canals which have part of their walls of ciliated columnar epithelium. Each of these fine ducts eventually terminates in a genital follicle. Oogonia and spermatogonia are budded off from the germinal epithelium of these follicles. Early oocytes are connected to the epithelium by a broad stalk but this gradually becomes more slender and finally ruptures to leave the mature ova free within the follicular cavity. Spermatogonia give rise, in turn, to concentric bands of spermatocytes, spermatids and spermatozoa, the latter converging towards the centre of the follicles in the form of dense lamellae.

## Methods Used for Assessing the Reproductive Cycle

Several methods have been used to assess the course of the reproductive cycle. These may involve direct observations of spawning in natural or laboratory populations as well as the macro- and microscopic appearance of the gonad throughout the year. Observations of spawning in field populations provide the most reliable evidence of natural spawning though these data may be difficult or impossible to obtain.

Alternatively, the reproductive period can be inferred from the appearance of larvae in the plankton, or the recruitment of juvenile mussels (= spat) to the populations. Data obtained using these indirect methods, however, are generally less reliable since larvae and spat may have been transported by currents over considerable distances from parental stocks which have experienced quite different environmental conditions. However, they can serve as valuable checks on data obtained by more direct methods.

The most reliable and detailed information regarding the annual reproductive cycle is that obtained from histological preparations of mussels sampled at regular intervals throughout the year. Several schemes have been used to classify the reproductive condition in *Mytilus*. While some of these simply rely on the general macroscopic features such as the colour, texture or thickness of the gonad, others are based on microscopic appearance of squashes or thin, stained sections of mantle tissue (Lubet, 1959; Wilson and Seed, 1974; Seed and Brown, 1977; Sunila, 1981; Kautsky, 1982a; Fell and Balsamo, 1985; King et al., 1989). From such preparations various stages in the reproductive cycle (developing, ripe, spawning and spent) can be recognized. Developing and spawning stages are usually further subdivided, thus resulting in several arbitrary stages into which any individual mussel can be assigned. The general reproductive condition of the population can then be assessed by calculating a mean gonad index. This is obtained by multiplying the number of mussels in each stage by the numerical ranking of that stage and dividing the resulting value by the total number of mussels in the sample. Gametogenesis leads to an increase in this index, while a decrease in the index denotes spawning.

One of the major disadvantages with such arbitrary classifications of gonad condition is that they are rather subjective, and do not fully recognize the occurrence of intermediate stages of development; the gonad index is thus a nominal rather than an interval measurement. Moreover, they provide no information on mantle nutritive storage cells. Consequently, some workers (Bayne et al., 1978; Lowe et al., 1982; Newell et al., 1982; Rodhouse et al., 1984a; Hawkins et al., 1985) have preferred to use more quantitative stereological methods. These enable the changes in the volume fractions of different components within the gonad (e.g. gametes, storage cells) throughout the course of gametogenesis to be established from point counts on test grids applied to random thin sections of mantle tissue. Rodhouse et al. (1984a), however, found that there was generally good agreement between the gonad index and gamete volume fraction (i.e. the proportion of mantle tissue that consists of follicles containing developing and ripe gametes) in *M. edulis* from Killary Harbour, western Ireland (Fig. 4.2). Stereology thus offers a simple technique whereby the main events in the reproductive cycle, including periods of energy storage and utilization, can be quantified and related to environmental variables. The technique has also

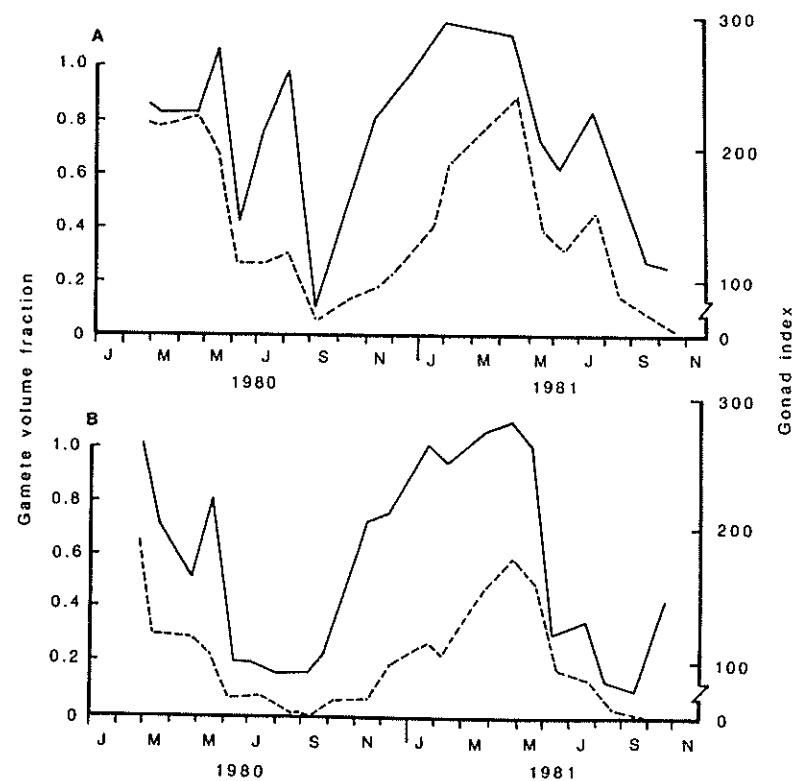


Fig. 4.2. Annual cycle of gamete volume fraction (dashed line) and gonad index (solid line) in (A) cultivated, and (B) wild *Mytilus edulis* from Killary Harbour, Ireland. (After Rodhouse et al., 1984a).

proved useful in quantifying the effects of various pollutants on gonad development in *M. edulis* (see p.452 Chapter 9).

Gonad indices have sometimes been expressed as a function of gonad weight and shell length (Suchanek, 1981). However, some caution is required when using gonad or mantle weights as indicators of gamete production since these tissues also contain variable amounts of stored nutrient reserves such as glycogen. Thompson (1984a) used the DNA content of male mussels to establish the course of the gametogenic cycle in a subarctic population of *M. edulis* in Newfoundland, Canada. Other workers (Wilson and Seed, 1974; Seed, 1975; Wilson, 1988) have assessed reproductive

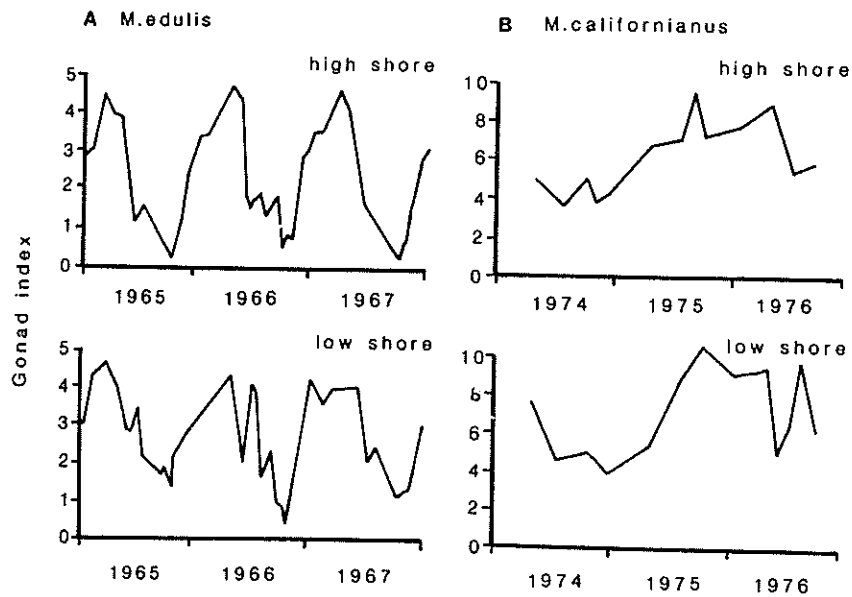


Fig. 4.3. Comparison of gonad development in high and low shore populations of (A) *Mytilus edulis* from Filey Brigg, England and (B) *Mytilus californianus* from Tatoosh Island, Washington state, North America; note the different gonad indices ranging from completely spent (0) to fully ripe (5 and 10 in *M. edulis* and *M. californianus* respectively). (After Seed, 1975 and Suchanek, 1981).

condition in terms of the density and size of oocytes in mantle sections. More recently, image analysis has been used in the case of oysters (Wilson and Simons, 1985), and could also presumably be applied to *Mytilus*.

### The Annual Cycle

Figure 4.3A illustrates the annual fluctuations in the gonad index of *M. edulis* from high and low intertidal sites in North-east England, over a three-year period. The gonad index used varies from 0 (completely spawned out) to 5 (fully ripe).

Redevelopment of the resting gonad commences during October or November and gametogenesis then proceeds throughout the winter so that by early spring the gonads of most mussels are morphologically ripe. During the spring months a period of partial spawning is followed by rapid gametogenesis until by early summer the gonads are again fully ripe. This second period of gametogenic activity is more evident among mussels in the more favourable feeding conditions of the lower intertidal zone. Additional, less intensive, spawnings may occur throughout the summer until by late August or September the gonad index reaches its lowest value, as most mussels enter their reproductively quiescent phase. Throughout late August, September and October the mantle tissue becomes progressively thickened with varying amounts of nutrient reserves, which are used subsequently to fuel gametogenesis throughout winter when food supplies may be more limiting. A significant feature of the annual cycle of the populations described above is the actual duration of the spawning period, with some gamete release apparently occurring throughout much of the year (see also Fell and Balsamo, 1985), albeit with seasonal peaks during the spring and summer. Neither body size nor tidal level appeared to have any marked or consistent effects on the timing of spawning (Seed, 1975; but see Campbell, 1969; Kautsky, 1982a). Male mussels, however, were generally at a rather more advanced stage of gametogenesis than females at any particular time (Seed, 1969a), possibly because sperm can be produced at a faster rate than ova, which have large yolky reserves. Newell et al. (1982) also noted that male mussels had a higher gamete volume fraction than females during the course of maturation.

Protracted reproductive periods resulting from repeated spawnings, particularly during the spring and summer, have also been reported for natural *M. edulis* populations elsewhere (Wilson and Seed, 1974; Seed and Brown, 1977; Briggs, 1978; Sunila, 1981; Lowe et al., 1982; Brousseau, 1983; Fell and Balsamo, 1985; McKenzie, 1986; King et al., 1989), and appear to be characteristic of many cultivated mussels growing under particularly favourable nutrient conditions (Lutz et al., 1980; Rodhouse et al., 1984a; Zhang, 1984; Wilson, 1987; Wallace, 1990). Other populations, however, may exhibit a single short spawning period lasting only a few weeks (Chipperfield, 1953; Kautsky, 1982a; Newell et al., 1982), suggesting that food is perhaps more limiting at other times of the year.

Bayne (1976) classifies bivalve reproductive strategies according to the relationship between spawning and storage cycles. Conservative species utilize nutrient stores accumulated during the summer and autumn for gametogenesis during the winter, and are thus partially buffered from adverse environmental changes. In opportunistic species, however, gametogenesis is more closely linked with the prevailing food supply, thus enabling them to capitalize on periods when feeding conditions are especially favourable. *M. edulis* is apparently quite flexible and can exhibit both types of strategy (Lowe et al., 1982; Rodhouse et al., 1984a). In some populations it clearly fol-



lows a conservative strategy, spawning in the early spring, thus enabling the developing larvae to exploit the spring phytoplankton bloom, which is so characteristic of coastal waters in temperate latitudes. In many populations, however, the spring spawning is followed by further opportunistic spawnings, which derive from energy resources accumulated concurrently with gametogenesis. Populations grown under particularly favourable culture conditions may be entirely opportunistic in their reproductive strategy (Rodhouse et al., 1984a). Mussels which spawn late in the year, when food supply may be at, or even below, maintenance levels, can be at considerable reproductive risk since winter stress may kill those with insufficient nutrient reserves. Late spawnings are to be anticipated, therefore, only when energy reserves surplus to those required for basal metabolism and necessary gamete production over winter occur. *Mytilus*, therefore, seems to have a remarkable ability to adjust its reproductive strategy according to the prevailing environmental conditions.

In addition to the annual variations in the timing of both gametogenesis and spawning which can occur within any particular mussel population, reproductive cycles in *Mytilus* also vary geographically. The reproductive cycles of several mytilids from various parts of their geographical range are extensively reviewed by Seed (1976) and Suchanek (1985). Marked variations also occur between coexisting populations of different species. Along the west coast of North America, for instance, *M. edulis* spawns over a relatively restricted period during the late autumn or early winter (October to February), whereas in the same region *M. californianus* apparently dribbles gametes continuously throughout the year though never spawning out completely (Fig. 4.3B). These differences seem to be related to other aspects of the life-history strategies of these two closely related mussels (Suchanek, 1981), and are thus probably important in facilitating their continued coexistence in many west coast habitats. Differences have also been reported in the reproductive cycles of coexisting populations of *M. edulis* and *M. galloprovincialis* from South-west England (Seed, 1971; Gardner and Skibinski, 1990).

### Factors Controlling the Reproductive Cycle

Although the reproductive cycle in *Mytilus* has been well-documented, we still have only a partial understanding of the complex interactions between those exogenous (e.g. temperature, food, salinity) and endogenous (e.g. nutrient reserves, hormonal cycles, genotype) factors that determine the initiation and duration of gametogenesis and spawning (Newell et al., 1982; see also Chapter 6). The proximate cues responsible for triggering spawning are probably of only brief duration and may be quite different

from those which control the growth and maturation of gametes, and which will thus operate over a more extended time-scale.

Many attempts have been made to determine the key factor(s) which synchronize the reproductive cycle to the prevailing environmental conditions. Of these, sea temperature, which varies seasonally and latitudinally in a moderately uniform manner, has perhaps received most attention, and the concept of a causal relationship between this factor, reproduction and geographical distribution has become widely established as a general zoogeographical principal. Bayne (1975) described a linear relationship between the rate of gametogenesis in *M. edulis* and the rate of temperature change measured as 'day-degrees' (see p.117); the duration of spawning, by contrast, was more variable and seemed to be related to nutritional status and fecundity. Gamete formation in *Mytilus*, however, is evidently not inhibited by low temperature, since differentiation in some populations can proceed even when the water temperature is close to zero (Kautsky, 1982a; Thompson, 1984a, b).

Reproductive cycles in *Mytilus* vary latitudinally both in terms of their onset and duration, with mussels from the warmer, more southerly, waters of the northern hemisphere generally reproducing earlier in the year than conspecifics further north. Moreover, the cyclical nature of gametogenesis and cycles of storage and utilization of reserves are typically less pronounced in more southerly populations (Gabbott, 1975). In Britain *M. edulis* populations on the west coast reproduce earlier in the year than those on the colder east coast (Seed, 1975), while in South-west England the Mediterranean mussel, *M. galloprovincialis* spawns several weeks later than *M. edulis* when the sea water temperature for that locality is at its maximum (Seed, 1971). Such observations suggest that sea temperature acts as a principle factor in controlling the broader aspects of the annual cycle of *Mytilus*.

In a study of several populations of *M. edulis* along the eastern seaboard of North America, however, Newell et al. (1982) found no discernible latitudinal trends in reproduction. Two populations on Long Island, at the same latitude and experiencing the same temperature regime, exhibited the greatest temporal differences in gametogenesis, with summer reproductive maxima separated by an interval of three months. Newell et al. (1982) attributed these differences to temporal and quantitative variations in the energy content of the available food. Again, working on Long Island, Fell and Balsamo (1985) also concluded that temperature was not a major factor determining the time of the reproductive period in *M. edulis*. Bayne and Worrall (1980) showed that gamete production in *M. edulis* is initiated by a rise in temperature only if sufficient nutrients are available, either as energy reserves or as recently ingested food. Some authors (Lubet and Aloui, 1987) have suggested that a 'temperature window' may exist outside which gametogenesis declines, or does not occur, but inside which the reproductive strategy will depend to a large extent on food availability. This window presumably will vary according to the temperature range

normally experienced by any particular population and to which it will therefore be adapted.

Food abundance certainly appears to be the primary factor controlling gonad growth in *M. edulis* in the Baltic (Kautsky, 1982a). No food storage occurs in these mussels since only during the spring phytoplankton bloom is there sufficient food to allow gametogenesis to proceed. Food shortage outside this bloom period presumably explains the absence of any secondary spawnings in these mussels. However, when caged mussels were maintained under more favourable feeding conditions, they ripened in January when the gonad index of the natural population was still close to its minimal value. Pieters et al. (1979) also indicated that a close relationship exists between food availability and gametogenesis in *M. edulis*. In coastal waters adjacent to industrial areas the gametogenic cycle of mussels may be subjected to stresses imposed by the input of toxic metals (Myint and Tyler, 1982). Reproductive failure has been reported in *M. edulis* during brown tide conditions (Tracey, 1988).

Thus, superimposed upon the overall effects of latitude, and therefore temperature, on the reproductive cycle are variations due to habitat-specific differences in the time and duration of maximum food availability. Any factor which results in altered food availability, or the ability of mussels to assimilate this food, will alter the nutrient storage cycle, and thus the timing of gametogenic events (Newell et al., 1982).

Rising, falling and fluctuating temperatures have all been reported to stimulate spawning in *Mytilus* (Chipperfield, 1953; Campbell, 1969; Wilson and Seed, 1974; Kennedy, 1977; Hines, 1979; Kautsky, 1982a; Wilson, 1987). Some workers have suggested that spawning occurs only within a critical temperature range (Zhang et al., 1980; Sprung, 1983), while others (Young, 1946; Sunila, 1981) have found little or no evidence that spawning is induced by temperature or temperature change. Thermal limits may be set by long-term average temperatures. Elvin and Gonor (1979), for example, speculate that in *M. californianus* average temperatures may set threshold levels for nerves responsive to thermal shock, and that rapid thermal changes then trigger the release of neurosecretions from cerebral ganglia and associated spawning events.

Physical stimulation caused by jarring or scraping the shell and/or by pulling or cutting the byssus threads will often cause ripe *M. edulis* to spawn (Suchanek, 1978; Lutz et al., 1980; Wilson, 1987). These are precisely the environmental cues received during periods of rough weather, which could also signal the presence of storm-generated patches of bare rock onto which mussels can settle. This pattern apparently correlates well with spawning and subsequent recruitment events for *M. edulis* on the west coast of North America (Suchanek, 1985). Several workers (Battle, 1932; Chipperfield, 1953; Wilson, 1987) have correlated spawning with phases of the moon and tidal fluctuations, while salinity changes may also initiate spawning in some mussels (Parulekar et al., 1982; but see Fell and Balsamo, 1985). Currently, the relative

contribution of these and other exogenous factors to spawning is uncertain. Whatever factors are involved in initiating spawning, the presence of gametes in the water stimulates other ripe mussels to spawn, thereby enhancing the chances of fertilization.

Thus, from the extensive literature, a wide range of exogenous factors have been suggested as controls for both gametogenesis and spawning in *Mytilus*. Of these, temperature and food supply seem to be particularly important. However, these and other factors probably interact with endogenous factors (see also Chapter 6) in a complex manner to control the initiation of the gametogenic cycle and synchronize spawning. In field populations, a major difficulty in demonstrating a simple causal relationship between single environmental variables and complex processes such as reproduction, is that many of these variables (e.g. temperature, food supply, salinity, light) often covary or interact, sometimes even synergistically. Data, particularly on European mussels, has shown that *Mytilus* has a remarkable ability to vary its reproductive cycle in response to annual fluctuations in exogenous conditions. The precise pattern which the reproductive cycle takes probably depends on external factors which time endogenous events in such a way that maximizes survival and reproductive success. It seems likely, therefore, that *Mytilus* does not exhibit a single reproductive strategy, but rather exhibits a variety of patterns depending on the particular environmental regime (Newell et al., 1982).

