

THE ECOLOGY OF ROCKY COASTS

essays presented to J.R. Lewis, D.Sc.

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CHAPTER VI

MUSSELS AND THEIR RÔLE IN STRUCTURING ROCKY SHORE COMMUNITIES

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6.1 Introduction

Molluscs represent the second most diverse group of animals and marine bivalves are the most abundant molluscs (Russell-Hunter, 1983). Of these, mussels (family Mytilidae) have achieved an impressive ability to dominate rocky shores on all continents. Their world-wide success as dominant space occupiers is most pronounced at exposed or semi-exposed sites in temperate habitats, especially on horizontal or gently sloping rocky substrata. The development of byssal attachment threads by adult bivalves, as in the extant genus *Mytilus*, has allowed them to exploit hard substrata and dominate rocky habitats. Associated with the evolution of the byssal apparatus is a typical reduction of the anterior end of the body and the enlargement of the posterior region, producing a triangular shape and heteromyarian condition (the 'typical' mussel form). Evolutionarily the use of byssal threads by adults may have been a neotenuous retention of byssus by byssate post-larval stages of some burrowing taxa (Yonge, 1962). In the Ordovician c. 40% of marine bivalves were endobyssate (i.e. they attached byssal threads to the inside of a partial or complete burrow), and their success was attributed to the use of byssal threads that allowed them to maintain a stable position at the sediment-water interface (Stanley, 1972). Stanley (1972) also suggested that from the Devonian to the Jurassic the Mytilidae evolved from largely endobyssate forms such as *Modiolus*, through an intermediate stage (the extinct genus *Promytilus*) to a greater diversity of epibyssate forms such as *Mytilus* spp. (that attach byssus directly to exposed hard substrata such as rock or wood). However, Yonge (1976) questioned this progression, suggesting instead that endobyssate species evolved from epibyssate forms and that the 'typical' mussel form is what has made the Mytilidae so successful. Initially mytilid mussels may have competed with brachiopods in offshore habitats since their early radiation occurred near-shore. Regardless of the cause of the great Permo-Triassic brachiopod extinction (Bretsky, 1969; Stanley, 1968, 1972; Suchanek and Levinton, 1974), the Mytilidae then became more numerous, subsequently radiating to offshore environments (Stanley, 1972), the deep-sea (Allen, 1983) and even into the Galapagos Rift communities as evidenced by the relatively recently discovered mytilid *Bathymodiolus thermophilus* Kenk and Wilson from c. 2500m depth (Corliss *et al.*, 1979; Rau and Hedges, 1979; Kenk and Wilson, 1985).

Mussels, especially those that live in exposed habitats, represent some of the most productive species on earth, rivalling the productivity of tropical rain forests and kelp beds (Whittaker, 1975), with a standing crop of up to $6.5 \text{ kg} \cdot \text{m}^{-2}$ and a productivity of c. $2.0 \text{ kg} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ for low littoral *Mytilus*

californianus Conrad beds at Tatoosh Island, Washington State, U.S.A. (Leigh *et al.*, in prep.). Because of their productivity and predictability mussels have been and still are being utilized heavily as a human food resource, having a history of harvest and cultivation for over 700 years in Europe (Mason, 1976). *Mytilus* spp. were also used for food and tools in prehistoric and historic times by native American Indians and by the Pilgrim settlers in 1622 (Miller, 1980). Because of their strength and size, *M. californianus* shells were used as tools (specifically whaling harpoon tips) by Makah Indians in Washington State.

With few exceptions, in most exposed or moderately exposed locations in temperate zone habitats, mytilid mussels form the foundation for complex rocky littoral communities. Here I shall discuss the distribution, structure, and dynamics of dominant littoral mussel beds (with additional reference to some important sublittoral mussel beds) and the communities of associated organisms which they support.

6.2 Geographical and Zonational Distributions of the Dominant Mytilidae

Although most mytilid mussel populations are found in littoral habitats, all of the Mytilidae appear to have the ability to live sublittorally. In fact, the occasional sublittoral individuals of typically littoral species (e.g. *Mytilus edulis* L. and *M. californianus*) are invariably more robust (Paine, 1976b; Suchanek, 1978). Recently several naturally occurring sublittoral mussel populations have received considerable attention (e.g. *Aulacomya ater* (Molina) and *Choromytilus meridionalis* (Krauss) in South Africa and *Modiolus modiolus* (L.) in New England, U.S.A.). Although this Chapter deals primarily with littoral mussels, I have included relevant information on these sublittoral forms as well. It appears that competition and especially predation are the factors that prevent most mytilid mussels from developing sublittoral populations (see below).