### Reproductive Output

Estimates of reproductive output or fecundity in *Mytilus* have usually been obtained either directly, by inducing mussels to spawn in the laboratory and then counting or weighing the gametes released, or indirectly from allometric equations relating weight loss on spawning to dry body weight or shell length (Thompson, 1979; Bayne and Worrall, 1980; Kautsky, 1982a; Sprung, 1983; Rodhouse et al., 1984b). Reproductive output in mussels, as in many other bivalves, can account for a substantial proportion of both total production and standing crop (Griffiths and Griffiths, 1987). It can also represent a significant energy subsidy to the pelagic system. Kautsky (1982a), for instance, estimated that the reproductive output of Baltic *M. edulis* was equivalent to half the zooplankton production, and was thus an important food source for herring larvae and carnivorous zooplankton. Individual female *M. edulis* (ca. 7cm shell length) can produce around  $7-8 \times 10^6$  eggs during a complete spawning, while even larger individuals can produce as many as  $40 \times 10^6$  eggs (Thompson, 1979).

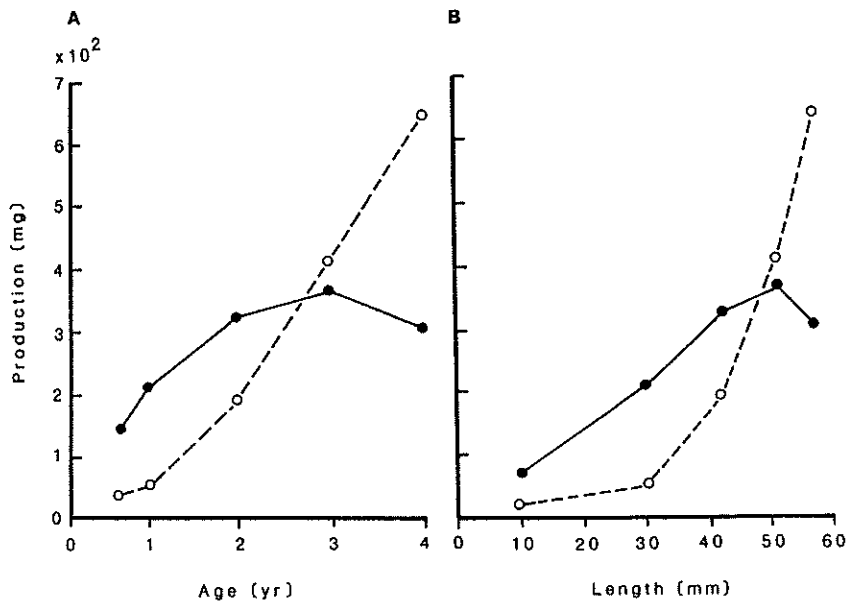


Fig. 4.4. Somatic (solid circles) and gamete (open circles) production as a function of age and shell length in low shore *Mytilus edulis* from Long Island, New York, North America. (After Rodhouse et al., 1986).

Energy which is surplus to metabolic requirements can be utilized for somatic growth and/or for gamete production (see p.122 and Chapter 5). However, the proportion of this energy surplus allocated to reproduction (= reproductive effort) varies according to body size or age (Bayne and Worrall, 1980; Kautsky, 1982a; Sprung, 1983; Thompson, 1984b; Rodhouse et al., 1986). Reproductive effort should not be confused with reproductive value which is the average expected lifetime fecundity (see for e.g. Bayne et al., 1983; Thompson, 1984b). Young mussels grow rapidly and convert little or no energy into reproduction, but with increasing size there is a gradual transition from somatic growth to reproduction, so that in the largest mussels most production (sometimes >90%) is channelled into gamete synthesis (Fig. 4.4). In these large individuals reproductive tissues may sometimes account for over 50% of the soft body weight (Thompson, 1979; Kautsky, 1982a). The reproductive effort of mussel populations will thus depend on their size (age) structure; those dominated by smaller, younger individuals will have a lower reproductive effort than populations consisting mainly of larger mussels, where gamete production may approach the total annual production. Okamura (1986) found that isolated individuals of *M. edulis*, or those growing in small clumps (6–9 mussels), grew more rapidly and had a greater reproductive effort than those in larger clumps (21–28 mussels). Moreover, mussels

in the centre of groups had reduced growth rates compared with those situated at the edge, whose growth and reproductive output was similar to isolated individuals. In natural populations most mussels occur within a matrix of very large groups where growth rate (see also p.121–122) and reproductive effort will therefore be substantially reduced.

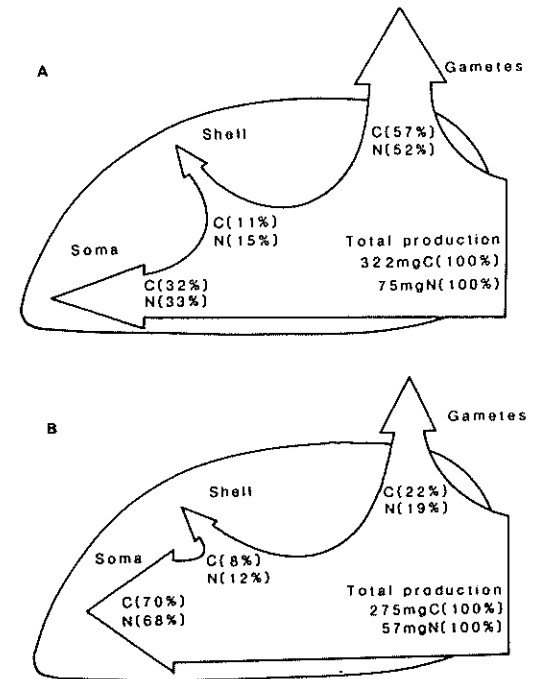


Fig. 4.5. Allocation of carbon and nitrogen in (A) wild and (B) cultivated *Mytilus edulis* from Killary Harbour, Ireland, once total cumulative production in the two populations is approximately equal. (After Rodhouse et al., 1984b).

Reproductive output is influenced by environmental variables such as temperature, food supply and tidal exposure, since these will broadly determine levels of net production. Bayne et al. (1983) reported a ten-fold difference between the maximum and minimum values for egg production, reproductive effort and reproductive value in *M. edulis* from six contrasted sites on the English and Welsh coasts. Fecundity may also vary from year to year, suggesting that the proportion of energy allocated to reproduction is adjusted according to the available food ration (Thompson, 1979). Bayne and Worrall (1980) compared growth and reproductive

output in *M. edulis* from two contrasting sites near Plymouth, England. The Lynher population received a richer food supply than the population at Cattewater, which was located near the outfall of a small electricity generating station, and was thus subjected to additional temperature stress during winter and spring. Consequently, the Lynher population had a greater overall production, spawned twice each year and expended up to 60% of its total production on reproduction. At Cattewater, production was lower, there was only a single spawning each year, and reproductive output accounted for 26% of total production.

*M. edulis*, however, appears to be able to buffer its reproductive effort from the full effects of environmental stress. Thus, while temperature extremes and desiccation in the upper intertidal zone produce higher metabolic costs, energy seems to be shunted away from somatic growth, rather than from gamete production (see Suchanek, 1985, and references therein). Sprung (1983) showed that although intertidal mussels at Helgoland produced significantly smaller eggs than those grown subtidally, (but see Bayne et al., 1983), they reached sexual maturity at a smaller body size and actually had a higher egg output relative to shell length. In Killary Harbour, western Ireland, naturally occurring intertidal mussels allocated a greater proportion of their energy budget to reproduction compared with mussels cultivated on ropes, which channelled more of their energy into somatic growth (Fig. 4.5). Such observations, perhaps rather surprisingly, suggest that *M. edulis* actually reduces its proportional allocation of resources to gamete production in the presence of environmental amelioration. Reproductive effort in *M. edulis*, however, varies with body size and age, and mussels from different populations, even those of similar shell length, may vary considerably in terms of age. Bayne (1976) found that even when *M. edulis* had been starved for 30 days it still continued to produce gametes, although it had to significantly deplete its energy reserves in order to do so.

Baltic mussels experience very low levels of predation (and low  $\text{Ca}^{2+}$  levels) and tend therefore to produce relatively thin shells with small adductor muscles. Accordingly, these mussels are able to allocate a considerably greater proportion of their energy budget to reproduction compared with mussels of similar size from fully marine areas (Kautsky et al., 1990). It is now known, however, that Baltic and North Sea *Mytilus* are genetically differentiated (see Chapters 1 and 7 and references therein), and that reproductive output in *Mytilus* also appears to be related to genotype (Hilbish and Zimmerman, 1988; Gardner and Skibinski, 1990). Rodhouse et al. (1986) found a positive correlation between fecundity and multiple locus heterozygosity, at least amongst larger mussels, which had grown beyond the size at which gamete production started to exceed somatic production.

### Condition

Condition indices in which the amount of flesh is related to the quantity of shell have been used extensively for many years, both in scientific research and in the commercial fishery. Many different methods exist for measuring condition (Lutz, 1980; Aldrich and Crowley, 1986; Davenport and Chen, 1987). A commonly used index, however, is that in which dry flesh weight is expressed as a proportion of the internal cavity volume of the shell (i.e. whole volume less the volume occupied by the actual shell valves). Methods utilizing wet flesh weight or volume are less sensitive due largely to the difficulty in standardizing the degree of wetness. Condition indices can be measured either for individual mussels or for whole populations. However, in view of the large amount of natural variability in condition, individual measurements are preferred whenever condition is investigated in relation to biological aspects, such as mortality or parasitic infection. The use of grouped data can be justified for population comparisons when the differences between sample means are more relevant than the degree of individual variation.

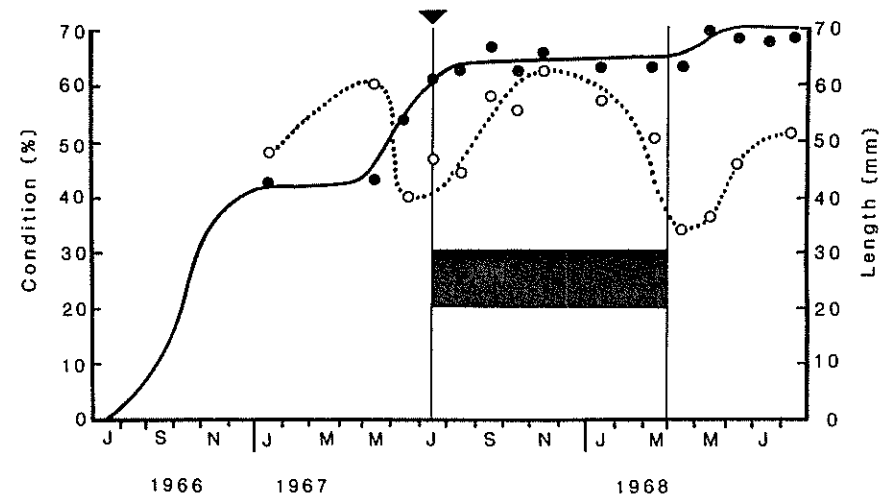


Fig. 4.6. Growth in shell length (solid circles) and condition, wet flesh volume as a percentage of the internal volume of the shell (open circles) of *Mytilus edulis* from Linne Mhuirich, Scotland; arrowhead denotes a mean length of 60mm, black bar the suggested time of harvesting. (After Mason, 1976).

Condition indices in *Mytilus* vary according to body size (Baird, 1958), season (Mason, 1976; Dix and Ferguson, 1984; Rodhouse et al., 1984a), level of parasitic infection (Kent, 1979; Thiesen, 1987; see also Chapter 12) and with local environmental conditions, especially the availability of food and degree of aerial exposure (Baird, 1966; Seed, 1980; Yamada, 1989). Seasonal changes are due to a complex interaction of those factors such as temperature, food supply and salinity which are thought to influence somatic growth and reproductive development. Figure 4.6 illustrates how the condition index of *M. edulis* in Linne Mhuirich, Scotland, increases during the autumn and winter months, when shell growth has virtually ceased. The subsequent steep decline in condition coincides with the main spring spawning period of these particular mussels. Marked differences in condition can also occur between mussels grown on the seabed and those grown in suspended culture on rafts (Fréchette and Bourget, 1985). Beatty and Aldrich (1989) also reported a significant increase in condition when mussels were only slightly elevated above the sea bottom. Such differences presumably reflect the better quality of digestible food and the generally lower concentration of sediment present in the water column, compared with the water at or immediately above the seabed itself.

## SETTLEMENT AND RECRUITMENT

Following spawning and external fertilization, developing mussel larvae spend a variable period of time as part of the temporary or meroplankton when they are passively drifted by water currents, often over considerable distances. In temperate waters *Mytilus* larvae are generally abundant throughout the spring and summer months though several studies (Seed, 1969a; Rodhouse et al., 1985) have recorded *M. edulis* larvae in the plankton throughout much of the year. Such extended periods of larval abundance are due, at least in part, to the protracted spawning periods which are known to characterize many mussel populations.

Because of the ongoing confusion in the literature with respect to the use of the terms settlement versus recruitment, the term settlement shall refer here to the process whereby larval individuals come in contact with, and permanently attach to, the substratum, a process which clearly includes metamorphosis (see also p.63–64 Chapter 3). Recruitment, on the other hand, shall be defined as the process of successful colonization after some specified period of time, during which some postsettlement mortality will generally have occurred. Because it is often difficult, or even impossible, to assess settlement in field populations, settlement is often inferred from recruitment data measured in days or even weeks after settlement has actually taken place.

In view of the difficulties inherent in following larval cohorts in the field, most larval life spans have been determined either directly from laboratory cultures or inferred from the time difference between spawning and the subsequent recruitment of juvenile mussels within the same geographical region (Suchanek, 1985). Estimates obtained using the latter approach, however, can be confounded by the immigration of larvae from distant mussel stocks in which the temporal spawning pattern may have been quite different. Although the larvae of *M. edulis* become competent to settle at a shell length of approximately 260µm they are able to delay their metamorphosis and remain within the plankton until they have grown to around 350–400µm (Bayne, 1965; Sprung, 1984). Fuller and Lutz (1988) found that in field populations the mean size of *M. edulis* postlarvae at the time of their settlement was 300–350µm (see larval settlement section Chapter 3). Any delay in metamorphosis, however, is accompanied by a decreased ability to discriminate between different settlement surfaces. Thus, although 2–4 weeks seems to be the normal duration of planktonic life for *M. edulis*, this can vary according to temperature, food supply and the availability of a suitable settlement surface, so that 10 weeks or more may elapse between fertilization and the settlement of postlarval mussels (= plantigrades).

Much of the early literature fails to distinguish between the primary settlement of early plantigrades (250–400µm) on filamentous surfaces and the secondary settlement of later plantigrades (>500µm) onto established mussel beds. The association between recently settled *M. edulis* and filamentous substrata has long been recognized (see Seed 1976 and references therein), but the significance of such observations was not fully appreciated until de Blok and Geelen (1958) showed that early plantigrades settled on filamentous surfaces such as hydroids and various algal species from which they subsequently disappeared. Early experiments with various substrata indicated a distinct preference by early plantigrades for filamentous surfaces but that this preference subsequently changed. The suitability of the substratum seemed to be related to its general surface texture rather than to any chemical attraction (but see Cooper, 1981). Maas Geesteranus (1942) showed that young mussels would settle on most types of substrata provided these were firm and had a roughened or discontinuous surface. He also showed that plantigrades would attach and detach themselves many times before finally settling on the established mussel bed. He argued that mussel beds attract further recruits by virtue of their surface texture and that the byssal threads of the mussels themselves seemed to be important in this respect. *Mytilus* species are now known to settle on a wide variety of filamentous substrata, including the byssal filaments of conspecific adults (Petraitis, 1978; Suchanek, 1981; Hosomi, 1984; Eyster and Pechenik, 1987), filamentous algae (Paine, 1974; Suchanek, 1978; Petersen, 1984a, b; King et al., 1990) and fibrous ropes used in the mytiliculture industry (Mason, 1976; Lutz, 1980).

Bayne (1964) demonstrated that mussels pass successively from the plankton to sites of temporary attachment on filamentous algae, and from these, via a secondary pelagic phase, to sites of more permanent attachment on adult beds. This secondary pelagic phase has been termed bysso-pelagic migration or byssus drifting, and is facilitated by the secretion of long fine byssus-like threads (Sigurdsson et al., 1976; de Blok and Tan-Mass, 1977; Board, 1983; Lane et al., 1985). Young postlarval mussels retain this ability to drift, up to a size of about 2–2.5mm. Growth to this size may take several months and a significant part of this time could, therefore, be spent undergoing repeated phases of bysso-pelagic migration. The primary attachment phase seems to be a natural prelude to final settlement and may have considerable adaptive value. An initial attachment period away from the established mussel bed effectively reduces intraspecific competition, and also prevents the small, vulnerable postlarval stages from entering the strong inhalant currents of larger mussels.

The relatively marked seasonal abundance of early plantigrades on filamentous algae reported by Bayne (1964) and King et al. (1989) was not observed by Seed (1969a) for wave-exposed rocky shores in North-east England, where high densities of these mussels persisted throughout much of the year. Filamentous algae, together with other algae such as *Corallina* and *Mastocarpus* (= *Gigartina*) appeared to provide an extensive pool of young mussels, many of which could be migrating onto the adult beds more or less at any time of the year, thus accounting for the sporadic and often unpredictable pulses of recruitment that characterize many *Mytilus* populations (Seed, 1969a; Dare, 1976; Lewis, 1977). Early plantigrades normally remain on their primary attachment sites until they are approximately 1–2mm in shell length, though some may actually remain there until they are twice this size. The time taken to achieve this size will depend on individual growth rates. However, many autumn-spawned plantigrades which settle late in the year, when conditions for growth are becoming increasingly unfavourable, frequently overwinter on the algae, leaving only with the onset of more favourable conditions during the following spring. While migration from primary attachment sites to the adult habitat appears to be due to changes in the ecological requirements of the plantigrades, many mussels will also be liberated involuntarily by the seasonal die-back of their host algae, or through the action of winter storms.

More recently evidence has emerged which indicates that in some populations early plantigrades of *M. edulis* may settle directly onto adult beds, without an initial growth phase on filamentous substrata as postulated by the primary-secondary settlement model (McGrath et al., 1988; King et al., 1990). The absence of mussels >400µm in plankton samples from Norwegian fjords has also been cited as evidence for the absence of a secondary pelagic phase (Böhle, 1971). Kautsky (1982a) similarly found no evidence for this phase in his study of Baltic mussels. Direct settlement of plantigrades onto adult beds has also been reported for *M. californianus* (Petersen,

1984a,b). The existence of varying modes of settlement may thus provide yet another example of the plasticity in the biology of *Mytilus*. Whether the mode observed on any particular shore is genetically-based or is a response to varying environmental conditions still has to be determined (McGrath et al., 1988).

The onset, duration and intensity of settlement and recruitment exhibits considerable spatial and temporal variation (see reviews by Seed, 1976; Suchanek, 1985). Seasonal patterns have normally been determined either by using artificial surfaces or by noting the relative abundance of plantigrades in samples of filamentous algae and/or established mussel beds. A wide range of artificial substrata has been used to collect settling plantigrades (see King et al., 1990); a major advantage of these collectors is that they present a constant surface area of relatively uniform textural composition and, when routinely deployed, they enable recruitment to be quantified over fixed intervals of time. Field studies have clearly demonstrated that smooth surfaces are generally unattractive to prospecting plantigrades and that maximum settlement occurs on roughened, scarred or fibrous substrata (Seed, 1969b; Dare et al., 1983; King et al., 1990).

When collected regularly throughout the year samples of filamentous algae and/or established mussel populations can provide useful semi-quantitative information concerning recruitment. Such data, however, provide only an estimate of the total number of plantigrades present at any given time; differences between successive samples therefore, represent a balance between the numbers of larvae settling and the subsequent loss of plantigrades through postsettlement mortality and growth out of the size categories being sampled. Furthermore, it is often difficult or even impossible to separate recently recruited mussels from the large numbers of small (<2.0mm) competitively suppressed individuals which characterize many *Mytilus* populations year round (Seed, 1969b; Kautsky, 1982b). These small, slow-growing mussels apparently become recruited to the breeding stock only after they have been effectively released from intense intraspecific competition, as larger mussels are lost from the population (Kautsky, 1982a,b). In this way the population is effectively stabilized and maintained at or near the carrying capacity of the area with respect to the available food and space. Only if settlement fails for several successive years will this appreciably affect the size of such populations. Kautsky (1982a) thus draws an interesting distinction between the initial recruitment of juveniles to the population, and subsequent recruitment from the persistent pool of small competitively suppressed mussels to the breeding stock.

*Mytilus* is highly gregarious and dense settlements often occur around the edges and in between individual mussels in established populations. Hosomi (1984) has shown that recruitment of *M. galloprovincialis* in Osaka Bay, Japan, was proportional to the density or biomass of the adult population, because recruitment occurred only amongst the byssal threads of adult mussels. Such gregarious behaviour is probably

adaptive since *Mytilus* occurs predominantly in the intertidal or shallow subtidal zones and will therefore be subjected to mechanical forces of water movement especially on wave-exposed coasts. The reduced surface area exposed to such forces by mussels living in dense clusters, together with the mutual support afforded by neighbouring individuals, makes clumps of mussels better able to withstand these forces than isolated individuals (Harger, 1972; Paine, 1974). Mussels living in clumps may also be less vulnerable to predators. Plantigrades, once settled, provide loci for further recruitment and so the colony gradually extends. Juvenile mussels reach established beds by their ability to attach and detach themselves from unsuitable surfaces until a favourable habitat is encountered, usually in cracks or crevices in the rock surface or amongst the matrix of byssal threads provided by conspecifics. Once established, mussel beds will tend to increase in size both through gregarious settlement and growth of individual mussels. The competitive dominance of mytilid mussels on many rocky shores is probably, at least partly attributable to their ability to crawl extensively over the substratum even for some time after their initial settlement.

### SOMATIC GROWTH

Growth has been extensively documented in *Mytilus* partly because of its commercial and ecological importance and partly because its growth history, as in many bivalves, is permanently recorded in the shell as a series of growth checks, a feature which makes these animals especially amenable to growth studies. Growth is usually assessed in one of two ways; either the size of the whole organism is related to age (= absolute growth), or the rate of growth of one size variable is related to that of another variable (= allometric growth). Reviews of growth in bivalves generally, and in *Mytilus* in particular, are provided respectively by Seed (1980) and Seed and Richardson (1990).

#### Methods for Estimating Absolute Growth

Although growth is most appropriately measured as the rate of change in biomass, in bivalves this can only be accurately determined once the animal has been removed from its shell; this is because live weight is strongly affected by variations in shell shape and thickness and by the amount of water retained in the mantle cavity (Griffiths and Griffiths, 1987). Consequently, shell length is a more commonly used

indicator of size, and this, in turn, can then be related to weight, volume or even energy content by one or more allometric functions (p.121–122).

#### Analysis of size frequency distribution

Where recruitment to the population is seasonal, individual year classes can often be identified as distinct modes in plots of size frequency distributions. Changes in the position of these modes over time enable the mean growth rate of each year class to be estimated. In *Mytilus* this method has limited application because extended periods of recruitment and variable individual growth rates usually result in an inevitable merging of age classes (Seed, 1976; Kautsky, 1982b; Craeymeersch et al., 1986). Occasionally, such overlapping distributions can be adequately resolved by using various graphical or mathematical techniques (Grant, 1989). However, even when size frequency analysis is used (Bayne and Worrall, 1980; Rodhouse et al., 1984a) it provides only a measure of the average growth of mussels within the population, and such estimates may have been substantially modified by size-specific natural mortality.

#### Use of growth checks on or within the shell

Surface growth rings on the shells of many bivalves, including mussels, have been used extensively in age determination. These rings are produced during periods of suspended shell growth, and may be associated with various environmental factors including seasonal changes in temperature or food availability, prolonged stormy weather, or even with the annual reproductive cycle. Consequently, they cannot be assumed to be annual in origin, and even when annual rings are present their use in age determination can be confounded by other nonannual growth checks. Earlier rings may also be worn away due to shell abrasion, and in older, slow growing mussels, rings at the posterior shell margin become closely packed and difficult to resolve.

The shell of *Mytilus* consists of three layers, a thin outer periostracum, a middle prismatic layer and an inner nacreous layer. The periostracum and prismatic layers are secreted by the mantle epithelium around the margins of the shell, while the nacreous layer is deposited by the general outer surface of the mantle, and thus effectively thickens and strengthens the shell. Acetate peel replicas of polished and etched longitudinal shell sections reveal a series of distinct growth bands within the middle and inner layers. Nacreous lines are formed annually (Lutz, 1976), whereas microgrowth bands within the prismatic shell have a tidal periodicity, and can thus be used to detect short-term as well as longer term variations in individual growth rates (Richardson, 1989; Richardson et al., 1990).

### Other direct measurements of shell growth

Successive measurements of marked or caged mussels can provide valuable records of the effects of size, season and environmental conditions on growth (Seed, 1976; Kautsky, 1982b; Page and Hubbard, 1987), providing that caging itself does not influence growth rate through its effects on water movement and food supply. Precise measurements of linear growth have been obtained using a sensitive laser diffraction technique first developed by Strømngren (1975). This method has been used in several laboratory-based studies to measure the effects of temperature (Almada-Villela et al., 1982), salinity (Gruffydd et al., 1984), photoperiod (Strømngren, 1976a, b), algal diets (Strømngren and Cary, 1984) and heavy metals (Redpath, 1985; see also Chapter 9) on the shell growth of *M. edulis*. More recently, a photographic technique which involves digitizing negative images of shell outlines has been used by Davenport and Glasspool (1987). Though less sensitive than the laser method, this technique allows the outlines and projected areas of shells to be calculated; the recorded images thus contain valuable information regarding changes in shell shape as well as size.

### Estimates from physiological measurements

An alternative approach to the study of mussel growth is that based on the energy balance equation. Here the growth potential or 'scope for growth' is estimated from physiological measurements of the various components of the energy budget (Navarro and Winter, 1982; Widdows et al., 1984; Thompson, 1984a; see also p.405–406 Chapter 8). When integrated over time and applied to individuals of different size these data can be used to derive an average growth curve. Scope for growth does not differentiate between energy that is used for somatic growth or reproductive output, but has considerable practical advantages in that it can be assessed over short-term laboratory experiments. It thus provides an excellent method for quantifying the responses of individual mussels to changing environmental conditions such as food supply, temperature, salinity and contaminants. In *Mytilus* a close correspondence between growth rates estimated from energy budgets, and actual growth rates measured by more direct methods, has been reported by several workers (Bayne and Worrall, 1980; Riisgård and Randløv, 1981; Hamburger et al., 1983).

### Quantitative expressions of growth

A habitat by virtue of its resource limiting environmental conditions imposes a maximum size beyond which further growth proceeds only slowly, if at all. The maximum attainable size ( $L_{\infty}$ ) under any set of environmental conditions can be approximated using the Ford-Walford plot, where length at age  $t + 1$  years is plotted

against length at  $t$  years (Cerrato, 1980). Maximum size is given where the line of best fit intercepts a point of zero growth when  $L_t = L_t + 1$ . This parameter is basic to many growth equations, two of which, the von Bertalanffy and the Gompertz have been widely used to describe and compare growth rates in *Mytilus* (Bayne and Worrall, 1980; Rodhouse et al., 1984a; Thompson, 1984b; Craeymeersch et al., 1986). Sigmoidal growth curves of the Gompertz type appear to be more characteristic of slower growing populations; faster growing populations generally lack any obvious inflexion point and for these the von Bertalanffy equation may provide a better description of growth (Griffiths and Griffiths, 1987). In the von Bertalanffy equation:

$$L_t = L_{\infty} [1 - e^{-k(t - t_0)}]$$

where  $k$  is the growth constant reflecting the rate at which maximum size ( $L_{\infty}$ ) is approached and  $t_0$  is another constant representing time when  $L_t = 0$ . The Gompertz equation is similar but uses the logarithms of length:

$$\log_{10} L_t = \log_{10} L_{\infty} [1 - e^{-k'(t - t_1)}]$$

where  $k'$  is the rate constant and  $t_1$  a constant representing time when  $L_t = 1$ .

Such equations do not reflect growth variations caused by seasonal fluctuations in temperature. Consequently, the product which integrates temperature and time (= day degrees) is sometimes incorporated as an independent variable (Ursin, 1963; Rodhouse et al., 1984a). Both equations assume that growth is determinate and that some maximum attainable size exists for any given population. Yet growth in many bivalves, including mussels, may not always be determinate, at least over their realized life span and may not, therefore, cease at any fixed adult size (Seed, 1980; Gardner and Thomas, 1987). Some workers (Davenport et al., 1984) have used polynomial expressions to describe shell growth in preference to the more commonly used growth equations (see also Chapter 5).

### Variability in growth rate

Growth rate in *Mytilus* varies according to size, age and environmental conditions. Even mussels of similar size and age grown under apparently identical conditions can exhibit widely different rates and it is now known that growth variation is at least partially determined by genotype (p.121 and Chapters 5 and 7). However, variations attributable to this source are probably minor compared with those resulting from environmental factors. For example, under heavy settlement, growth in *M. edulis* individuals can vary as much as 10-fold (Trevelyan, 1991). Under optimal conditions *M. edulis* can attain lengths of 60–80mm within two years, whereas in the marginal



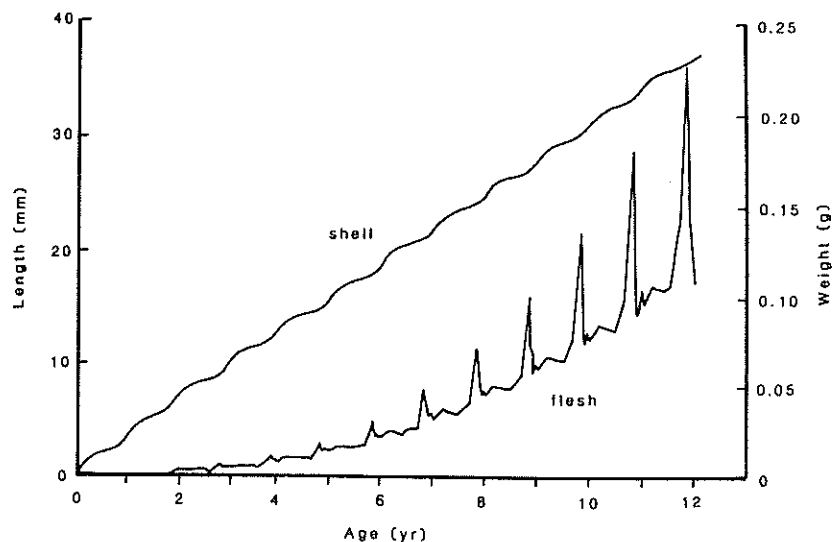


Fig. 4.7. Seasonal patterns of shell and flesh (dry weight) growth in *Mytilus edulis* from the Baltic. (After Kautsky, 1982b).

conditions of the high intertidal zone growth is substantially reduced, and mussels may reach lengths of only 20–30mm after 15–20 years (Seed, 1976). *M. californianus* can achieve faster growth rates and attain a much larger body size (up to 250mm) than *M. edulis* (Paine, 1976a; Suchanek, 1981; Yamada, 1989). Various environmental factors influence growth rate in *Mytilus*, and these are generally such that in temperate waters shell growth is rapid during the spring and summer, and slow or absent during the colder months. Flesh weight, by contrast, exhibits pronounced seasonal peaks associated with the annual reproductive cycle. Thus the pattern of growth in temperate water populations consists of alternating increments in shell length during the spring and summer and flesh weight during winter (Fig. 4.7).

### Environmental Modulators of Growth

#### Temperature

Almada Villela et al. (1982) examined the effect of several constant temperatures on *M. edulis* and found that between 3°C and 20°C linear growth increased logarithmically; above 20°C growth declined sharply, while at lower temperatures (3

and 5°C) it proceeded only very slowly. These workers further noted that while a cyclical temperature range occasionally produced better growth than either of the temperatures at the extremes of the experimental regime, no constant pattern emerged. The absence of any adverse effects of fluctuating temperature and the ability to acclimate to temperature changes, at least over part of their physiological range, indicates that *Mytilus* is well-adapted to life in the constantly changing environmental conditions usually associated with coastal and estuarine waters.

A relationship between growth and temperature is clearly demonstrated when shell length is plotted against age in day degrees. However, growth rates expressed in these terms are not always consistent, which suggests that factors other than temperature (e.g. food supply) are probably involved (Wilson, 1977; Thompson, 1984b). A major difficulty in correlating single environmental variables with growth rate in field populations is that the correlation, although obvious, may not be causal. Page and Hubbard (1987) concluded that the temporal patterns of growth in *M. edulis* on a production platform off the Californian coast were determined mainly by variations in phytoplankton, and that temperature could be virtually eliminated as an important growth regulator over the range (10–18°C) normally experienced by these mussels. Similarly, in a study of mussels in western Sweden, Loo and Rosenberg (1983) found that low temperatures (<5°C) did not seem to limit growth whenever these coincided with the spring phytoplankton bloom. Physiological studies on *M. edulis* have also demonstrated that between 10 and 20°C water temperature has little effect on scope for growth (Bayne et al., 1976).

#### Salinity

Brackish estuaries and lagoons are favourable habitats for mussel growth but this probably reflects the increased food levels in these environments rather than any beneficial effects of reduced salinity. Indeed, lowered salinity may have a detrimental effect on growth and can even be lethal to mussels under extreme conditions (Almada-Villela, 1984; Gruffydd et al., 1984). *M. edulis*, however, can survive considerably reduced salinities and will even grow as dwarfed individuals in the inner Baltic, where salinities can be as low as 4–5‰ (Kautsky, 1982b). Results from reciprocal transplant experiments suggest that differences in growth rate and maximum size between North Sea and Baltic mussels are mainly due to physiological adaptations to environmental salinity (Kautsky et al., 1990).

Bøhle (1972) found that at various steady state salinities mussels gradually acclimated to lowered salinity levels. Acclimation to fluctuating salinities, however, did not occur to the same extent, presumably because the period of exposure to the lowest salinities was too brief. *M. edulis* can effectively isolate itself from low salinity by closing its valves and maintaining a relatively high osmotic concentration within

the mantle fluid (Davenport, 1979; Aunaas et al., 1988). However, since feeding is suspended while the valves remain closed, growth rate will inevitably be depressed.

The influence of salinity on growth may be due to reduced metabolic efficiency. Tedengren and Kautsky (1986), for example, found that at ambient salinities the oxygen to nitrogen ratio was consistently lower in Baltic mussels than in those from the North Sea. Since a lowered O:N ratio is energetically unfavourable (Bayne et al., 1985), this would contribute to the lower growth rate and smaller maximum size of Baltic mussels.

#### Food supply and tidal exposure

Probably the single most important factor in determining growth rate is food supply, since this provides the necessary energy to sustain growth. Mussels are efficient filter feeders removing particles down to 2–3 $\mu$ m with 80–100% efficiency (Møhlenberg and Riisgård, 1977). The total amount of particulate material present in suspension (= seston) contains several potentially utilizable food types. These include bacteria, phytoplankton, fine organic detritus and material of inorganic origin, though the precise nutritional contribution that each of these makes to the diet varies seasonally, and among mussels of different size (Rodhouse et al., 1984a; Page and Hubbard, 1987). Dissolved organic matter may also contribute to the energy intake of *Mytilus* (Manahan et al., 1983; Siebers and Winkler, 1984).

Several authors have identified seasonal and regional variations in both the quantity and quality of utilizable food as important determinants of mussel growth (Ceccherelli and Rossi, 1984; Fréchette and Bourget, 1987). Field growth rates often exceed those recorded in the laboratory, irrespective of food supply and temperature. Kiørboe et al. (1981) suggest that this may be due to the stimulatory effects of resuspended bottom material which, as well as serving as an additional food supply, may also enable the mussel to exploit its full clearance potential. Despite the broad correlation between growth rate and particulate food, mussels can buffer their shell growth during short-term temporal variations in food availability by utilizing glycogen reserves accumulated prior to and during gametogenesis (Bayne et al., 1983).

Mussels only feed when they are submerged. At some point along the intertidal gradient, therefore, the energy required for metabolism during aerial exposure will exceed that available during the feeding period. Figure 4.8 illustrates the progressive reduction in growth rates with increasing tidal elevation in the black mussel *Choromytilus meridionalis*, as well as the exceedingly rapid growth rates under the most favourable conditions. Baird (1966) estimated that the point of zero growth in *M. edulis* was approximately 55% aerial exposure though this will presumably vary

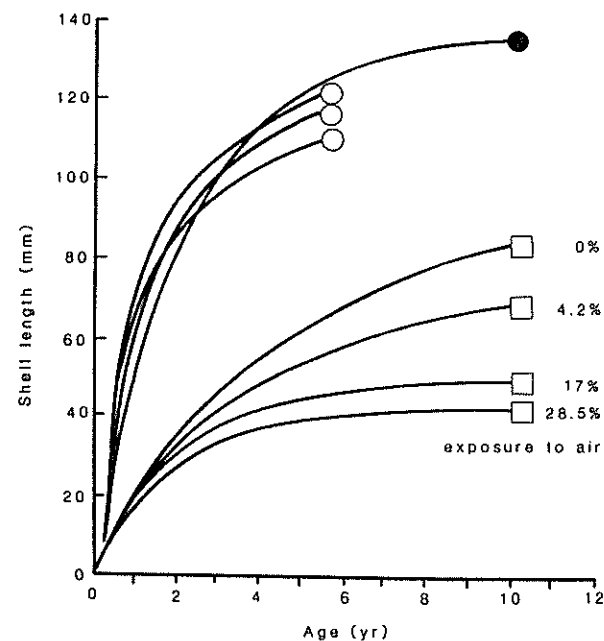


Fig. 4.8. Growth rates of South African *Choromytilus meridionalis* at different sites and tidal levels; Table Bay, offshore (solid circles), Saldanha Bay, raft culture (open circles) and False Bay (open squares). (After Griffiths and Hockey, 1987).

according to local conditions, such as the degree of wave splash. While growth declines with tidal exposure (see also Yamada (1989) for *M. californianus*), life expectancy often increases, since predation pressure in the upper shore is substantially reduced. However, when old slow growing mussels are transferred to more benign conditions downshore they are able to grow rapidly (Seed, 1968), indicating that the potential for growth remains intact for many years, even among mussels that have been prevented from exploiting this potential, owing to unfavourable environmental conditions. The relationship between growth rate and water depth reported by several workers (Rodhouse et al., 1984a; Page and Hubbard, 1987) is generally thought to reflect variations in food availability within the water column.