Mytilus edulis and its species complex is the most widely distributed mytilid entity, having a circum-polar distribution in temperate habitats of both the northern and southern hemispheres (Soot-Ryen, 1955; Seed, 1976b). Until recently, on Pacific coasts, *M. edulis* (the 'bay mussel') had been considered an inhabitant of more protected embayments (Ricketts and Calvin, 1939; Harger, 1970a,b, 1972a,b). However, it has now been shown to occur abundantly and persistently in some of the most exposed rocky shore sites known, such as Tatoosh Island, Washington and Torch Bay, Alaska (Suchanek, 1978). These findings are consistent with the generally eurytopic nature of *M. edulis* in habitats world-wide, especially with respect to temperature, salinity, and siltation. However, more work is needed to explain why it does not occur abundantly in exposed habitats elsewhere, such as in Oregon and California.

Few other mussel species are widely distributed; however, four deserve mention. *Aulacomya ater* occurs littorally and sublittorally in Chile, South Africa and the Kerguelen Archipelago (sublittoral forms not reported here). *Modiolus modiolus* is found in typically dense beds sublittorally on the East coast (New England) and West coast (San Juan Archipelago, Washington) of the U.S.A. and in Europe. On the shore it is more sporadic, sometimes being found as dense beds in rock pools (Torch Bay, Alaska) or as scattered individuals in dense *Mytilus californianus* beds (Tatoosh Island, Washington). *Perna perna* (L.) typically occupies littoral and sublittoral sites in Venezuela and on the East and West coasts of Africa. Finally, *Septifer bilocularis* L. never forms dense beds, but occurs as scattered individuals littorally in crevices or under stones and/or sublittorally on the East coast of Africa and on the shores of Australia. The remainder of the dominant space-occupying mussels have, for the most part, contiguous geographical distributions. A review of common or dominant world-wide mytilid mussels is given in Table 6.1, with information on geographical and vertical distributions, size and relevant references.

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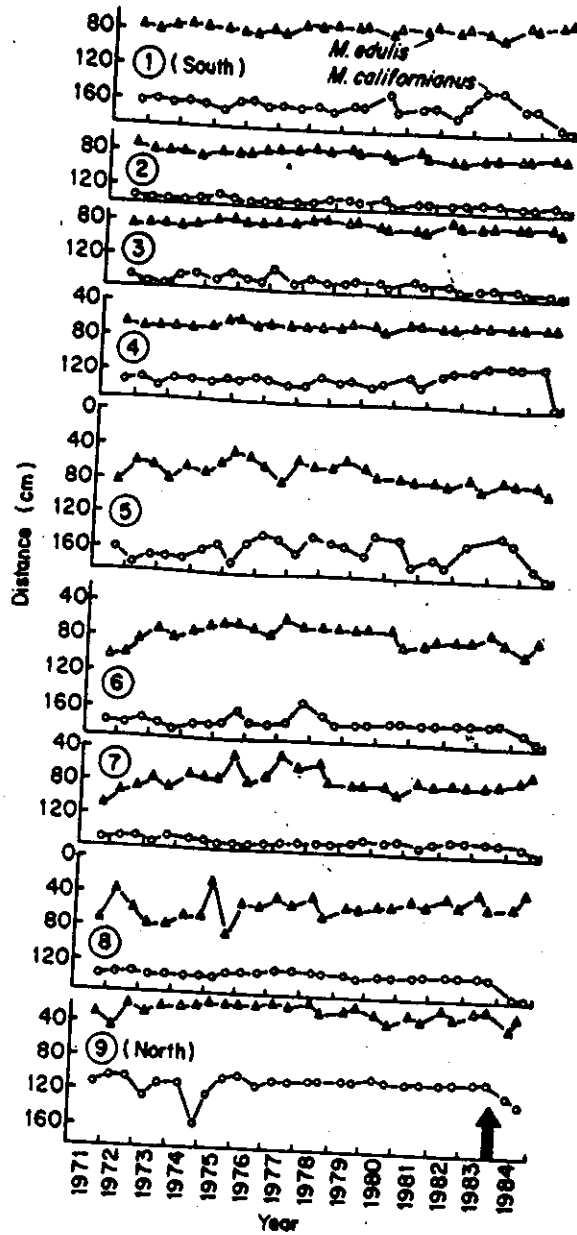


FIG. 6.1. Upper limits for *Mytilus edulis* and *Mytilus californianus* from 1971-84 at Tatoosh Island, Washington. Relative distances were measured from 9 permanent markers fixed to the rock substratum above the mussel beds. Site markers no. 1 and no. 9 at the southern and northern ends (respectively) of the transect line. Heavy arrow on abscissa denotes time of major freeze in December, 1983. Data courtesy of R.T. Paine.