### Other factors

Light seems to have a detrimental effect on growth in *Mytilus*. Continuous darkness, reduced levels of irradiance, wavelengths below 600–700nm and photoperiods of 7h or less, all significantly increased the linear growth rate in *M. edulis* (Strømgren, 1976a, b). Enhanced growth during periods of darkness was accompanied by increased defaecation, which suggests that the effect may be due to increased feeding activity (Nielsen and Strømgren, 1985). This view is supported by the observation of Ameyaw-Akumfi and Naylor (1987) who found evidence of circadian rhythmicity in shell gaping of *M. edulis*, with a greater duration of shell closure occurring during the hours of expected daylight. Strong wave action can significantly reduce growth rate in *M. edulis*, presumably by reducing feeding efficiency; this apparently does not occur in *M. californianus*, a species better suited to high-energy environments (Harger, 1970; Suchanek, 1981). Although pea crabs were once considered to be harmless commensals (Wells, 1928, 1940; MacGinitie and MacGinitie, 1949) it is now clear that they are parasitic on *Mytilus* species. Infested mussels typically exhibit reduced growth rates and shell shape distortions, and are generally in poorer condition compared to noninfested mussels (Seed, 1969c; Anderson, 1975; Bierbaum and Ferson, 1986). Reduced food intake by the mussel and/or reduced filtration rates are the most likely factors in lowering mussel fitness. (Pregenzer, 1979, 1981; Bierbaum and Shumway, 1988). Intraspecific competition for food and space can lead to extreme variations in growth rate. *M. edulis*, which recruited into a population consisting of one-year-old mussels, grew at less than half the rate of those recruiting onto an adjacent bare rock surface (Seed, 1969b). In populations consisting of several age classes even greater growth reductions occur, as the majority of small mussels trapped amongst the byssal threads of larger conspecifics are at a severe competitive disadvantage (see also Dare and Edwards, 1976; Kautsky, 1982b). Environmental contaminants such as tributyltin, heavy metals and petroleum hydrocarbons can all cause significant reductions in growth rate, often at exceedingly low concentrations (for references see Seed and Richardson, 1990).

Several environmental factors can thus modulate growth in *Mytilus*. Of these perhaps the availability of a suitable food resource is the most important since, without this, sustained growth cannot occur. Given adequate food several factors, particularly temperature, salinity and aerial exposure may interact, sometimes synergistically, resulting in various rates and seasonal patterns of growth. Such interactions, and the tendency for some variables to covary, makes it extremely difficult to identify the precise influence of any single factor on growth in natural mussel populations.

### The importance of genotype

The relationship between growth rate and genotype has been demonstrated in several bivalves including *Mytilus* (see p.352–357 Chapter 7). Particular attention has focussed on the strong positive correlation between individual growth rate and the degree of heterozygosity measured at several polymorphic enzyme loci (Koehn and Gaffney, 1984; Zouros et al., 1988). Several recent studies have revealed that more heterozygous *M. edulis* individuals have lower energy requirements for maintenance metabolism, and a higher efficiency for protein synthesis (Diehl et al., 1986; Hawkins et al., 1986). The higher energy status of these individuals may thus be reflected in faster somatic growth in juvenile mussels (Koehn and Gaffney, 1984), or in higher fecundity and production in those which have attained reproductive size (Rodhouse et al., 1986). In addition to growing faster, more heterozygous mussels also tend to achieve more uniform average growth rates (Koehn and Gaffney, 1984).

### Allometric growth

So far we have considered how linear growth rate can be modulated by environmental and genetic factors. However, mussels, like most organisms, exhibit progressive changes in their relative proportions with increasing body size. The relationship between any two size variables ( $x$  and  $y$ ) can be expressed by the allometric equation  $y = ax^b$  where  $a$  and  $b$  are constants. The exponent or growth coefficient  $b$  represents the relative growth rate of the two variables, while  $a$  is the value of  $y$  when  $x$  is unity. In its linearized logarithmic form this becomes  $\log y = \log a + b \log x$ . The slope ( $b$ ) and intercept ( $A$ ) of such transformed data are estimated by regression analysis (Brown et al., 1976; Aldrich and Crowley, 1986). Changes in relative proportions may simply be associated with the maintenance of physiologically favourable surface area to volume ratios as body size increases; alternatively, they may reflect adaptive responses to changing environmental conditions (see p.191–193 Chapter 5).

Of the various environmental factors that are known to influence shell shape in bivalves, population density (= crowding) seems to be particularly important in the case of *Mytilus* (Seed, 1968, 1973, 1978; Brown et al., 1976). The shells of densely packed mussels are proportionately more elongate with higher length to height ratios than those from less crowded conditions. This effect, which is exaggerated in older individuals, presumably has adaptive value since the posterior feeding currents will be effectively elevated above neighbouring conspecifics. Such ontogenetic and phenotypic variations in the allometric relationships of *Mytilus* and other bivalves are discussed in more detail elsewhere (Seed, 1980) and will not, therefore, be considered further in this account. The allometric equation has also found extensive use in physiological investigations, and in studies of mussel production for

estimating flesh weights from measurements of shell length. Here dry flesh weight is usually regressed against length for population samples taken at regular intervals throughout the year. These regressions are then compared by covariance analysis and used to estimate the mean weight of mussels of standard length. Temporal variations in these adjusted mean weights are then presumed to reflect changes in productivity, fecundity or physiological condition (Bayne and Worrall, 1980; Kautsky, 1982b; Rodhouse et al., 1984a, b; Thompson, 1984a). However, this procedure, which assumes that changes in the covariate (length) are trivial, has recently been criticized by Hilbish (1986), who showed that shell and soft tissues in *M. edulis* can exhibit markedly different seasonal growth patterns (but see Beatty and Aldrich, 1989). Where such uncoupling of growth occurs, seasonal variations in flesh weight adjusted to mussels of a standard length should perhaps be interpreted with caution.

## PRODUCTION

Production represents the net gain in body energy and occurs when the energy content of the absorbed ration exceeds metabolic requirements (see details in Chapter 5). This energy surplus can then be utilized for somatic and/or gamete production. Although reproductive output is thus an essential component of total production, in many studies it is often ignored, and commonly used definitions of production take into account only somatic growth. The partitioning of surplus energy between somatic growth and gamete production and its relationship to age is of fundamental importance within the context of life history strategies (Seed and Brown, 1978; Thompson, 1979). If energy intake falls below the maintenance ration then body reserves are utilized and negative growth (= degrowth) may occur. Production of individual mussels can be measured directly in the field or under controlled laboratory conditions, as actual rates of somatic growth and reproductive output; alternatively, it can be estimated indirectly as 'scope for growth' (Griffiths and Griffiths, 1987; see also p.114 and Chapters 5 and 8).

The methods by which production is calculated for individual mussels can also be applied to populations or even to whole communities (Asmus, 1987), provided that certain group attributes, such as size (= age) distributions and changes in population density, are taken into account. The data thus obtained are then generally expressed in terms of ash free dry weight (AFDW) or energy flux per unit area of habitat ( $\text{kJ m}^{-2} \text{yr}^{-1}$ ). Estimates of production are extremely sensitive to variations in the size (age) composition of the population as well as to changing environmental conditions. Increase in body size, for instance, is usually accompanied by a transition from somatic production to gamete production (Thompson, 1984b; Rodhouse et al., 1985; Craeymeersch et al., 1986), while growth efficiency declines as total production fails to

keep pace with the increase of respiratory energy expenditure. Consequently, production is often estimated separately for the different age or size classes represented within the population.

Although there have been relatively few studies of production in natural mussel populations, available data indicate that production levels in *Mytilus* can be extremely high and may rival even those reported for other highly productive systems such as tropical rain forests and kelp beds (Whittaker, 1975; Leigh et al., 1987). In Morecambe Bay, England, for instance, production by two year classes of *M. edulis* (1968 and 1969) amounted to  $62.89 \times 10^3$  and  $86.40 \times 10^3 \text{ kJ m}^{-2} \text{yr}^{-1}$  respectively, some 2.5 to 3 times their maximum standing crop (Dare, 1976; see also p.137). Most production occurred in the first year following settlement and although these mussels survived into their third year, production had virtually ceased after sixteen months (Fig. 4.9) due to the high rates of mortality, mainly from physical factors, that characterize this particular population. Production of organic material in the shell was 32–34% of organic flesh production; thus, while the organic component of the shell of *M. edulis* is small (probably <5% of total shell weight), production is high by virtue of the large bulk of shell in the population (see also Gardner and Thomas, 1987). Dare (1976) draws attention to the large amount of production that is made available to decomposers and to the detrital food chain in mussel populations of this sort. This contrasts with

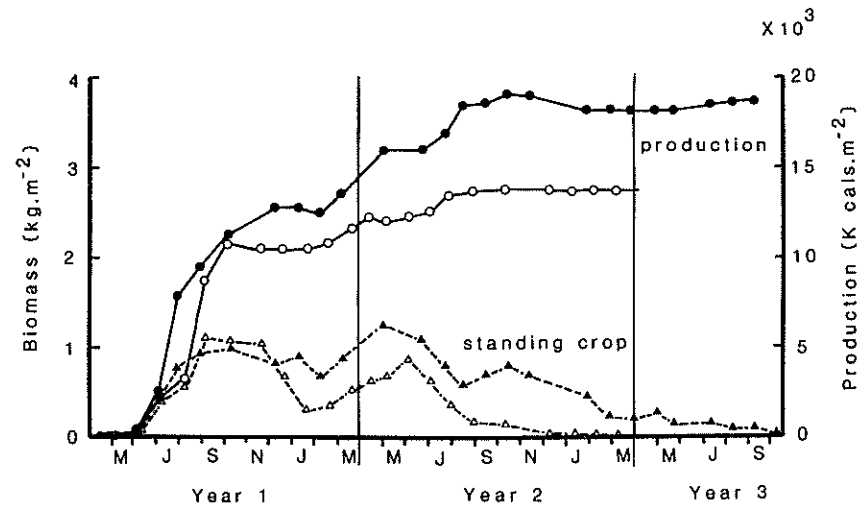


Fig. 4.9. Standing crop (dry biomass) and production of dry flesh in the 1968 (open symbols) and 1969 (solid symbols) year classes of *Mytilus edulis* from the low shore, Morecambe Bay, England. (After Dare, 1976).

other populations such as those in the Ythan Estuary, Scotland, in which predation apparently accounts for most of the annual mussel production (Milne and Dunnet, 1972; Baird and Milne, 1981).

The Morecambe Bay population studied by Dare is perhaps rather unusual in that it consisted entirely of young, fast-growing mussels with a considerable rate of turnover. In populations where the biomass tends to be dominated by older, slower growing individuals production levels are usually much lower with typical values generally falling within the range of  $2.0 \times 10^3$  and  $14.5 \times 10^3$  kJ m<sup>-2</sup> yr<sup>-1</sup> (Milne and Dunnet, 1972; Rodhouse et al., 1985; Asmus, 1987). High levels of production, comparable to those reported by Dare (1976), however, have been recorded in populations of *M. galloprovincialis* (Ceccherelli and Rossi, 1984; Hosomi, 1985) and *M. californianus* (Leigh et al., 1987), as well as in populations of *M. edulis* elsewhere (Dare and Edwards, 1976). In Killary Harbour, western Ireland, production levels of cultured mussels exceeded those of wild shore mussels by an order of magnitude (Rodhouse et al., 1985). The shore population, however, was dominated by larger, older mussels (40–60mm) with a high reproductive output. Consequently, these mussels contributed significantly to the larval population of this particular inlet. Carbon flow per unit area in a Swedish mussel culture described by Loo and Rosenberg (1983) was approximately ten times lower (ca. 13.5kg m<sup>-1</sup>) than in Killary Harbour (Rodhouse et al., 1985). Production levels in *Mytilus* vary seasonally due to the timing of events such as the spring phytoplankton bloom and the onset of spawning. Other factors including temperature will also presumably contribute to the strength of the seasonal effect. Variations amongst mussels grown under similar environmental conditions strongly suggest that genetic differences may also partially determine the level of secondary production (Mallet and Carver, 1989 and Chapter 7).

Flow-through plastic tunnels have recently been used to determine the uptake and release of materials in the tidal waters passing over natural mussel beds (Siebers and Winkler, 1984; Dame and Dankers, 1988; Prins and Smaal, 1990). Such studies elegantly demonstrate that intertidal beds of *Mytilus* are capable of removing substantial amounts of particulate material from the water column, transforming some of this into biomass, and releasing some constituents as dissolved waste products. Dense assemblages of filter feeding organisms like mussels can thus function as central processors of estuarine and coastal materials, and by regenerating nutrients could, therefore, play a central role in controlling levels of eutrophication and primary production in inshore waters.

## MORTALITY

### Survival and Longevity

Survivorship curves for *Mytilus* have generally been constructed either from changes in the relative abundance of mussels (e.g. numbers m<sup>-2</sup>) belonging to different year classes represented within the population, or by following the survival of marked cohorts of approximately similar size or age. Unfortunately, individual year groups in mussel populations are not always clearly defined, although their overlapping size frequencies can sometimes be adequately resolved (see p.113). Estimates of mortality obtained from changes in population density can also be confounded by the immigration or emigration of mussels between successive sampling dates. The demography of bivalve populations has been extensively reviewed by Cerrato (1980).

Figure 4.10 illustrates the survival of *M. edulis* settlements at two low intertidal sites in Morecambe Bay, England, and shows that few mussels in these populations survived beyond their second or third year (see also Emmett et al., 1987). By following the survival of marked cohorts at three tidal levels on an exposed rocky shore on the North-east coast of England, Seed (1969b) similarly found that mortality in the lower shore was severe, mainly as a result of intense predation. At higher tidal elevations, however, reduced levels of predation led to enhanced survival, although growth rates were considerably reduced. Thus, while lowshore populations consisted almost entirely of mussels that were under three years old, highshore populations often contained twenty or more year classes (Seed, 1969b). Senility, therefore, is unlikely to be a major source of mortality in *Mytilus* under most ecological conditions. Long-lived specimens of *M. edulis* (18–24 years) have also been reported by other workers (Thiesen, 1973), while *M. californianus* appears to experience even greater longevity, with some individuals possibly surviving for 50–100 years in certain relatively undisturbed populations (Suchanek, 1981).

Thiesen (1968) estimated the mortality (cause unspecified) of *M. edulis* in a fishery in the Danish Wadden Sea by observing the amounts and size of mussels laid and refished on the different mussel banks. He concluded that mortality was size-dependent, with the mean annual mortality varying between 68% and 34% in mussels of 25mm and 50mm shell length, respectively. These figures contrast with values of between 74% and 98% for the short-lived but fast-growing Morecambe Bay population studied by Dare (1976). Several workers (Seed, 1969b; Ceccherelli and Rossi, 1984) have suggested that faster growing mussels may be less long-lived because they will attain the size limit imposed by the environment much more rapidly than those living in habitats where growth rates are much slower. Mortality, like growth and reproduction, may also be genetically determined (see Chapter 7 and references therein).

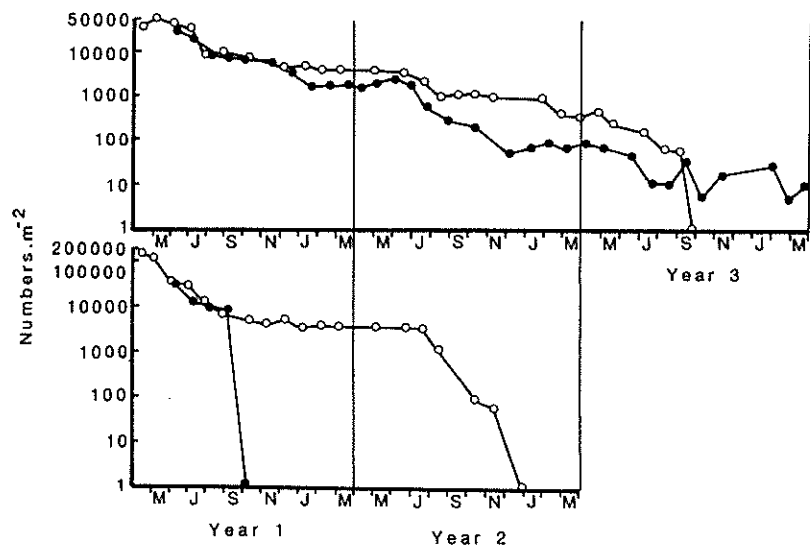


Fig. 4.10. Survival curves for the 1968 (solid circles) and 1969 (open circles) year classes of *Mytilus edulis* at two low shore sites in Morecambe Bay, England. (After Dare, 1976).

## Causes of Natural Mortality

### Physical factors

While *Mytilus* is highly adaptable and especially tolerant of a wide range of environmental conditions, extremes of physical factors such as storms, temperature and desiccation, and excessive deposition of silt are all known to cause mortality in mussels. These factors will vary seasonally and their combined and/or synergistic effects can occasionally result in spectacular mass mortalities.

Mortality from high temperatures and/or desiccation is well-documented (Suchanek, 1978; Peterson, 1979; Tsuchiya, 1983) and physiological intolerance to desiccation is probably the single most important factor determining the upper limits of mussel zonation (p.89–91). Juveniles are especially vulnerable and thus generally tend to settle gregariously into established mussel clumps, where they are presumably afforded somewhat greater protection. Low temperatures can be equally damaging. In Alaska, littoral *M. californianus* exposed to freezing conditions suffered 100% mortality, whereas *M. edulis*, a more eurythermal species, remained alive even after

spending several months frozen solid in ground ice (Suchanek, 1985). Ice crushing or scouring, however, is known to result in heavy mortalities of *M. edulis* populations in boreal regions such as Baffin Island (Stephenson and Stephenson, 1972), Glacier Bay, Alaska (Suchanek, 1985) and the Gulf of St. Lawrence (Bergeon and Bourget, 1986).

Storm generated waves and wave-driven logs can also cause extensive mussel mortality (Dayton, 1971; Lubchenco and Menge, 1978; Witman and Suchanek, 1984; Suchanek, 1985; Denny, 1987 and see section: Disturbance and Recovery, below). Storms are known to act in a density-dependent manner on *M. californianus* (Harger and Landenberger, 1971), and since *M. edulis* has a less robust shell and weaker byssal attachment than its congener, the effects of storm damage in mixed populations depends on the relative abundance of the two species (Harger, 1970, 1972). *M. edulis*, however, is known to be able to adjust its attachment strength according to the prevailing conditions, particularly the degree of water movement (Price, 1982; Young, 1985).

Excessive levels of silt and inorganic detritus (Ceccherelli and Rossi, 1984) and biodeposits (= mussel mud) produced by the mussels themselves (Tsuchiya, 1980) can also be extremely damaging. Thus, while *M. californianus* can attach strongly, and is otherwise well-adapted to waveswept environments, it does not crawl as effectively as *M. edulis*. Consequently, it suffers burial and heavy mortality from excessive siltation in more protected embayments. Suffocation by excessive biodeposits and subsequent destruction of the beds by waves and tidal scour were also identified as major causes of mortality in *M. edulis* in Morecambe Bay (Dare, 1976) and the Menai Strait in North Wales (Dare and Edwards, 1976). Pollution probably only becomes a significant mortality factor when mussels are stressed or perhaps weakened by disease (Sunila and Lindström, 1985).

### Biological factors

The natural enemies of mussels fall into four main categories: predators, parasites, pathogens and competitors for food and space. Parasites and pathogens are discussed in detail in Chapter 12 and with the exception of pea crab infestation, already dealt with on p.120, will not, therefore, be considered further in this section. Organisms which bore into the shell (e.g. *Cliona*, *Polydora*) may cause mortality indirectly by weakening the shell structure, thus increasing the mussel's vulnerability to predators. Blooms of toxic algae can occasionally result in heavy mortalities (Tracey, 1988) although, like many parasitic infections, their effects appear to be mainly sublethal. High levels of natural mortality have also been reported in some populations of *M. edulis* at times of metabolic stress (Emmett et al., 1987). This appears to be related to the relatively poor condition of postspawned mussels when nutrient reserves in the

mantle are at their lowest levels, and is therefore often most severe among larger mussels which have the highest reproductive effort (Worrall and Widdows, 1984). Alternatively, it may be associated with high temperatures (>20°C), particularly at times when food is in short supply (Incze et al., 1980).

Predation is undoubtedly the single most important source of natural mortality in *Mytilus*. Moreover, many mussel predators such as crabs (Jubb et al., 1983; ap Rheinallt, 1986), starfish (Menge, 1972; O'Neill et al., 1983), gastropod molluscs (Hughes and Dunkin, 1984; Hughes and Burrows, 1990) and shorebirds (Incze et al., 1980; Durrell and Goss Custard, 1984; Feare and Summers, 1985; Meire and Ervynck, 1986; Bustnes and Erikstad, 1990; Raffaelli et al., 1990) are known to forage selectively on specific size ranges of *Mytilus*. Consequently, these predators have the potential to influence population size structure as well as overall abundance and local distribution patterns (p.91–94). However, coexistence is often facilitated by virtue of temporal (= size) and spatial refuges, where the impact of the predator is significantly reduced (Seed, 1969b, 1992; Dayton, 1971; Paine, 1974, 1976a; Bayne and Scullard, 1978; Elner, 1978; Campbell, 1983). Because mussels can effectively escape predation by growing out of the size range normally taken by any particular predator, the length of time for which they remain vulnerable will thus depend on growth rate, and this in turn is a function of geographic location and tidal elevation.

The dogwhelk *Nucella* (= *Thais*) *lapillus* is a widely distributed littoral predator in northern Europe and along the Atlantic coast of North America. It is especially abundant on wave-exposed shores, where it feeds extensively on both barnacles and mussels (Seed, 1969b; Menge, 1983). The occurrence of dogwhelks on mussel beds, however, is highly seasonal (Tongiorgi et al., 1981) and during the colder months adult whelks aggregate in crevices and pools as part of their breeding cycle (Feare, 1971a). Emergence from winter aggregations occurs in spring, and over the summer months large numbers of dogwhelks can often be found foraging on *M. edulis* in the middle and lower shore (Fig. 4.11). Feeding in *N. lapillus*, however, may be severely curtailed during periods of desiccation or strong wave action (Hughes and Burrows, 1990). Dogwhelks are also major predators of *M. californianus* along the west coast of North America (Paine, 1974; Suchanek, 1978; Palmer, 1983). However, when given a choice, both *Nucella canaliculata* and *N. emarginata* showed a strong preference for *M. edulis* (Harger, 1972; Suchanek, 1978, 1981). The precise mechanism for such selection is uncertain but is presumably based upon the increased time or energy expended on drilling a thicker shell (containing an extra prismatic layer in *M. californianus*) and/or the potential lower calorific value of *M. californianus* tissue (Suchanek, 1981; Palmer, 1983). Whatever the reason, laboratory experiments have shown that *N. canaliculata* fed on *M. edulis* grow at a significantly faster rate than those fed on *M. californianus* (Palmer, 1983). Mussels attacked by dogwhelks are easily

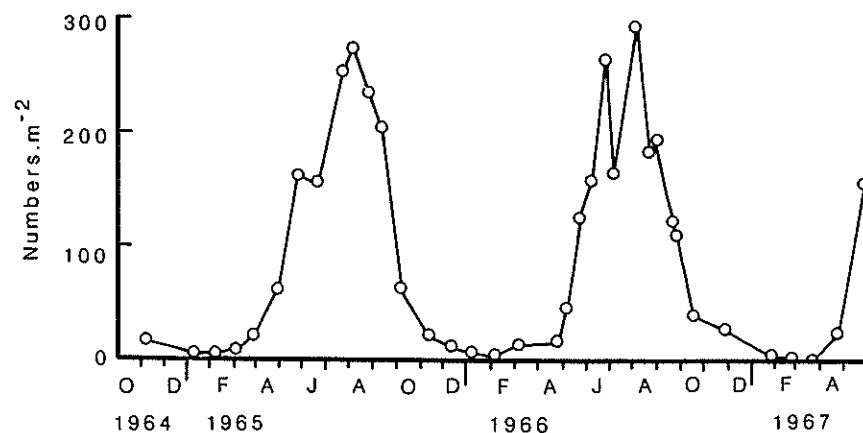


Fig. 4.11. Seasonal abundance of *Nucella lapillus* on low shore *Mytilus edulis* beds at Filey Brigg, England. (After Seed, 1969b).

identified by the small hole drilled through the shell. Most mussels are drilled through the thinnest part of the shell (Seed, 1969b), or above the underlying digestive gland, which is rich in glycogen and is easily digested (Hughes and Dunkin, 1984). Dogwhelks take from several hours to well over a day to handle prey and usually move net distances of <0.2m between meals (Hughes and Drewett, 1985). Feeding rates vary from about 0.1–0.6 mussels whelk<sup>-1</sup> day<sup>-1</sup> depending on shell thickness and temperature (Stickle et al., 1985). Seed (1969b) found large numbers of drilled mussels in the low intertidal zone on the North-east coast of England and attributed the absence of *Mytilus* near deep crevices and pools to locally intense predation as dogwhelks entered and left their dense winter aggregations. Similar high levels of dogwhelk predation have been reported among low-shore populations of *M. edulis* in Alaska, where the average percentage of drilled shells ranged from 61% at protected sites, to 95% on more wave-exposed areas (Suchanek, 1978).

In addition to dogwhelks, several other gastropods such as *Ocenebra*, *Urosalpinx*, *Acanthina*, *Ceratostoma* and *Jaton* are also known to feed on mussels (see Seed, 1976 for references). *Mytilus*, however, is not entirely defenseless as shown by its ability to immobilize predatory gastropods by means of its byssal threads. This method of defense, in which several individual mussels may actually cooperate in subduing the predator, has been observed in response to both dogwhelks (Wayne, 1980; Petraitis, 1987) and oysterdrills (Carricker, 1981). Gastropods are not considered to be important predators of mussels in the Danish Wadden Sea (Thiesen, 1968), nor in Morecambe Bay, England, (Dare, 1976). Similarly, *Thais clavigera* was not identified as an important predator of mussels by Hosomi (1984) in his detailed study of *M. galloprovincialis* in Japan.

Starfish are major mussel predators in many areas. *Asterias rubens* is often present at low densities on most rocky shores in northern Europe but periodically its numbers rise dramatically so that it effectively blankets much of the middle and lower shore. Such areas may then become almost totally denuded of *Mytilus* (Seed, 1969b). Dare (1976, 1982) also recorded large invasions of *A. rubens* in Morecambe Bay; starfish densities up to 450 m<sup>-2</sup> were recorded and the swarm, which at one time covered 2.25ha of ground, may have cleared up to 4000t of first year mussels between June and September. Such swarms of starfish are often very patchy and unpredictable in their occurrence, but are clearly a major factor in controlling the distribution and abundance of *M. edulis* in the lower shore and sublittorally (see Fig. 4.1). As a result of transplantation experiments, Kitching et al. (1959) concluded that *Marthasterias glacialis* was partially responsible for preventing the establishment of *M. edulis* sublittorally in Lough Ine, South-west Ireland, while on the west coast of North America *Pisaster ochraceus* effectively controls the distribution of *M. californianus* on the lower shore. Continued removal of this starfish results in the encroachment by the mussels into areas not previously occupied, eventually producing a virtual monoculture of mussels occupying the primary substratum (Paine, 1974). Asteroid starfish have also been identified as important predators of *M. edulis* on both the Pacific (Suchanek, 1978; Paine, 1980) and Atlantic (Peterson, 1979; Menge, 1983) coasts of North America. Interestingly, a close association between *M. edulis* and the anemone *Metridium senile* appears to afford the mussel significant protection against its asteroid predator *Asterias forbesii* (Kaplan, 1984).

In the low-salinity waters of both the Baltic and Glacier Bay, Alaska, however, the scarcity of mussel predators has effectively allowed *M. edulis* to become the dominant space occupying organism down to depths of 30m and 3m respectively (Kautsky, 1981, 1982b; Suchanek, 1985). Moreover, in view of the low predation pressures (and presumably the low Ca<sup>2+</sup> levels) experienced by Baltic mussels, selection has favoured individuals with thinner shells and smaller adductor muscles, but with a higher fecundity (Kautsky et al., 1990). Consequently, when these mussels are transplanted to fully marine sites in the North Sea, they are more readily attacked and easily pulled open by *Asterias*. Hancock (1965) showed experimentally that mussels with larger adductor muscles were less vulnerable to starfish predation.

In the low intertidal zone of exposed rocky shores of the Pacific North-west Paine (1976a) has documented size-limited predation on *M. californianus* by the seastar *Pisaster ochraceus*. From a series of laboratory choice experiments, in which *P. ochraceus* selected medium-sized *M. californianus*, rejecting both small- and large-sized individuals, McClintock and Robnett (1986) conclude that this species is maximizing energy intake, and minimizing time spent foraging and handling. However, Paine's (1976a) field observations do not support this evidence, since *P. ochraceus* chose *M. californianus* of all sizes, especially small individuals.

Several other reports have shown size-limited predation on mussels: Elner (1978) for *Carcinus maenas* on *M. edulis* (maximum size taken = 70mm); Campbell (1983) for *Asterias forbesii* on *M. edulis* (maximum size taken = 70mm); Briscoe and Sebens (1988) for *Strongylocentrotus droebachiensis* on *M. edulis* (maximum size = 16mm). With unlimited food supply and reduced predation, even *M. edulis* (typically viewed as a relatively small species) can attain sizes (up to 140mm in length at Bodega Harbor, California) well beyond most predators' capabilities (see Suchanek 1978).

Among the many avian predators of mussels, oystercatchers (*Haematopus* spp.) and eider ducks (*Somateria* spp.) are both known to feed extensively on *Mytilus* (Dunthorn, 1971; Heppleston, 1971; Incze et al., 1980; Zwarts and Drent, 1981; Swennen et al., 1983; Goss-Custard and Durrell, 1987; Bustnes and Erikstad, 1990; Raffaelli et al., 1990), and immense flocks of these birds can sometimes be responsible for heavy mortalities, particularly on commercial mussel beds in wave-protected environments. In some years flocks of eider (>4000 birds) in the Ythan Estuary, North-east Scotland, can account for most of the surplus mussel production (Milne and Dunnet, 1972; Baird and Milne, 1981). More than 60% of the adult eider diet is represented by mussels. Raffaelli et al. (1990) showed that over a 60-day period a flock of 500 eiders removed approximately 4500 mussels m<sup>-2</sup> mostly from the preferred (10–25mm) size range. When feeding on mussels eiders remove entire mussel clumps along with the focal prey item, thus generating bare patches within the mussel bed. Eiders can, therefore, have a significant impact on the population dynamics of *M. edulis*, not only through direct predation, but also as a result of increased mortality of the large numbers of mussels shaken from clumps (Raffaelli et al., 1990).

*Mytilus* is often the principal food supply of oystercatchers during the winter months and mussel production appears to be the major factor limiting the density of overwintering flocks in certain areas (Craeymeersch et al., 1986). In the East Scheldt, Holland, oystercatchers consumed about 40% of the annual mussel production (Meire and Eryvynck, 1986). Mussels encrusted with barnacles, however, were rarely taken and there appeared to be strong selection against thicker-shelled mussels. In experiments using mussels as prey, Leopold et al. (1989) showed that oystercatchers tended to select mussels that were easiest to open. Drinnan (1958) estimated that oystercatchers in the Conwy Estuary, North Wales, could ingest their own body weight of wet shellfish per day, with individual birds consuming up to 574 mussels (average length 25.7mm) or 186 mussels (37.5mm) during each low-tide period. By the end of the winter period a significant proportion of the larger mussels had been removed from the population. On more wave-exposed shores small numbers of oystercatchers feed mainly on limpets and dogwhelks and consequently fewer mussels are taken in these habitats (Feare, 1971b). Using exclusion cages, Marsh (1986) showed that birds (black oystercatchers, surf birds and gulls) significantly reduced recruitment of juvenile *M. californianus* and *M. edulis*. Moreover, on surfaces previously lacking



mussels, clumps of *Mytilus* became established within the exclosures but not in the control plots. Other birds that are known to feed on littoral mussels include scooters, sandpipers, knot, turnstones and even crows (Dare and Edwards, 1976; Feare and Summers, 1985; Yamada, 1989; Whiteley et al., 1990).

Crabs, particularly *Carcinus* and *Cancer*, can include large numbers of *Mytilus* in their diet (Kitching et al., 1959; Perkins, 1967; Walne and Dean, 1972; Elner, 1981; Menge, 1983; Ceccherelli and Rossi, 1984; Jensen and Jensen, 1985; Davidson, 1986; Ameyaw-Akumfi and Hughes, 1987; Gardner and Thomas, 1987). Many of the more recent studies of crab predation have focussed on predator preferences, the mechanics of shell crushing and energy maximization (Elner, 1978; Elner and Hughes, 1978; Jubb et al., 1983; Cunningham and Hughes, 1984; ap Rheinallt, 1986). Mortality from crab predation is generally most intense in the lower shore and sublittoral zone, where crabs are particularly abundant, and where they are able to forage for longer periods of time. Ebling et al. (1964) reported extensive crab predation in Lough Ine, South-west Ireland, and tentatively attributed the absence of *M. edulis* sublittorally in many localities to this cause. In the Menai Strait, North Wales, Davies et al. (1980) found that *M. edulis* protected by crabproof fences survived well, whereas unprotected control plots soon became completely denuded of live mussels.

Small mussels are especially vulnerable since these can be easily crushed by virtually all size ranges of crabs, whereas larger mussels are available only to larger crabs with strong chelae. Crabs will often actively select smaller mussels even when larger mussels, which they are capable of opening, are freely available. Vulnerability to crab predation will, therefore, generally decline as mussels increase in body size. Adult *Carcinus maenas* varies in colour from green to red depending at least partially on the length of intermoult. Red and green varieties are now known to have distinct physiological, ecological and behavioural characteristics (Reid and Aldrich, 1989; Kaiser et al., 1990). Green crabs are physiologically more tolerant of extreme conditions, but red crabs are structurally stronger and able to exploit a wider range of prey. In laboratory experiments red crabs exhibited a significant preference for larger *M. edulis* and usually dominated green crabs in aggressive disputes over prey. Harger (1972) showed that both *Cancer antennarius* and *Pachygrapsus crassipes* had a preference for *M. edulis* over *M. californianus*. Predation rates were such that mussels required 6–8 weeks from the time of settlement before they were large enough to escape predation by these crabs, and Harger (1972) concluded that, in order to survive on most rocky shores inhabited by crabs, mussels would have to settle at densities in excess of 10000 m<sup>-2</sup>. When these two mytilids co-occurred the thicker-shelled *M. californianus* was afforded some protection by the presence of its more vulnerable congener.

One predator, whose profound effects on the abundance and distribution of at least two *Mytilus* species has not been recognized widely, is the sea otter *Enhydra lutris* (VanBlaricom, 1988). In central California, sea otters create numerous discrete gaps in

*M. californianus* beds (VanBlaricom, 1988), similar to those formed by log or wave damage (Paine and Levin, 1981), by removing clumps of mussels (of all size classes), which are then sorted and consumed on the sea surface by pounding the mussels on a flat stone on the sea otter's chest, or against other mussels. From these clumps sea otters typically consume individual *M. californianus* from 40–120mm length. Yet even those not selected for consumption and discarded by the sea otters will most certainly experience mortality from other benthic predators, burial on the seabed or eventual stranding in upper intertidal regions as a result of wave action. For the size range of mussels (up to 150mm length) observed in this region there was therefore no effective (size) refuge from sea otter predation (*sensu* Paine, 1976a). Thus, although sea otters are selective in terms of size preference the result of their foraging activities affects all size classes of mussels. Otters usually dive repeatedly in one region during high tide, typically increasing the area of an individual gap by this method, although some observations have been made of sea otters climbing up onto the exposed intertidal zone to forage on mussels (Harrold and Hardin, 1986; and see VanBlaricom, 1988). Although most foraging occurs during the period from January to June, there is tremendous variability in sea otter foraging rates; this variability may be linked to differences in prey quality, or even differences in individual foraging preferences and behaviour (VanBlaricom, 1988).

From data gathered before the 1989 Exxon Valdez oil spill, *M. edulis* comprised up to 40% of the diet of sea otters from Green Island, Prince William Sound, Alaska (Estes et al., 1981; VanBlaricom, 1987, 1988). As with *M. californianus*, clumps of *M. edulis* are removed, then sorted and crushed with the canines and/or consumed whole at the sea surface without the aid of tools. No observations were made of predation during low tide. In contrast to the foraging method used on *M. californianus*, sea otters remove *M. edulis* clumps independently of one another, thereby creating a more patchy landscape with smaller foraging gaps in the mussel beds, except in regions of extreme predation pressure, where vast areas are denuded. Since the largest *M. edulis* found were ca. 90mm, these mussels also could not attain a refuge in size from sea otter predation.

In southern California, nocturnal spiny lobsters (*Panulirus interruptus*) exert a significant influence on the population dynamics of intertidal *Mytilus* spp. (Robles, 1987). Despite continuous recruitment of *Mytilus* into these habitats, no established mussel beds are present at these sites. Here whelks, fish and lobsters consume *Mytilus* but only the lobsters specialize on the mussels. It is not surprising that these lobsters can have such a dramatic impact on mussels since it takes them less than 1.5min on average to consume a small (<20mm) *M. californianus*. While intertidal mussel-foraging by lobsters occurs throughout the year, lobster densities and resultant impacts on mussels during the autumn/winter period are less than half of those during spring and summer (Robles, 1987). American lobsters (*Homarus americanus*) in

Nova Scotia also have a dramatic influence on *M. edulis* populations (Elner and Campbell, 1987), especially at night (Lawton, 1987). Analyses of stomach contents from both adults and juveniles reveal that mussels (*Mytilus edulis* and *Modiolus modiolus* combined) comprise 9.6–16.2% of the lobster diet, although Elner and Campbell (1987) argue that *M. edulis* is the more important prey species.

Fish are well known predators of mussels. In Morecambe Bay, England, Dare (1976) found that the stomachs of 15 flounders, *Platichthys flesus* (23–38cm in length), contained the umbones of an average of ca. 150 young mussels (2–570 fish<sup>-1</sup>). All sizes of mussels from 1 to 15mm were eaten, corresponding to the size range of this population. Eight plaice, *Pleuronectes platessa* of similar size had each eaten 105 mussels on average (30–175), while dabs, *Limanda limanda*, were also reported to feed on mussel spat in this region. Edwards et al. (1982) suggest that fish, especially the cunner (*Tautogolabrus*) may play a significant role in controlling the vertical distribution of *M. edulis* in New England.

Apart from the major groups of mussel predators already mentioned, mammals, including seals and walrus, and even turtles are also reported to feed on mussels (Seed, 1976; Hurd et al., 1979; Suchanek, 1985), while the grazing activities of sea urchins (Briscoe and Sebens, 1988) and limpets (Seed, 1969b; Connell, 1972) may account for some mortality of small, recently recruited mussels, particularly in the low shore. Polychaete worms (Hosomi, 1980) and the polyclad *Stylochus mediterraneus* (Galleni et al., 1977) are also predators of *Mytilus*.

Although sea urchins are known to consume kelp, their omnivorous habit is now being more appreciated, and their consumption of and control over mussel populations is more evident. From observations and field and laboratory experiments in the Gulf of Maine and the St. Lawrence Estuary, it is clear that the sea urchin *Strongylocentrotus droebachiensis* can essentially eliminate *M. edulis* from subtidal habitats (Himmelman et al., 1983; Briscoe and Sebens, 1988). *S. droebachiensis* is a facultative specialist that typically selects *M. edulis* when algal resources are depleted, but its effect is probably not as significant as that of seastars or predatory fish (Briscoe and Sebens, 1988).