TABLE 6.1

Geographical and vertical distributions of the dominant Mytilidae of the world
('-' indicates no data found).

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
North America: Pacific				
<i>Modiolus modiolus</i> (L.)	Arctic Ocean to Monterey, California	littorally and dense beds sublittorally	-	Soot-Ryen (1955) Suchanek (in prep.) Suchanek (pers. obs.)
<i>Mytilus californianus</i> Conrad	Aleutian Islands, Alaska to Isla Socorro, Mexico	mid-littoral and sublittoral (to - 73m)	≥ 266	Ricketts and Calvin (1939) Berry (1954) Soot-Ryen (1955) Chan (1973) Paine (1976a,b) Levinton and Suchanek (1978) Suchanek (1978)
<i>Mytilus edulis</i> L.	Arctic Ocean to Cabo San Lucas, Baja California	high- to low-shore and occasionally sublittoral to - 29m (- 220m?)	140	Soot-Ryen (1955) Suchanek (1978) Lutz (1980)
<i>Mytilus edulis diegensis</i> Coe	Northern California to Baja, California	littoral to slightly sublittoral in bays and sloughs	108	Coe (1945, 1946)
North America: Atlantic				
<i>Geukensia demissa</i> (Dillwyn) (= <i>Modiolus</i> (= <i>Brachidontes</i>) <i>demissus</i>) Dillwyn	Gulf of St. Lawrence to northeast Florida	in salt marshes from mid- to low-shore and occasionally on pilings	120	McDougall (1943) Kuenzler (1961a,b) Lent (1967, 1968, 1969) Pierce (1970) Abbott (1974) Lutz and Castagna (1980) Seed (1980a,b) Bertness and Grosholz (in prep.)
<i>Modiolus modiolus</i> (L.)	Arctic Seas to New Jersey	rocky and gravelly substrata generally sublittoral to at least 183m	150	Soot-Ryen (1955) Rowell (1967) Abbott (1974) de Schweinitz and Lutz (1976) Witman (1980, 1983, 1984)

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TABLE 6.1 *Cont'd*

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
<i>Mytilus edulis</i> L.	Arctic Ocean to South Carolina (and Cuba?)	mid-littoral to sublittoral	107	Scattergood and Taylor (1950) Soot-Ryen (1955) Abbott (1974) Peterson (1979) Lutz (1980) Menge (1983, pers. comm.)
South America: Pacific				
<i>Aulacomya ater</i> (Molina)	Callao, Peru to the Strait of Magellan	low-shore and sublittoral (to at least - 20m)	200	Soot-Ryen (1955) Knox (1960) Tomicic (1966, 1968) Lozada (1968) Marincovich (1973) Lozada <i>et al.</i> (1974) Suchanek (pers. obs.)
<i>Choromytilus chorus</i> (Molina)	Pacasmayo, Peru to Orange Bay, Tierra del Fuego	littoral and sublittoral	300	Soot-Ryen (1955) Sruardo (1960) Lozada <i>et al.</i> (1971) Arcena <i>et al.</i> (1974) Yañez (1974) Walne (1979) Tomicic (pers. comm.) Suchanek (pers. obs.)
<i>Mytilus edulis</i> L. (= <i>M. edulis chilensis</i> Hupe)	Valparaiso, Chile to Beagle Channel, Argentina	mid- to low-littoral	120	Soot-Ryen (1955) Knox (1960) Padilla (1973) Reid (1974) Yañez (1974) Suchanek (1978) Miranda and Acuna (1979) Langley <i>et al.</i> (1980)
<i>Perumytilus (Brachidontes) purpuratus</i> (Lamarck)	Ecuador to the Strait of Magellan	high- to low-littoral	41	Soot-Ryen (1959) Alveal (1970) Marincovich (1973) Viviani (1975) Castilla (1981) Paine <i>et al.</i> (1985) Suchanek (pers. obs.)
<i>Semimytilus algosus</i> (Gould)	Paíta, Peru to Valparaiso, Chile	low-littoral and sublittoral (to - 9m)	≥ 21	Soot-Ryen (1955, 1959) Olsson (1961) Marincovich (1973) Paine <i>et al.</i> (1985) Suchanek (pers. obs.)

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TABLE 6.1 *Cont'd*

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
South America:				
Atlantic				
<i>Aulacomya ater</i> (Molina)	southern Brazil to Strait of Magellan and Falkland Islands	littoral and sublittoral to at least 15m depth	-	Soot-Ryen (1955) Knox (1960) Lozada <i>et al.</i> (1974)
<i>Brachidontes rodriguezii</i> D'Orb. (? = <i>Perumytilus purpuratus</i> (Lamarck))	Santa Cruz, Argentina to Strait of Magellan	littoral	30	Penchazadeh (1973)
<i>Mytilus edulis</i> Linne (= <i>M. edulis platensis</i> Orbigny)	southern Brazil to Argentina	-	-	Knox (1960) Penchazadeh (1971) Abbott (1974) Seed (1976b)
<i>Perna perna</i> (L.)	Venezuela to the Strait of Magellan	-	-	Soot-Ryen (1955) Davies (1970) see also Seed (1976b)
Europe				
<i>Modiolus modiolus</i> (L.)	Iceland and Barents Sea to northern Britain and sporadically to the Bay of Biscay	low-littoral in pools and sublittoral to - 200m	200	Coleman and Trueman (1971) Coleman (1973) Roberts (1975) Seed and Brown (1975, 1977, 1978) Brown <i>et al.</i> (1976) Brown and Seed (1977) Comely (1978, 1981)
<i>Mytilus edulis</i> L.	White Sea to the Mediterranean and in northern Africa	high-littoral to sublittoral	90	Kitching <i>et al.</i> (1959) Lewis (1964) Kitching and Ebling (1967) Seed (1969a,b) Stephenson and Stephenson (1972) Kautsky and Wallentinus (1980) Kautsky (1982)
<i>Mytilus galloprovincialis</i> Lamarck	mostly Mediterranean and Ireland to the Black Sea	high-littoral to sublittoral	90	Lewis and Seed (1969) Seed (1971, 1972, 1974, 1978b) Gosling and Wilkins (1981) Skibinski <i>et al.</i> (1978, 1980, 1983) Skibinski and Beardmore (1979) Gosling (1984) Lubet <i>et al.</i> (1984)

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TABLE 6.1 *Cont'd*

<i>Mustel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
Africa: Atlantic Ocean				
<i>Aulacomys ater</i> (Molina)	at least in South Africa	mid-littoral to sublittoral	95	Velimirov <i>et al.</i> (1977) Griffiths (1977, 1980a) Griffiths and King (1979a,b) Pollock (1979) Field <i>et al.</i> (1980) Griffiths and Seiderer (1980) Seiderer <i>et al.</i> (1982) Stuart, Field and Newell (1982) Stuart, Newell and Lucas (1982) Wickens and Griffiths (in press)
<i>Choromytilus meridionalis</i> (Krauss)	at least in South Africa	mid-littoral and sublittoral (to - 30m)	101	Griffiths (1977, 1980a,b) Griffiths (1981a,b,c,d) Griffiths and Seiderer (1980) Griffiths and Buffenstein (1981) Penney and Griffiths (1984) Wickens and Griffiths (in press)
<i>Perna perna</i> (L.)	sporadically from Mauritania to the Cape of Good Hope	mid-littoral to sublittoral	112	Stephenson and Stephenson (1972) Berry (1978) Griffiths (1981a) Wickens and Griffiths (in press)
Africa: Indian Ocean				
<i>Brachidontes variabilis</i> (Krauss)	northern Mozambique to lower Natal	scattered littoral	-	Stephenson and Stephenson (1972) Jackson (1976)
<i>Perna perna</i> (L.)	Mozambique to the Cape of Good Hope	mid-littoral to sublittoral	-	Stephenson and Stephenson (1972) Jackson (1976)
<i>Septifer bilocularis</i> L.	at least Mozambique to Natal	scattered littoral	-	Stephenson and Stephenson (1972) Jackson (1976)