It is clear, therefore, that similar suites of predators operate on *Mytilus* in different parts of its geographical range. The impact of many of these predators is often highly seasonal. Crabs and dogwhelks, for example, are generally most active during the spring and summer months, whereas the impact of many avian predators such as oystercatchers occurs mainly during the colder winter months, when huge flocks may be temporarily resident in the coastal zone. Figure 4.12 summarizes the major sources of mortality of *M. edulis* in Morecambe Bay, England, and shows how these mussels become vulnerable to different sources of mortality as they grow, and how this mortality is related to season.

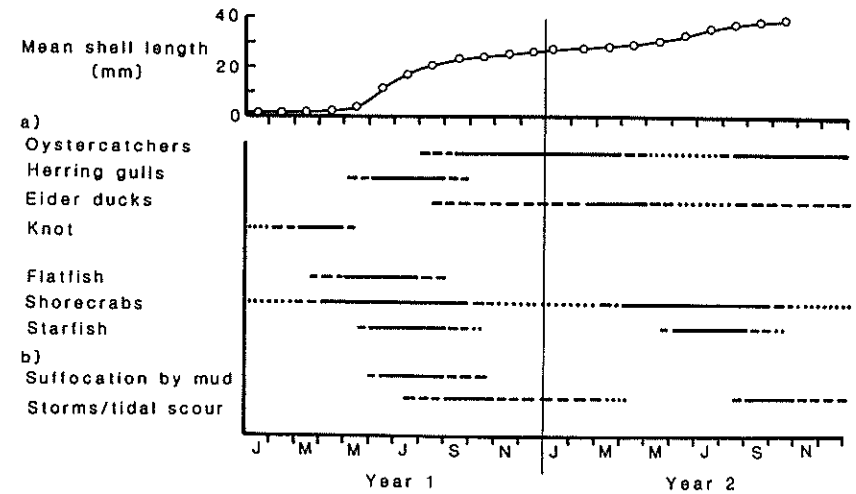


Fig. 4.12. The major identified sources of *Mytilus edulis* mortality from (a) predators and (b) biophysical factors in Morecambe Bay, England, and their effective periods relative to the seasonal growth rate of the mussel population; maximum effects denoted by heavy lines, slight effects by dotted lines. (After Dare, 1976).

Mussels are the supreme competitors for space amongst the ground-covering organisms on horizontal or gently sloping rocky shores (Lewis, 1977) and only rarely do we see other species displacing them from mid to lowshore sites under these conditions. On steeper rock faces mussels are generally less effective spatial competitors and consequently tend to be replaced by barnacles or algae (Lewis, 1964; Paine, 1974; Menge, 1976). Occasionally, however, when two mytilid species co-occur, as do *M. californianus* and *M. edulis* along much of the west coast of North America, interspecific competition can often result in the partial exclusion of one species (Harger, 1972; Suchanek, 1985). Nevertheless, these mussels exhibit very different life history strategies which facilitate their widespread coexistence (Suchanek, 1981).

In a fascinating account of an introduced species, one mytilid (*Mytilaster minimus*) found in the Mediterranean Sea may now be experiencing competitive interference from a second mytilid species (*Brachidontes variabilis*) that migrated through the Suez Canal (Safriel and Sasson-Frostig, 1988). The two species have virtually identical habitat requirements, although different densities of each are found under different conditions of wave exposure. Results of field experiments indicate that adult *B. variabilis* disproportionately inhibit both survivorship and mean shell length of *M. minimus* recruits, but environmental patchiness probably permits coexistence (Safriel and Sasson-Frostig, 1988).

Intraspecific competition can also be a major source of mortality as a result of overcrowding when many of the underlying mussels are suffocated or starved of food. Self-elimination due to intense competition for space is most acute in rapidly growing mussel populations (Griffiths and Hockey, 1987; Richardson and Seed, 1990). Occasionally, this results in the formation of 'hummocks' in which the centrally placed mussels are forced clear of the substratum (see p.147 for possible alternative explanations of hummock formation). Eventually, the whole mussel matrix becomes unstable and is then easily detached by strong wave action or tidal scour (Seed, 1969b; Dare, 1976). In terms of population dynamics, however, this should perhaps be considered as emigration rather than mortality, though many of the detached mussels are transported to unfavourable habitats and subsequently die. Mussel populations experiencing slower growth rates, particularly those with a small terminal body size, will generally exhibit lower rates of competition-induced mortality, although they will remain vulnerable to predators for much longer periods. Such populations are, therefore, more likely to be controlled by predation rather than by competition (Griffiths and Hockey, 1987). In the Exe Estuary, England, McGroarty et al. (1990) showed that the mortality of *M. edulis* during their first winter was strongly and positively density-dependent. This provided a powerful regulating mechanism by which the adult population was effectively stabilized despite wide annual variations (up to  $\times 17$ ) in the density of juvenile mussels.

Fouling organisms are increasingly being recognized as significant sources of mortality in littoral and sublittoral mussel populations (Paine, 1979; Suchanek, 1985). Mortality usually occurs when mussels are dislodged as a result of the increased weight or shearing stresses in the form of drag or lift imposed on them by the fouling organisms, especially by barnacles and seaweeds (Witman and Suchanek, 1984; Denny, 1987). Feeding currents may also be restricted or even totally occluded if the valve openings are overgrown. Even without causing outright mortality, fouling organisms may lower the fitness of mussels by reducing body tissue and/or gamete development (Paine, 1976). The mechanism responsible for such lowered fitness is probably related to reduced food intake, or to the greater expenditure of energy on maintenance and the production of byssus for more secure anchorage (see also p.143–144). Fouling, especially by ascidians, is often a major problem on rope grown mussels (Mason, 1972 and see p.487 Chapter 10). Fouling organisms, however, are not always detrimental to their hosts. A recent period of freezing temperatures along the Pacific coast of North America resulted in mass mortality of *M. californianus*. However, mussels, which were insulated with the epiphytic alga *Endocladia muricata*, survived the freeze, whereas those without the epiphyte died (Brosnan, 1990).

## THE *MYTILUS* BED COMMUNITY

### The *Mytilus* Matrix and Associated Fauna

*Mytilus* aggregations are highly productive assemblages. *Mytilus californianus*, the largest *Mytilus* species from the North American continent, typically has a range of mussel abundance of 459–11,098 individuals  $m^{-2}$  (mean  $5,795 \pm SD 3,451$ ) (Suchanek, 1979), a calculated mussel meat standing crop of 1.3–6.5kg  $m^{-2}$  dry wt (energy = 29–144J  $mm^{-2}$ ) and a mussel meat productivity of ca. 0.2–1.9kg  $m^{-2} yr^{-1}$  dry wt (energy = 3.8–42J  $mm^{-2} yr^{-1}$ ), rivalling the productivity of some of the most productive rainforests (Leigh et al., 1987). This compares with *M. edulis* communities from the Bay of Fundy with mussel abundance of 700–4,000 individuals  $m^{-2}$  (Newcombe, 1935), Narragansett Bay, Rhode Island, where whole mussels represent ca. 77% (11kg  $m^{-2}$ ) of the total community dry weight and the mussel meat represents ca. 82% (1.5kg  $m^{-2}$ ) of the total community meat dry weight (Nixon et al., 1971); Morecambe Bay, England, where mussels have a maximum standing crop value of 1.5kg  $m^{-2}$  AFDW (Dare, 1976), and the northern Wadden Sea (North Sea) with numerical abundance values of ca. 1,631  $\pm$  151 individuals  $m^{-2}$ , a range of standing crop values for whole mussels of 0.9–1.4kg  $m^{-2}$  AFDW (which is ca. 25 times higher than other communities in the Wadden Sea), and a range of whole mussel productivity values from 0.2–0.6kg  $m^{-2} yr^{-1}$  AFDW, 93% of which is due to the mussels themselves, and 7% to the organisms found in association with the mussels (Asmus, 1987). In comparison, Craeymeersch et al. (1986) found mean densities of *M. edulis* in the southwestern Netherlands of 1,590  $m^{-2}$  and annual productivity of mussel flesh of 0.16kg  $m^{-2} yr^{-1}$  AFDW, whereas Kautsky (1982a) found densities of 36,000–158,000  $m^{-2}$  (see Thompson, 1984b) in subtidal Baltic Sea populations. These extremely productive populations most likely result from a significant lack of predatory pressures on *Mytilus* in totally submerged populations (Kautsky, 1981). *M. galloprovincialis* communities from Italy show similar trends, with numerical abundance values for mussels of 333–11,536  $m^{-2}$  (extrapolated from 600cm<sup>2</sup> samples) which comprise ca. 4.7–91.2% of the benthic community biomass at these sites (Tursi et al., 1985). Comparable values for the closely related mytilid, *Perna perna*, yield mussel numerical abundance values of 633–1587  $m^{-2}$  (extrapolated from 100cm<sup>2</sup> samples), and standing crop estimates for whole mussels of 0.4–1.4kg  $m^{-2}$  AFDW, of which *Perna* alone represents 82–94% (Jacobi, 1987a).

*Mytilus* assemblages have long served as the focal point for numerous empirical and theoretical studies on population and community ecology, especially the importance of predation and disturbance events on structuring marine intertidal communities. In the past, most attention has been focussed on *Mytilus* population dynamics *per se*, although many investigators have referred to the mussel populations as *Mytilus* communities or mussel communities, probably because they represent neatly

identifiable entities and dominant biomass structural components within specific regions of the intertidal zone (Shelford et al., 1935; Hewatt, 1937; Rigg and Miller, 1949). Paine's (1966, 1969) seminal works on the regulation of *Mytilus* 'community' diversity by predation, and Dayton's (1971) analysis of physical disturbance on *Mytilus* populations, have stimulated a wide variety of studies on processes responsible for regulating community structure in rocky intertidal systems, as well as many other habitats. However, these studies have dealt almost exclusively with the dominant biomass component (mussels) and/or other primary space occupiers, with little reference to the diverse biological community found associated with the mussels. Hewatt (1935), Newcombe (1935) and Ricketts and Calvin (1939) were among the first to address taxonomic complexity within *Mytilus* beds, but not until recently has the full extent of this diversity been appreciated and more fully documented (see Suchanek, 1979, 1980, 1985; Kanter, 1978, 1980, and Paine and Suchanek, 1983 for *M. californianus* beds; Tsuchiya, 1979 and Tsuchiya and Nishihira, 1985, 1986 for *M. edulis* beds; Tsuchiya and Bellan-Santini, 1989 for *M. galloprovincialis* beds).

As *Mytilus* beds age and grow, they increase not only their biological component, the living mussels, but they also enlarge their physical component, producing structurally complex entities that are capable of harbouring a diverse assemblage of associated fauna and flora. Bed thickness, connectedness between individuals and sediment loading are all increased within the bed, changing dramatically the microhabitats under, between and around the mussels. Although only the bottom layer of mussels is attached to the primary substratum, individuals in subsequent layers solidify the bed structure by interconnecting byssal threads to many neighbouring individuals. This usually forms a dense structure with numerous interstices, which provides refuge for a myriad of associated fauna. Thus, *Mytilus* beds are composed primarily of three components: (1) a physical matrix of interconnected living and dead mussel shells, which may occur as a monolayer or multilayer up to five or six mussel layers deep, (2) a bottom layer of accumulated sediments, mussel faeces and pseudofaeces, organic detritus and shell debris, and (3) a taxonomically diverse assemblage of associated fauna and flora (Suchanek, 1979).

The data given below on associated fauna and flora pertain primarily to characteristics of naturally occurring mussel beds, although there are also data on associated organisms in cultured *Mytilus* populations (Plessing, 1981; Mattsson and Linden, 1983).

Considerable progress has been made in understanding the development of diverse *Mytilus* communities (Suchanek, 1979, unpublished results; Tsuchiya and Nishihira, 1985, 1986). Unless indicated, the information presented below has been gleaned from the works cited in the preceding sentence. In general, mussel bed thickness and structural complexity increase with mussel bed age. Sediments and debris accumulate in direct proportion to the thickness of the beds. Further mussel recruitment

promotes even greater physical and/or chemical changes and as more layers are added, existing microhabitats are modified and new ones created. Observations by Newcombe (1935) indicate that for a *M. edulis* bed on soft substrata, sediments beneath the bed become more anoxic with increased mussel cover, thereby eliminating some infaunal bivalve species such as *Mya arenaria*. Nixon et al. (1971) found that *M. edulis* beds in Rhode Island contained ca. 14.4kg m<sup>-2</sup> dry wt of trapped sediment with a mean organic content of 3.86%. For *M. californianus* beds ca. 24cm thick from Tatoosh Island, Washington, dry weight of sediment can exceed 80kg m<sup>-2</sup> (Suchanek, 1979).

Mussel beds can attain considerable thickness, with intertidal *M. edulis* beds reaching 10cm thickness (Nixon et al., 1971), subtidal *M. edulis* beds being reported as thick as ca. 120cm (Simpson, 1977), and intertidal *M. californianus* beds attaining a maximum thickness of ca. 40cm (Suchanek, unpublished results). In *M. californianus* beds, mussel shells also increase the ratio of shell surface area to rock surface area by multipliers of ca. 5 (in monolayered beds) to 30 (in multilayered beds), providing considerable increased substrata for settlement of associated fauna and flora (Suchanek, unpublished results). Within the interstices of this matrix light, temperature and wave action are diminished, whereas sedimentation and relative humidity are increased. Figure 4.13 illustrates the significant changes in microhabitat regimes as both temperature and relative humidity are altered at various depths within *M. californianus* beds on the west coast of North America at Tatoosh Island, Washington and Bodega Bay, California (from Suchanek, unpublished results). On a sunny day, temperatures at the base of a 25cm thick *M. californianus* bed can be 5-13°C cooler than at the surface, whereas relative humidity can increase by ca. 15%, affording greater protection to species with more restricted physiological tolerances to these parameters.

Community diversity within mussel beds is surprisingly high. Species richness (S) and the Shannon-Wiener diversity index (H') increase with both mussel bed age and thickness. *M. edulis* from Northern Ireland had at least 34 associated species within the interstices of the bed, of which nearly half are Crustacea (Briggs, 1982). For *M. edulis* beds in Japan, Tsuchiya and Nishihira (1985, 1986) found that S was greatest in older and larger beds, and H' and Margalef's equitability index (J') were higher at the perimeter and central portions of adult beds than in young beds or old beds. Although 69 species representing eight phyla were found in this community, 98% of the individuals encountered were accounted for by three phyla: Annelida (46%), Arthropoda (39%), Mollusca (13%), and no algae were reported. Surprisingly, Asmus (1987) found no correlation of increased biomass of associates with increased *M. edulis* density in the northern Wadden Sea. Also surprising is the low species richness (12 taxa), and no significant increase of species richness of associated fauna inside *M.*

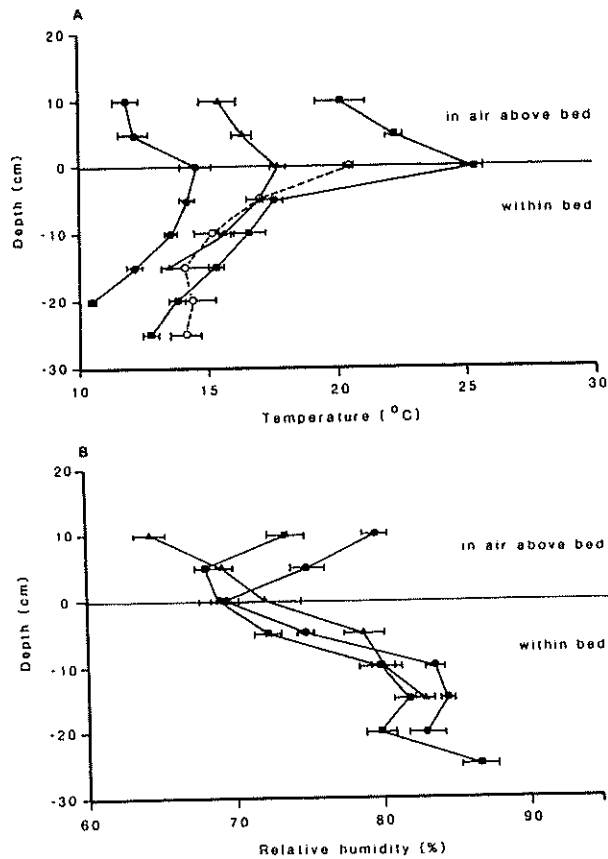


Fig. 4.13. Variations in (A) temperature and (B) relative humidity above and within dense beds of *Mytilus californianus* from three sites in Bodega Bay, California, North America (closed symbols), and one site at Tatoosh Island, Washington state, North America (open symbols); central symbols are mean values (typically  $N = 5$ ), error bars are  $\pm 1$  SE.

*edulis* beds, as compared with those found outside mussel beds in Maine, U.S.A., documented by Commito (1987).

For *M. californianus* in Washington, Suchanek (1979, 1980) sampled mussel beds over a variety of thicknesses, tidal heights and exposure conditions. He found that  $S$  (but not  $H'$  or  $J'$ ) increased with mussel bed age, and decreased with tidal height at most study sites to a maximum of about 135 taxa for any one sample (ca. 30 x 30cm)

yielding a total community  $S$  of over 300 taxa representing three divisions of macroalgae, 12 phyla of invertebrates and 3 species of bony fish. Nearly 90% was accounted for by four phyla: Arthropoda (38%, with barnacles alone comprising 24%), Mollusca (35%), Bryozoa (9%) and Annelida (7%). All sites showed a significant increase in  $S$ ,  $H'$  and  $J'$  with increasing mussel bed thickness. Species richness showed a significant inverse correlation with tidal height and only suggestive (nonsignificant) positive trends with increasing wave exposure. For samples of ca. 0.10m<sup>2</sup>,  $S$  ranged from ca. 25 species at upper intertidal low-wave exposure sites, to 135 species at low intertidal high-wave exposure sites. As a comparison, *Perna perna* beds from Brazil also harbour a diverse fauna, with Crustacea (70%), Polychaeta (6%) and Cnidaria (6%) making up the most numerically abundant taxa, although no quantitative species richness or diversity values were given (Jacobi, 1987a).

Selected taxa specialize on specific microhabitats within the mussel matrix. Some prefer the organically rich sediments at the base (bivalves, sipunculids and some polychaetes); some prefer the interior facies of old broken mussel shells (bryozoans and hydroids); and some only the surface mussels (algae and most barnacles), although other species are distributed throughout the entire vertical strata (sea cucumbers, anemones, boring clionid sponges, crabs, nemertean and errant polychaetes) (Suchanek, 1979). While there is some overlap between groups, associated fauna and flora can be divided into three major categories based on their interaction with, or relative position within, the mussel matrix (Suchanek, 1979). 'Epizoans', typically ranging from 17–33% of the associated species, are sessile forms that use the mussel shells directly as a substratum; they either grow on or bore into mussel shells. Examples include all attached algae, barnacles and hydroids. 'Mobile fauna' (58–74% of associates) may include representatives from many trophic and/or taxonomic groups, but at least have the ability to move freely throughout the mussel matrix. Examples include porcellanid crabs, numerous amphipods and isopods and free-roving gastropods. 'Infauna' (5–21% of associates) are those organisms that are associated with, and usually directly dependent upon, the sediment and/or accumulated detritus at the base of the mussel bed, and are species typical of most soft sediment environments. Examples include sipunculids, sediment dwelling polychaetes and ophiuroids. Furthermore, while some sediment contributes to habitat heterogeneity and the promotion of diversity for some taxa, an excess in mussel beds has been found to adversely affect some amphipod assemblages (Tsuchiya and Nishihira, 1985; Jacobi, 1987b).

The specialization that derives from the microhabitat differences encountered by fauna and flora within different regions of the mussel matrix results in a predictable vertical stratification. For example, because algae need high levels of incident radiation, they are always found on the upper surfaces of the mussel matrix. The common sea cucumber found in *M. californianus* beds, *Cucumaria pseudocurata*,

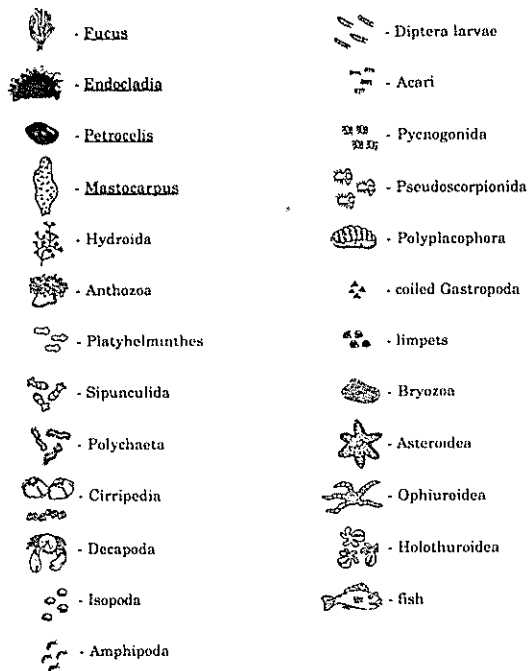
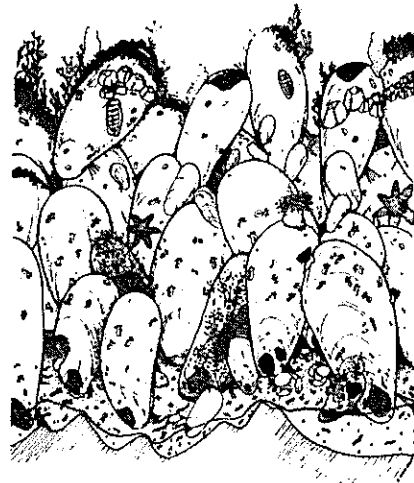


Fig. 4.14. Diagrammatic cross section through a dense *Mytilus californianus* bed from Tatoosh Island, Washington state, North America, showing vertical stratification of typically abundant fauna and flora.

from data obtained in laboratory tanks, has the ability to move throughout the bed, but typically chooses sites in the mid to lower region, and specializes in the consumption of *Mytilus* faeces and pseudofaeces (Suchanek, unpublished results). Figure 4.14 is a diagrammatic cross-section through a *M. californianus* bed showing the vertically stratified nature of these typical associated fauna and flora (from Suchanek, 1979). The specific nature of preferred site selection within a mussel matrix by associated fauna has been shown even on the scale of individual mussel shells. Laihonen and Furman (1986) reported site-specific settlement of a barnacle epibiont, primarily near the siphonal aperture, on *M. edulis* from the Baltic Sea.

### *Mytilus* Dislodgement by Biota

Habitat energy regimes can influence greatly the byssal attachment strength of intertidal mussels, and therefore play a critical role in protection from dislodgement. Byssal attachment strength of *M. californianus* is significantly greater than that of its smaller congener *M. edulis* and is significantly greater at the edges of a bed than at the periphery (Witman and Suchanek, 1984). Other information on differences in attachment strengths between *M. galloprovincialis* and *M. edulis* is provided in Skibinski and Gardner (1991). Attachment strength for *M. edulis* from exposed habitats is ca. 15 times higher than in protected habitats (Witman and Suchanek, 1984), and in experiments where *M. californianus* were held down under plastic covered mesh in exposed rocky intertidal habitats, those mussels that were held down firmly seldom or never laid down byssal threads (Suchanek, unpublished results). However, those that were loose under the plastic developed numerous byssal attachments, presumably in order to stabilize their positions. These data indicate that *Mytilus* detects and responds to movement by wave energy or drag forces by the production of increased numbers of byssal threads.

Despite increased production of byssal threads, excessive fouling by epibionts can increase significantly the risk that mussels will be dislodged from the primary substratum (Dayton, 1971, 1973; Paine, 1979; Witman and Suchanek, 1984; Witman, 1987). In general, low-profile epizoans (e.g. sponges, bryozoans, encrusting coralline algae) that form thin encrustations and do not increase the vertical relief of the mussel, do not place mussels at much risk of dislodgement, but those epibionts (e.g. macroalgae, kelp, barnacles) that increase the effective height of mussels above the mussel bed plane will lead to increased drag and lift amplification and higher risk of dislodgement (Witman and Suchanek, 1984; Denny, 1987; Suchanek, unpublished results). Another generalization is hypothesized for encrusting epizoans (e.g. tunicates, sponges) which might occlude the feeding gape of mussels, and thereby

cause death, dislodgement or lowered fitness through a weakened state due to starvation (Paine, 1976b; Suchanek, unpublished results).

### Symbiosis

At least four types of symbioses, commensalism (+0), amensalism (-0), parasitism (+-) and mutualism (++), have been reported between mussels and their associates. Barnacle settling patterns on live *M. edulis*, result in significantly faster barnacle growth rates as a result of enhanced food resources, indicating a commensal relationship (Laihonon and Furman, 1986). Over 76% of those barnacles settling on live mussels chose the region closest to the siphonal aperture and, during a 10-week period, grew an average of 4mm larger (rostrum-carinal length) than those settling on dead mussel shells. No significant difference in growth rates was observed between mussels with and without barnacle fouling. It is interesting to note that in many cases *M. edulis* is able to clean itself by sweeping its prehensile foot over the dorsal part of the shell (Thiesen, 1972), whereas *M. californianus* lacks that capability. Although fouling does occur on *M. edulis*, this may help to explain why Tsuchiya and Nishihira (1985, 1986) reported no algae fouling *M. edulis* in their study of associated organisms (see above).

In southern California, U.S.A., facultative red algal epiphytes have a negative effect on both the survivorship and reproductive capabilities of *M. californianus* and provide virtually no protection to the mussels (Dittman and Robles, 1991). In an epiphyte removal experiment, overgrown mussels had significantly lower growth rates and gonad weights than comparable individuals that were cleaned of their epiphytes.

In Oregon, U.S.A., the red alga *Endocladia muricata* can have a variable influence on *Mytilus*, depending on the environmental conditions (D. Brosnan, 1990 and personal communication, 1990). Under heavy wave action *M. californianus* individuals that are heavily fouled with *Endocladia* are dislodged at a significantly higher frequency than those without fouling. *Endocladia* also likely interferes with mussel feeding and growth, resulting in a clearly amensal relationship. However, as described already (p.136) mussels that are fouled by *Endocladia* are also insulated from extremes in temperature, and survive drastic freezes at significantly higher rates than those without such epiphytic growth, producing a commensal (or possibly mutualistic) relationship.

The lack of shell cleaning ability by *M. californianus* may help to explain why associated grazers (e.g. limpets, snails and chitons) are especially important in reducing excessive epibiotic fouling on this species, and why a mussel-grazer mutualism may be essential in maintaining community stability for this assemblage

of mussels and associates (Suchanek, 1979). *M. californianus* beds harbour high densities of mobile grazers, ca. 3–16 times that of the surrounding open rock substratum. Several factors contribute to these increased densities since *M. californianus* beds provide significant benefits to grazers: (1) increased surface area on mussel shells increases grazer food resources; (2) modified microhabitat regimes within the interstices of the mussel matrix provide protection from extremes in physical variables such as relative humidity and temperature, and (3) the mussel bed matrix provides mobile grazers with a spatial refuge from visual predators. Grazers, in turn, provide significant benefit to the mussels: (1) they remove potentially harmful epibiota, reducing the risk that mussels might be fouled extensively and then dislodged when they encounter high-wave conditions, and (2) grazers enhance the speed of mussel bed recovery from disturbance by nearly seven-fold. As a result, grazers stabilize the physical mussel matrix, within which a diverse community of associates has developed. In so doing, this mutualistic association also enhances the stability of the entire mussel bed community (Suchanek, 1979, 1985).

Grazers not only reduce algal cover on the mussels themselves, but often produce distinctive patterns (browse zones) within and around *Mytilus* beds that indicate the intensity and extent of grazing (Suchanek, 1978; Sousa, 1984). Figure 4.15 illustrates the nature of browse zones at the perimeter (upper) and within disturbance gaps (lower) in *M. californianus* beds from Shi-Shi, Washington state, showing the relative distance travelled by molluscan grazers foraging out from the mussel matrix. Similar patterns are found in *Perumytilus purpuratus* beds in Chile (Suchanek, unpublished results). In a series of experiments Suchanek (1979) erected experimental barriers that prevented the movement of grazing molluscs at the exterior and interior edges of *M. californianus* beds at Tatoosh Island and Shi-Shi, Washington, and demonstrated that browse zones are indeed created by the foraging activities of molluscan grazers. Since the mussel bed matrix provides refuge from visual predators such as birds, mobile grazers typically remain within the interstices of the bed during low tide. When *M. californianus* beds are submerged grazers usually migrate out ca. 20cm from the edges of the bed, creating a halo effect of reduced algal cover (Suchanek, 1978, 1979, and Fig. 4.15 upper). When disturbance gaps are formed in the central portions of these same *M. californianus* beds, grazers also forage ca. 20cm into the gaps to consume algae within that zone (Fig. 4.15 lower). This effectively alters the successional sequences and replacement order of gap colonizing species (see section: Recovery from disturbance, p.149ff).

## DISTURBANCE AND RECOVERY OF *MYTILUS* BEDS

### Disturbance

The integrity and physical stability of *Mytilus* beds depends directly on the attachment strength of their byssal threads. In general, mussels appear to respond to increased wave force by the production of greater numbers of byssal threads. *M. edulis* produce more byssus during stormy winter periods than in calm summer periods (Price, 1980, 1982) and *M. californianus* produce stronger (more numerous) attachments at the edges of beds than in the central regions (Witman and Suchanek, 1984). However, when byssal thread attachments are disrupted, individual or groups of mussels within the matrix are dislodged and disturbance gaps are formed. These gaps within mussel beds may be initiated by either physical factors (Dayton, 1971; Levin and Paine, 1974, 1975; Paine and Levin, 1981; Sousa, 1985; Denny, 1987), or biological processes (Paine, 1966, 1969, 1974, 1979; Dayton, 1971, 1973; Suchanek, 1978; Witman and Suchanek, 1984; Paine et. al., 1985; VanBlaricom, 1988). Wave action (Dayton, 1971; Paine and Levin, 1981), epizoism (Denny, 1987), or predation (Van Blaricom, 1988) are likely to lead to subsequent expansion of these disturbance gaps.

The mechanism of initial gap formation in *Mytilus* beds may involve a single process or a combination of processes: log battering, wave action, fouling, and hummocking. Log damage seems to occur more frequently in regions of heavy logging (Dayton, 1971). Wave action most likely involves a combination of drag (Witman and Suchanek, 1984) and fluid dynamic lift (Denny, 1987) from breaking waves, especially if mussels are significantly fouled by epibiota. Heavy fouling, particularly by the brown algae *Fucus* and *Postelsia* and the barnacle *Semibalanus cariosus*, is especially common in regions where mobile predators or grazers are absent, or in low density. Heavy fouling by these three taxa is common on dislodged *M. californianus* that have been washed ashore along outer coast beaches (Witman and Suchanek, 1984; Suchanek, unpublished results). Hummocking, the phenomenon where mussel clumps are raised above the ambient level of the bed because they lack byssal attachments to the primary substratum but remain attached to each other, is a common feature of some *M. californianus* beds in Washington.

Hummocks may be formed by intense intraspecific pressures as young mussels grow larger within the matrix of the bed forcing other individuals upwards without making firm byssal attachments to the primary substratum. Or, they may also be formed by biological agents such as decapods, either purposefully or mistakenly nipping at *Mytilus* 'feet' as the mussels attempt to extend them to secure byssal attachments. Hummocks are often connected to other hummocks by small tunnels with the same characteristics, and are typically inhabited by vast numbers of crabs such as *Petrolisthes* spp. (Fig. 4.16). Because of the weak attachment of these hummocks to

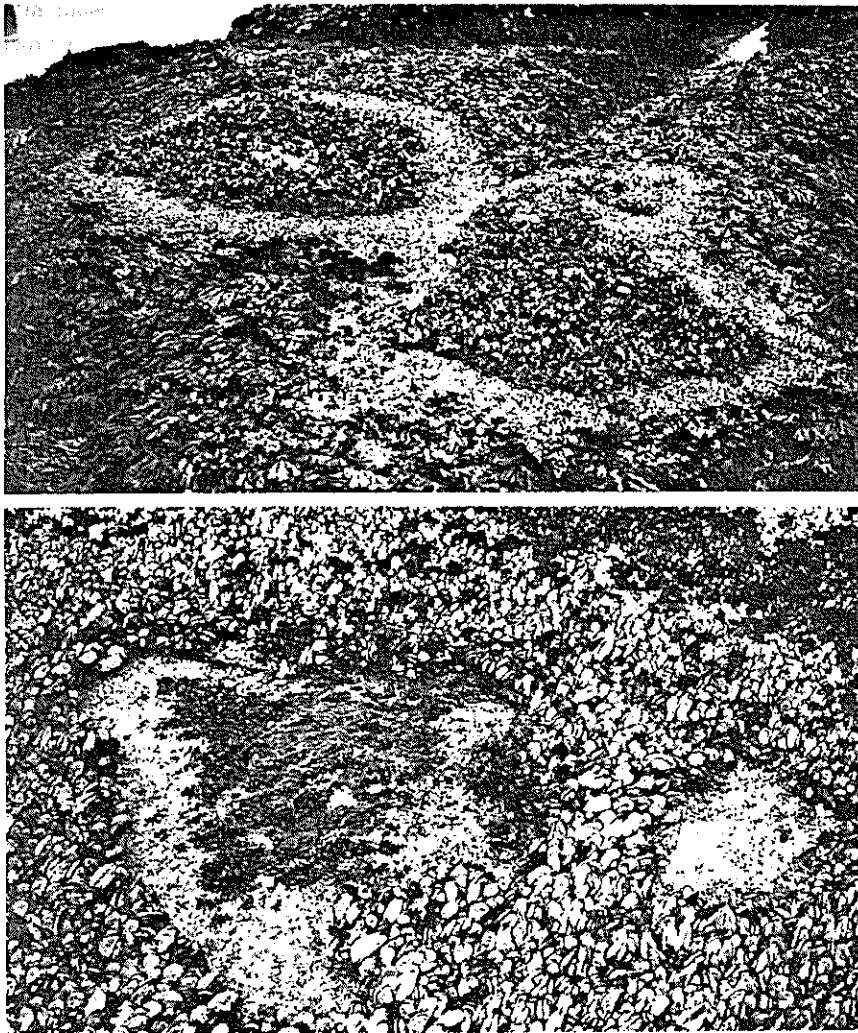


Fig. 4.15. Browse zones of bare space created by molluscan grazers associated with *Mytilus californianus* beds in Washington state, North America. External browse zones, about 20 to 30cm into the surrounding *Fucus* cover (upper), surround two isolated *M. californianus* beds at Shi-Shi. Internal browse zones (lower) extend inwards about 20cm into the *Porphyra* covered central region of a natural disturbance gap at Tatoosh Island. The smaller disturbance gap in (lower) has a diameter of about 20cm and therefore is devoid of all algal growth (see text).





Fig. 4.16. Diagram of hummocks in *Mytilus californianus* beds at Tatoosh Island, Washington state, North America. Note that such hummocks are typically connected by tunnels or passageways and populated with high numbers of porcellanid crabs.

the primary substratum, they may serve as initiation sites in the formation of disturbance gaps (Denny, 1987).

Gap formation in *Mytilus californianus* mussel cover resulting from wave or log damage occurs most frequently during the winter season and can disrupt up to 65% of some mussel beds in one season; studies over six winters (199 site-years of data) showed typical removal rates of ca. 0.4–5.4% of the mussel cover per month, with 89% of the disturbances affecting <25% of the beds each winter (Paine and Levin, 1981). The remaining observations span the range from 25–65% and might, more appropriately, be termed catastrophes, not an event to which *M. californianus* beds are typically exposed each winter. Gaps which occur in summer are smaller and may form 5–10 times slower (Paine and Levin, 1981). The initial size of disturbance gaps from wave or log damage in *M. californianus* beds ranges from the size of an individual mussel to areas of ca. 57.5m<sup>2</sup> and the distribution of gap sizes approximates a log-normal (Dayton, 1971; Suchanek, 1979; Paine and Levin, 1981). Subsequent enlargement may result in a nearly 5000% increase in gap size (Dayton, 1971), most likely as a result of weaker byssal thread attachments in the central portions of the beds, where the gap was initiated, than at the edges (Witman and Suchanek, 1984). Only 1.6% of such disturbance gaps subsequently enlarged when they were formed during or just prior to summer months (when wave action is minimal), but over 21% of comparable gaps enlarged when they were formed during or just prior to winter months (Paine, 1989).

Biological disturbances that disrupt the *Mytilus* matrix, such as predation by crabs and seastars or epizoism by algae (e.g. *Fucus* or *Postelsia*), usually occur on the scale of individual or few mussels, although the actions of the predatory seastar *Pisaster* can result in larger gap formation in *M. californianus* beds. This is done by the removal

of one or several mussels from the matrix, which can then undergo enlargement as described above.

Sea otters also cause disturbance gaps in both *M. edulis* and *M. californianus* beds. At one site in central California, sea otter predation removed about 20% of the *M. californianus* cover, where the mean size of gaps was 0.25m<sup>2</sup> (range = 0.03–1.34m<sup>2</sup>) (VanBlaricom, 1988). In this study sea otters created more gaps than did wave/log damage. The size-frequency distribution of these gaps is quite similar to those produced by wave or log damage in Washington state (Paine and Levin, 1981), although wave or log damage produced more smaller and more larger gaps in mussel beds than did sea otters. In Alaska, a major immigration of male sea otters is believed to have been responsible for a large-scale *M. edulis* mortality event (100% in some regions) in Prince William Sound during the winter of 1979–80, but the mussel beds recovered quickly and returned to moderately dense coverage in 1984 (VanBlaricom, 1988).

Twenty six percent of sea otter generated gaps enlarged before they healed, which in some cases took over two years (VanBlaricom, 1988). This increased the chance that various subsections of the gap might be set to different successional ages, and therefore might experience different successional processes; thus, making the patch mosaic of primary space occupiers even more complex in regions inhabited by sea otters, than in areas where gaps are formed from wave or log damage.

Within the context of the variable disturbance events described above, *Mytilus* beds have been characterized as having 'mosaic' patterns composed of disturbance gaps with a wide variety of alternative primary space occupiers, most of which are found in gaps of varying ages and varying successional stages.

#### Recovery from disturbance

Nearly complete recovery from physical and/or biological disturbance is a characteristic common to *Mytilus* beds throughout the world. Most *Mytilus* assemblages are fairly dominant and persistent features of the habitats in which they occur, and their superior ability to regain lost space has been interpreted as a deterministic process (e.g. Paine, 1974, 1984). Parameters that influence this reclamation process are: size of initial disturbance gap, season of disturbance, height of mussel bed on the shore, angle of substratum, age of bed and intensity of larval settlement.