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TABLE 6.1 *Cont'd*

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
India and Southeast Asia				
<i>Mytilus smaragdinus</i> Gmelin (? = <i>Perna</i> (= <i>Mytilus</i>) <i>viridis</i>) (L.)	South China Sea: Philippines, Thailand and Singapore	littoral to sublittoral	> 300?	Jones and Alagarwami (1968) Davies (1970) Obusan and Urbano (1968) E.L. Tan (1971) W.H. Tan (1975a) Blanco (1973) Ling (1973) Sribhibhadh (1973) Tham <i>et al.</i> (1973) Korringa (1976) Parulekar <i>et al.</i> (1982)
Kerguelen Archipelago				
<i>Aulacomya ater</i> (Molina)	Kerguelen Islands	high- to low-littoral	-	Arnaud (1974) Bellido (1981) Lawrence and McClintock (in prep.)
<i>Mytilus edulis</i> L. (= <i>M. desolationis</i> Lamy) (= <i>M. kerguelensis</i> Fletcher)	Kerguelen Islands	high littoral	-	Knox (1960) Arnaud (1974) Bellido (1981) Lawrence and McClintock (in prep.)
Japan				
<i>Mytilus edulis</i> L.	northern Japan	mid-littoral	> 60	Hoshiai (1960, 1961, 1964) Hoshiai <i>et al.</i> (1964) Tsuchiya (1979, 1980, 1982, 1983)
<i>Mytilus galloprovincialis</i> Lamarck	southern Japan	mid-littoral to sublittoral	112.5	Hosomi (1977, 1978, 1980)
<i>Septifer virgatus</i> (Wiegmann)	northern Japan	mid-littoral	> 60	Hoshiai (1961, 1964) Hoshiai <i>et al.</i> (1964) Tsuchiya (1979, 1983)

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TABLE 6.1 *Cont'd*

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
U.S.S.R.				
<i>Crenomytilus grayanus</i> Soot-Ryen	Kuril Islands south to the Philippine Islands	mid-littoral to sublittoral	> 128	Saito and Sakamoto (1951) Soot-Ryen (1955) Sadykhova (1967, 1970a,b,c) Levinton (pers. comm.)
<i>Mytilus edulis</i> L.	-	-	-	Kuznetsov and Mateeva (1948) Mateeva (1948) Palichenko (1948) Savilov (1953)
Australia and Tasmania				
<i>Brachidontes rostratus</i> (Dunk.) (? = <i>Brachidontes variabilis</i>)	South Australia to New South Wales and Tasmania	sparsely in upper to mid-littoral	-	Guiler (1950, 1951, 1955) Bennett and Pope (1953, 1960) Knox (1960, 1963) Wilson and Hodgkin (1967) Stephenson and Stephenson (1972)
<i>Mytilus edulis</i> L. (= <i>M. edulis planulatus</i> Lamarck)	Fremantle, Western Australia to Port Stephens, New South Wales and throughout Tasmania	low-littoral and sublittoral (to - 18m)	-	Guiler (1950, 1951) Bennett and Pope (1953, 1960) Allen (1955) Knox (1960, 1963) Wilson and Hodgkin (1967) Stephenson and Stephenson (1972)
<i>Septifer bilocularis</i> L.	in Western Australia south to Cape Leeuwin	littorally in crevices and under stones and sublittorally (to - 5.5m)	-	Wilson and Hodgkin (1967)

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TABLE 6.1 *Cont'd*

<i>Mussel species</i>	<i>Geographical range</i>	<i>Vertical range</i>	<i>Maximum known length (mm)</i>	<i>References</i>
<i>Xenostrobus (Modiolus) pulex</i> (Lamarck)	Victoria and Tasmania	upper littoral	-	Guiler (1950, 1951, 1955) Bennett and Pope (1953, 1960) Knox (1960, 1963) Wilson and Hodgkin (1967) Stephenson and Stephenson (1972)
New Zealand				
<i>Aulacomya maoriana</i> Iredale	North and South Island	scattered widely from high- to low-littoral	-	Knox (1953, 1960) Batham (1958) Stephenson and Stephenson (1972) Kennedy (1976, 1977)
<i>Mytilus edulis</i> L. (= <i>M. planulatus</i> Lamarck) (= <i>M. edulis aoteanus</i> Powell)	North and South Island and some distant island possessions	mid-littoral to sublittoral	-	Knox (1953, 1960) Batham (1958) Kennedy (1976, 1977)
<i>Perna (Mytilus) canaliculus</i> Gmelin	North and South Island	mid-littoral to sublittoral (to - 18m)	180	Knox (1953, 1960, 1963) Batham (1958) Greenway (1969a,b, 1975) Paine (1971) Stephenson and Stephenson (1972) Kennedy (1976, 1977) Luckens (1976)
<i>Xenostrobus (Modiolus) pulex</i> Lamarck (= <i>Modiolus neozelanicus</i> Iredale)	North and South Island	high- to low-littoral	20	Knox (1953, 1960) Batham (1958) Paine (1971) Kennedy (1977)

6.3 Factors Limiting Mussel Zonation

6.3.1 Upper limits

While there may be significant fluctuations in some mussel populations, especially at lower shore levels, upper limits are often very constant over long periods of time (Lewis, 1964, 1977b; Paine, 1974, 1984). Lewis (1977b) has presented 10 years' data showing a consistent percentage cover of high shore *Mytilus edulis* at Robin Hood's Bay, England. At Tatoosh Island, Washington, Paine (1974, 1984) has shown a constancy in the upper limit of the *Mytilus californianus* zone over 12 years (1971-83). Similar trends in the upper limit of the *M. edulis* zone at Tatoosh Island over five years are seen in Suchanek (1978), with moderately predictable seasonal fluctuations caused by summer mortality as a result of desiccation. Evidence of periodic desiccation was clearly visible at Tatoosh Island during August, 1984, when 'windrows' of thousands of empty (non-drilled) *M. edulis* shells (many with viscera remaining) were piled up on high-shore platforms (pers. obs.).

Thirteen years' data on the upper limit of both *M. edulis* and *M. californianus* are presented in Fig. 6.1 (data courtesy of R. T. Paine). These data represent linear (not vertical) distances (cm) measured each spring and autumn down from 9 markers permanently fixed into the rock substratum, to the upper limits of both the *M. edulis* and *M. californianus* zones. This transect is positioned along a North (no. 9) to South (no. 1) inclined slope. The rock angle is steepest at the South end, resulting in a shorter linear distance for each unit change of vertical height. These data show moderate stability for the upper limits of both species, especially *M. californianus*, with occasional events disrupting this level. The greatest fluctuations in the *M. californianus* upper limit (e.g. at markers no. 5 and no. 9) are associated with winter disturbance patches which incorporated a portion of the upper edge. Also, a freeze in December, 1983 (at arrow on abscissa), significantly lowered this upper limit at all marker sites (see below). In the field *M. edulis* appears less affected by winter storms, but typically suffers some mortality at the upper edge from desiccation each summer.

While reduced food intake at higher-shore levels may result in slower growth rates and eventually smaller-sized adults (Baird, 1966; Seed, 1976b; Griffiths, 1981b; Griffiths and Buffenstein, 1981), physiological intolerance to desiccation is probably the single most significant factor determining the upper limits of mussel zonation. Several authors have noted casually that mussels can survive above the upper limit of their normal littoral zone when protected in cracks or crevices (Batham, 1958; Griffiths, 1981a; Lawrence and McClintock, in prep.) or have suggested desiccation as an upper limiting factor (Paine, 1974; Hosomi, 1978). Actual mortality from high temperatures and/or desiccation in upper zones has also been well documented (Coe, 1946; Luckens, 1976; Suchanek, 1978; Peterson, 1979; Griffiths, 1981a; Tsuchiya, 1983). In an excellent series of field and laboratory studies Kennedy (1976) determined the influence of desiccation and temperature on three species of rocky shore mussels (*M. edulis aoteanus* Powell, *Perna canaliculus* Gmelin and *Aulacomya maoriana* Iredale) in southern New Zealand. These results indicated strongly that the relative positions of the three mussel species on the shore were consistent with their respective tolerances to temperature and, especially, desiccation. Particularly important findings in this study were the combined and/or synergistic effects of temperature, wind, relative humidity and species-specific or age-specific behavioural differences on desiccation-related mortality. Furthermore, juveniles were more susceptible to desiccation than adults and tended to settle or aggregate into clumps of conspecifics or other mussel species, a result supported by evidence from studies on other mytilids (Luckens, 1976, for *Perna canaliculus* in New Zealand; Suchanek, 1978, 1981, for *M. californianus* in Washington; Bertness and Grosholz, in prep., for *Geukensia demissa* (Dillwyn) in New England).

Contrary to popular belief, it is not only drastic changes in temperature that affect bivalve mortality. Small temperature differences can have dramatic effects on the survival of bivalves and may ultimately

determine their local as well as geographical distributions. In laboratory tests it has been shown that an increase of 1.0°C can change mortality rates from low to high levels for some bivalves (Kennedy and Mihursky, 1971), and that differences in thermal tolerance between four species of infaunal bivalves correlated well with their relative latitudinal, tidal and infaunal positions. Dickie (1958) showed that environmental temperature differences as small as 0.3°C can increase mortality by 25% in scallops. Currently we lack comparable data on mussels, but attention is drawn to the works of Henderson (1929), Wells and Gray (1960), Read and Cumming (1967), Lent (1968), Waugh (1972), and Bayne *et al.* (1976) that deal specifically with the effects of small temperature differences on survival and/or distributions for various species of Mytilidae.