Paine and Levin (1981) provide substantial documentation on the basic recovery process for mid intertidal *M. californianus* beds. In their study, recovery of very small gaps was almost instantaneous (0.2cm day<sup>-1</sup>) due to leaning or collapse of the adjacent mussel matrix, especially if the surrounding matrix was thick. For intermediate sized gaps (<3.0m<sup>2</sup>) their recovery was slower (0.05cm day<sup>-1</sup>) and more dependent on lateral movement of mussels from the edges of the disturbance gap. For very large gaps

mussels may settle directly from the plankton onto the primary substratum or onto filamentous substrata within the gap. Alternatively, mussel recolonization into large gaps can be enhanced by two other mechanisms. Firstly, *M. californianus* larvae tend to settle most heavily onto conspecific byssal threads; therefore, byssal threads of adult mussels that have been dislodged from other regions and reattach within the gap, provide foci for mussel larvae settling from the plankton (Suchanek, 1978, 1981), thus enhancing gap healing. Secondly, mussels dislodged from the primary substratum leave remnant byssal threads, which remain in the gap for several months after a major disturbance, and these threads can act as similar foci for mussel larval settlement/recruitment (Suchanek, unpublished results; see also p.108–112).

A predictable series of biological events accompany the recolonization of disturbance gaps in mid intertidal *M. californianus* beds in Washington (Suchanek, 1979; Paine and Levin, 1981). Remnant byssal threads typically remain on the primary substratum for about 10mo. During this period, the substratum is first colonized macroscopically by diatoms and filamentous algae, as well as by barnacles and *M. edulis*. The latter may persist as a fugitive in these gaps up to three years from the initial disturbance event, with coverage sometimes reaching 70–80% of the gap at extrapolated densities of ca.  $12,400 \pm 5990$  individuals  $m^{-2}$  (Suchanek, 1978, and unpublished results). This allows ample time for *M. edulis* to attain reproductive size and spawn (Suchanek 1978, 1981). During this phase the gap substratum is also colonized by numerous algae and balanomorph and gooseneck barnacles, during which time *Nucella* dogwhelks, at mean densities of ca.  $50\text{--}75 m^{-2}$ , consume a majority of the *M. edulis* (Suchanek, 1978, 1981; Paine and Levin, 1981). Typically, ca.  $85 \pm 14\%$  of the dead *M. edulis* shells surveyed within the boundaries of these gaps show clearly identifiable *Nucella* drill holes (Suchanek, 1978). Similar processes appear to occur in *M. californianus* gaps in California, but the *M. edulis* are consumed at such a rapid rate that they likely never reach reproductive size (Sousa, 1984).

*M. californianus* first colonizes these gaps about 20–26mo after the initial disturbance, and rapidly increases its coverage of the substratum to over 80% after about 36mo, with a matrix about 14cm thick, consisting of 2–3 mussel layers. After 60–80mo the substratum is completely reclaimed by *M. californianus*, with a 15–20cm thick matrix comprising 3–4 mussel layers. Figure 4.17 illustrates this sequence of recolonization events at a site on Tatoosh Island, Washington state over 15 years. After complete coverage of the substratum the mussel bed continues to increase in thickness to a maximum of about 40cm with 5–6 mussel layers.

Seasonality is also critical to the sequence of recovery events that follow. In addition to an increased rate of gap enlargement during winter seasons, as compared with summer seasons (see above), the rate of recovery is also significantly reduced during winter months (Suchanek, unpublished results). Figure 4.18 shows the maximum monthly rate of gap closure ( $cm^2 mo^{-1}$ ) for 55 relatively small (ca.  $900cm^2$ )

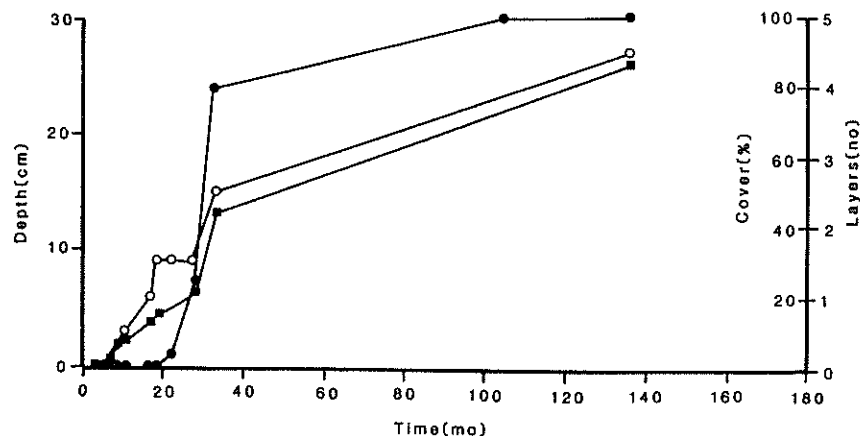


Fig. 4.17. Changes in mussel bed depth (solid squares), number of mussel layers (open circles) and mussel cover (solid circles) during the re-establishment of a *Mytilus californianus* bed at Tatoosh Island, Washington state, North America, following a storm which completely denuded the substratum in November 1975 (time = 0).

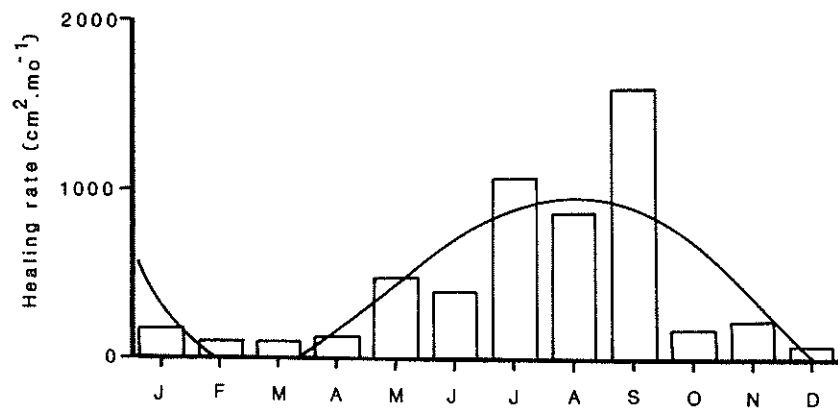


Fig. 4.18. Maximum monthly rate of disturbance gap closure (= healing rate) for 55 artificially created gaps in *Mytilus californianus* beds at Tatoosh Island and Shi-Shi, Washington state, North America, during 1974–1978. Data were pooled for all tidal heights; fourth order polynomial curve fitted to data points.

artificially created gaps in *M. californianus* beds at Tatoosh Island and Shi-Shi, Washington monitored over a four year period (Suchanek and Duggins, unpublished results). This healing rate/time relationship is described best by the 4th order polynomial  $y = 980.3 - 1048.1x + 321.2x^2 - 31.4x^3 + 0.9x^4$ ,  $R^2 = 0.62$ . Gaps healed much faster during the months from May through September than during any other period. Healing in these gaps was accomplished mostly through mussel movement (leaning and re-attachment of byssal threads), rather than by larval settlement/recruitment. This series of experiments also revealed that the initial period of gap healing (immediately after gap initiation) has the highest rate of closure during summer months, especially for gaps that occur in thick, multilayered mussel beds. The mechanism(s) responsible for this phenomenon is unclear. Since mussels tend to produce more byssal threads during periods of stronger wave action (see above), one might hypothesize that winter would be a period when more healing would occur through the extension and production of more byssal threads, thereby resulting in lateral movement; but the data do not support this prediction. Alternatively, mussels may discriminate between rough and calm sea conditions by changing the nature of byssal thread production. In rough winter conditions they might produce many byssal threads in their immediate vicinity in an attempt to become as rigidly attached to the underlying substratum as possible. During calmer summer conditions they might extend their foot to attach byssal threads further away in order to reclaim substratum lost during disturbance events.

Patch size as well as seasonality is important in determining the identity and timing of colonizing fauna and flora that occupy recovering disturbance gaps. Suchanek (1978, 1981), Paine and Levin (1981) and Sousa (1984) discuss several aspects of competitively subordinate taxa (including *M. edulis* and several barnacles and algae) that colonize in winter—a period when the probability of finding a colonizable gap is greatest. Winter gaps provide excellent opportunities for barnacle larvae (e.g. *Balanus glandula* and *Semibalanus cariosus*) and certain algal taxa that are abundant in spring, but not in summer. Gaps formed during summer periods may be colonized initially by a very different assemblage of fauna and flora; in some cases barnacles colonizing immediately after a winter disturbance patch may persist and remain on the primary substratum throughout the lifespan of the *Mytilus* bed, often providing a basement of live barnacle tests to which the mussels are attached (Suchanek, 1979; D. Brosnan, personal communication, 1990). Along the New England and Alaskan shorelines, the colonization of *Balanus* in disturbed areas appears to be more than an incidental event in the recovery process as barnacle tests act as significant recruitment sites for *M. edulis* (Menge, 1976; Suchanek and Duggins, unpublished results).

Since gap size also determines the ability of mobile grazers to reach and consume colonizers in the interior regions of gaps in *M. californianus* beds (see above and Suchanek, 1978, 1979; Sousa, 1984) size is intimately related to the overall recovery

process, and especially the interaction between alternative space occupiers and mussels. Floral and faunal assemblages affected by grazers within the browse zone (typically ca. 10–20cm width—see Fig. 4.15 lower) are completely different than those within the central regions of gaps (usually more than 40cm diameter) (Suchanek, 1978, 1979; Sousa, 1984). For instance, during the early stages of gap colonization, diatoms and the red alga *Porphyra* occupy 80–90% of the primary substratum within the central portions of large gaps, but are nearly or completely absent within the browse zones (Suchanek, unpublished results). Many other algae and some sessile fauna are similarly but not as dramatically affected. However, other genera (e.g. *Alaria*, *Hedophyllum* and *Petrocelis*) appear to benefit from the grazing pressures exerted in the browse zone, probably because these genera have poorer competitive abilities and/or better antigrazer defenses. Moreover, some genera (e.g. *Halosaccion*) may benefit from grazing pressures during early stages of gap recolonization but be excluded completely from the browse zone during later stages (Suchanek, unpublished results). One of the most significant benefits that grazers can impart to *M. californianus* populations is an enhanced rate of recovery from disturbance. *M. californianus* beds at Shi-Shi, Washington, which had grazers experimentally removed, recovered lost space seven times slower than beds with their full complement of grazers (Suchanek, 1979).

Angle of substratum is important in determining not only the relative cover of *Mytilus*, but also the rate of recovery from disturbance. In regions of lower wave intensity (e.g. the relatively protected fjords within Glacier Bay, Alaska, or on any protected dock or piling) *Mytilus* spp. very effectively colonize vertical substrata. However, in regions of intense wave action *Mytilus* is not at all effective in maintaining a persistent and dominant coverage on vertical or nearly vertical slopes. In New England *M. edulis* dominates horizontal and inclined substrata, but does not compete very effectively with barnacles on vertical substrata (Menge, 1976). For *M. edulis*, the combination of gravity and wave action appears to dislodge individuals from the substratum; for *M. californianus* competition from the stalked barnacle *Pollicipes* also seems to be a contributing factor in its inability to dominate vertical slopes. In terms of recovery rate, on more steeply angled slopes the leaning component of gap healing (Paine and Levin, 1981) contributes more to gap recovery than on horizontal substrata, especially on the uphill side of the gap.

Recovery time from a major disturbance is variable for different species of *Mytilus*, but for most *Mytilus* assemblages it is a long-term process. *M. edulis* appears to colonize and recover from perturbation more quickly than other species. On a regional scale its recruitment typically shows temporal predictability, but spatial predictability is low and is dependent upon available areas of disturbed primary substratum. In Washington, for example, where *M. edulis* is typically a fugitive in the mid to low intertidal zone, it commonly recruits into disturbance gaps within the dominant *M. cali-*

*ifornianus* cover, although not all gaps are colonized heavily (Suchanek, 1978). At Washington sites, where *M. edulis* is eliminated from the substratum by extremes in temperature, such as the very high intertidal zone where it is dominant, it recovers lost space typically within 1–3 years (data extracted from Paine, 1986). Recovery of *M. edulis* in New England is enhanced by the presence of barnacles on the primary substratum (Menge, 1976). Substratum with prior barnacle cover yielded nearly 100% recovery by *M. edulis*, whereas substratum without barnacles was virtually devoid of mussels. In Mutsu Bay, Japan, an artificial removal of *M. edulis* from a rocky shore resulted in complete recovery within three years (Hoshiai, 1964; Tsuchiya, 1983). In artificially created disturbance gaps (50 x 50cm) in Torch Bay, an Alaskan fjord, *M. edulis* populations had not completely recovered (range = 5–90% recovery) after almost seven years (Suchanek and Duggins, unpublished results). Here, exposure dictated recovery rates with gaps at intermediate exposure sites healing about twice as fast as those at very exposed sites.

In several studies after 3–5 years of data collection, very little recovery had been noted in disturbed *M. californianus* assemblages (Hewatt, 1935; Cimberg, 1975; Sousa, 1984), even though mussel larval settlement in this species occurs continuously throughout the year (Suchanek, 1981). An eight-year data-set by Castenholz (1967) also showed no recovery within that time period. Paine and Levin (1981) provide excellent data and a model of gap healing in *M. californianus* beds, and show that recovery from disturbance in mid intertidal mussel beds, measured as a cycling time (or rotation period) for these beds ranges from ca. 8–35 years depending on location. That is, mussel beds or portions of mussel beds destroyed by some disturbance event will recolonize and return to their original condition within this time period. While these results are consistent with other studies for mid intertidal horizontal *M. californianus* beds (Suchanek, unpublished results), some long-term data sets show variable agreement with these predictions for both vertical slopes and high intertidal mussel beds on horizontal platforms.

In a 21-year data set from a large intertidal stack at Trinidad Head, California (Cimberg, 1975 and personal communication, 1990), *M. californianus* showed minimal or no recovery after both artificial and natural mussel removals on a near vertical slope (Fig. 4.19). In 1968 *M. californianus* dominated a 30–40cm band around the stack (Fig. 4.19left). That year all biota was removed from a 20cm vertical swath on both the seaward and leeward sides of the stack, and the site was monitored for long-term changes. In 1972 the remainder of the mussel band was eliminated by heavy *Pisaster* predation (Fig. 4.19centre) and showed no recovery through 1989 (see example in Fig. 4.19right). Since the stack is completely surrounded by sand, it is unclear how *Pisaster* colonized it, but it could have been the result of a massive larval settlement.

A 16-year data set at Shi-Shi, Washington from a *M. californianus* bed on horizontal substrata shows similar results (Suchanek and Duggins, unpublished

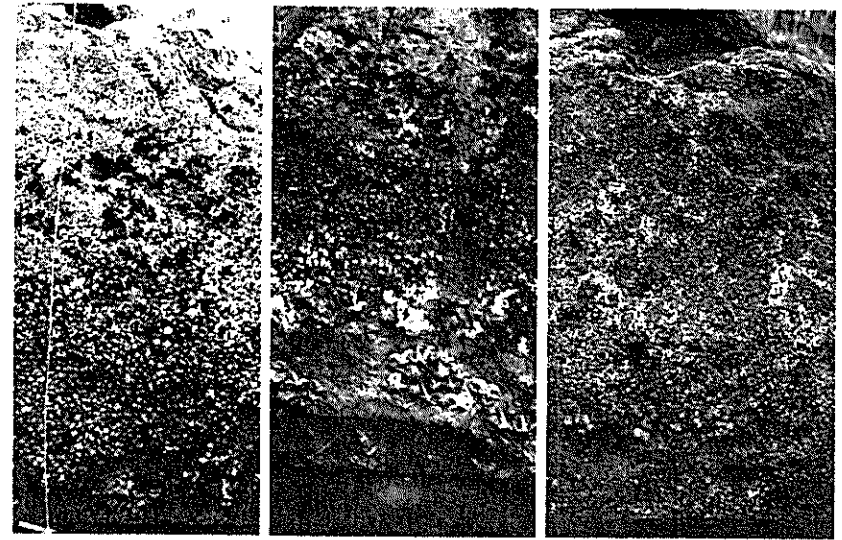


Fig. 4.19. Serial photographs of an intertidal stack at Trinidad Head, California, North America. In 1968 *Mytilus californianus* occupied a continuous band around the bottom portion of the stack (left). In 1972 *Pisaster* predation resulted in the elimination of all *M. californianus* from the stack (centre). Also note in (centre) a centrally located 20cm vertical swath denuded in 1968. As of 1989, *M. californianus* has not recolonized this site (note condition in (right) taken in 1986). All data and photographs from R.L. Cimberg (personal communication, 1990).

results). From 1974 through 1976 artificial disturbance gaps (ca. 30 x 30cm) were created in the high intertidal mussel bed region, but where *M. californianus* still occupied 100% of the substratum as a monolayer. Healing rates of these gaps were variable and several enlarged their area, but none healed completely. Because of the slow recovery rates, and the fact that some had continued to enlarge, the mathematically calculated mean projected healing times of these gaps (n = 6) for data through 1988 was  $600 \pm 1139$  years. It is highly unlikely that recovery would take this long since a massive larval settlement/recruitment event would probably result in complete recolonization of this intertidal region. However, during the winter of 1988/1989 a severe freeze virtually eliminated the entire upper vertical 0.3m of the *M. californianus* beds at this site (also see discussion on p.89–91). During the last visit to this site (August 1990) the mussel beds surrounding these gaps and contributing to gap healing were nonexistent. Therefore, the former gaps have technically enlarged infinitely in size so that the region is one entire 'gap' and the recovery process for this entire mussel bed must start again from virtually bare rock, and it is unclear how long this may take.

The *Mytilus* beds at Shi-Shi are located in a region that is relatively less exposed than comparable beds at Tatoosh Island. Differences between and within these sites in the rates of recovery for disturbance gaps in intertidal mussel beds suggest that both exposure and tidal height play a significant role in the relative 'stability' (i.e. rate of recovery) of the dominant space occupiers. In the Washington study sites, gaps at high intertidal and less exposed sites recover much more slowly than comparable gaps at mid and low intertidal and more exposed sites. These results are in general agreement with those of Lewis (1977), who reported that mussel assemblages found in upper intertidal zones and in the most sheltered sites, experience the least amount of change per unit time. Lewis (1977) presents these data as evidence for increased 'stability' (i.e. lack of change). However, if some disturbance disrupted these mussel assemblages, it is highly likely that the rate of change back to the original condition (i.e. the rate of recovery) would be much slower at those sites than at lower intertidal and more exposed sites. Therefore, without entering into a semantic discussion about the term 'stability', the dynamics (or at least relative rates of change) in *M. edulis* beds in North-west Europe are comparable to those in *M. californianus* beds in Washington. The most likely limiting factor controlling recovery rates for *Mytilus* beds in upper intertidal sites in Washington is larval settlement and subsequent recruitment by mussels. In Europe, upper intertidal habitats also contribute greatly to long-term mussel bed 'stability' by virtue of their role as refuges from predation by *Nucella* and *Asterias* (Lewis, 1977).

Paine (1984) has used *M. californianus*, and the processes that allow it to return to dominant space occupier status, as a clear example of ecological determinism. While this principle is accurate for those mussel beds at mid to lower exposed rocky intertidal sites, those mussel beds on vertical substrata, or at high intertidal sites, are much more variable and may display alternative stable states (*sensu* Sutherland, 1974) for long periods of time. The examples given above for long-term data sets at Trinidad Head, California (Cimberg, 1975 and personal communication, 1990) and Shi-Shi, Washington (Suchanek and Duggins, unpublished results) provide evidence for these alternative states. Data from Trinidad Head indicate that *M. californianus* was replaced as the dominant primary space occupier on almost vertically sloped substrata, primarily by the barnacles *Semibalanus cariosus* and *Chthamalus dalli*, over a period of at least 17–21 years (R.L. Cimberg, personal communication, 1990). Data from Shi-Shi over a 16-year period indicate that on high intertidal horizontal substrata, *M. californianus*, once removed, can be replaced by a variety of fauna and flora, primarily *Semibalanus cariosus* and the brown alga *Fucus gardneri*; the mathematically projected healing times exceed many hundreds of years (Suchanek and Duggins, unpublished results). It is with great interest that these disturbance sites will continue to be monitored for as long as possible.

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