The importance of behavioural differences between species should not be underrated as an important factor affecting the littoral distributions of mussels. For example, short periods of gaping by the epibyssate mussel *Modiolus modiolus* when subjected to air contribute significantly to water loss and subsequent mortality and may be closely related to its typical low littoral to sublittoral distribution in England (Coleman and Trueman, 1971; Coleman, 1973). A different view of air-gaping is reported for an endobyssate modiolid, *Geukensia* (= *Modiolus demissa*), which air-gapes both for aerial respiration and for evaporative cooling, allowing this species to penetrate high-shore habitats in salt marshes (Kuenzler, 1961a,b; Lent, 1968, 1969). The significant differences here are that despite water loss, *G. demissa* (i) has a much higher upper thermal tolerance limit (37°C), some 14 degrees higher than that of *M. modiolus*, and (ii) lives in semi-protective burrows in marsh mud (Bertness, 1980; Bertness and Grosholz, in prep.), further reducing the effects of desiccation. In fact, if epibyssate species (such as *Mytilus* spp., *Choromytilus* spp., and *Perna* spp.), did evolve from endobyssate forms (such as the modiolid *Geukensia demissa*) then this radiation (Stanley, 1972), although involving only minor morphological changes, may have necessitated significant behavioural and/or physiological adaptations for survival in intertidal regions where aerial exposure can be dangerous or even fatal.

Freezing can be equally as important as desiccation in determining upper zonal limits for some mussel species. The range of *Mytilus californianus* extends from the Aleutian Islands, Alaska to Baja, California (Soot-Ryen, 1955). Throughout its range *M. californianus* lives in sympatry with *M. edulis*, but is a dominant space occupier in the mid- to low-shore only from Sitka, Alaska southwards (Ricketts and Calvin, 1939). When this occurs, *M. californianus* outcompetes *M. edulis* and relegates it to a high-shore band (Suchanek, 1978, 1981). North of Sitka the smaller *M. edulis* dominates much of the littoral zone, in some places (e.g. Glacier Bay, Alaska) covering over 5.5 vertical metres of space (Suchanek and Duggins, in prep.). *M. edulis* is much more eurythermal and has an exceptional tolerance to winter freezing (Bayne *et al.*, 1976). In fact, in the Hebron Fjord, Labrador, entire beds of *M. edulis* remain alive after spending six to eight months frozen solid in ground ice at -20°C and below, after which they are chipped out by the Eskimos for food in the spring (Kanwisher, 1955).

In locations such as Torch Bay, Alaska, when littoral *M. californianus* are exposed to freezing, they suffer 100% mortality (Suchanek, 1978); hence their local distribution is restricted to shore pools, extremely low-shore sites or sublittoral habitats (Suchanek and Duggins, in prep.). Occasionally, even in more temperate climates *M. californianus* can be affected by freezing. In December, 1983, a major freeze occurred in Washington State and the upper limit of the Tatoosh Island populations of *M. californianus* was lowered significantly (Fig. 6.1), leaving a gap between the lower limit of *M. edulis* and the upper limit of *M. californianus*. Lag periods exist between the time when mussels die and the time their shells are washed free of the matrix of binding byssal threads; in the case of *M. edulis* and *M. californianus*, dead shells may take as long as six to eight months to wash out of the system completely (Suchanek, 1978 and Fig. 6.1). In addition, the exceptionally hot summer of 1984 could have exacerbated this situation by eliminating even more *M. californianus* at the upper limit. Populations of

M. edulis experienced some fluctuations up or down in the upper limit, but no uni-directional trend was observed in association with this freeze (Fig. 6.1).

6.3.2 Lower limits

Several observational and/or experimental studies have shown how biological factors (i.e. predation and competition) contribute greatly to setting the lower limit at which mussels can survive. Some of the pioneering work in this area was done by Newcombe (1935b) in the Bay of Fundy, who strongly implicated a sea urchin (*Strongylocentrotus*), a dogwhelk (*Purpura* = *Nucella*), and especially two species of sea stars (*Asterias*) as predators on, and determinants of, lower limits for *M. edulis* populations. Paris (1960) also suggested such predator-control of *Mytilus* in the San Juan Islands of Washington State. In Ireland, Kitching *et al.* (1959), Ebling *et al.* (1964) and Kitching and Ebling (1967) have described a suite of predators that feed on *M. edulis* (the crabs *Carcinus* and *Liocarcinus* (= *Portunus*), the whelk *Nucella* and the sea star *Marthasterias*), and suggest strongly that the sea star was the agent controlling the littoral distribution of this mussel. The distribution of littoral *M. edulis* in New England is controlled by a guild (*sensu* Root, 1967) of predators: the whelk *Nucella* (= *Thais*); two sea stars, *Asterias* spp.; and three crabs, *Cancer* spp. and *Carcinus* sp. (Menge, 1976, 1978a,b, 1979, 1983; Lubchenco and Menge, 1978; Menge and Lubchenco, 1981). In the mid-zone of protected shores they claim that *Nucella* is the only important predator, although this has been questioned by Edwards *et al.* (1982) who feel that fish (specifically the cunner *Tautoglabrus*) may play a significant rôle in controlling the vertical distribution of both *Mytilus* and *Modiolus* at these sites (also see reply by Menge, 1982b). In the low littoral at protected sites Menge and Lubchenco felt that the entire guild of predators is at work with the crabs, the sea stars and the whelk (in decreasing order of importance) controlling *M. edulis* as well as barnacles. At low littoral sites exposed to heavy wave action they reported that predators do not control *M. edulis* and, therefore, it achieves long-term spatial dominance, in some places reaching into the sublittoral zone (Menge, pers. comm.). In New Jersey, similar control of *M. edulis* populations on dock pilings and a rocky jetty were noted by Peterson (1979). There the predators are two crabs (*Callinectes* and *Neopanope*) and the sea star *Asterias*.

Predator-controlled lower limits of three other mytilid species have been shown experimentally by R.T. Paine in a series of removals of predatory sea stars: *Pisaster* in Washington (Paine, 1974), *Stichaster* in New Zealand (Paine, 1971) and *Heliaster* in Chile (Paine *et al.*, 1985). In each case the dominant mussels at these sites (*Mytilus californianus*, *Perna canaliculus* and *Perumytilus purpuratus* (Lamarck) respectively) extended their vertical range downward in the littoral zone. When predators were allowed to return to these sites, the *Perumytilus* system returned to the original condition. In some cases, *Perna* and *Mytilus* were able to grow beyond the size capable of being consumed by the sea stars (Paine, 1976a) and thus these manipulations created temporarily altered states which may persist for ten (for *Mytilus*) to thirty years (for *Perna*) (Paine *et al.*, 1985).

Other examples of predation controlling the lower limits of mussel distributions have been implied from laboratory feeding experiments by Seed (1980a) for the crabs *Callinectes* and *Panopeus* on *Geukensia*. Seed felt that this mechanism was especially probable on wharf pilings and sea wall sites, but possibly not as important in salt marshes where the prey are less accessible.

Competition has also been shown to control lower littoral limits for mussels. Experimental manipulations on *Perna* in New Zealand by Paine (1971) have shown that in addition to being controlled at its lower limit by the predatory starfish *Stichaster*, *Perna* can be outcompeted by the giant kelp *Durvillea* which occurs in the lower littoral. When the latter species is removed *Perna* settles and proliferates in the available space. Further evidence for the influence of competition on lower limits was given by Suchanek (1978, 1981) for *Mytilus edulis*. In Washington *M. edulis* occurs in (i) a high

littoral band occupying c. 0.3m vertically, (ii) in the mid- to low-shore in gaps formed in the dominant *M. californianus* band, and (iii) in holdfasts of the kelp *Lessoniopsis*. Whenever *M. californianus* is removed, either naturally by winter storms or artificially by ecologists, *M. edulis* colonizes these lower littoral sites. In Alaska, where *M. californianus* often freezes on the shore (see above), the more tolerant *M. edulis* occupies a major band in the littoral where *M. californianus* would normally be expected to occur (Suchanek and Duggins, in prep.).

The control of mussel upper limits by physical factors (such as heat and desiccation) and lower limits by biological factors (predation and competition) fully support those findings of Connell (1961a,b) for rocky shore barnacle distributions and his speculations that these factors also control other littoral forms.

6.4 Population Dynamics and Life History Patterns of Mussels

6.4.1 Reproductive cycles and spawning

Reproductive cycles and spawning periods in mytilid mussels are tremendously variable, both with respect to fluctuations between different species at the same location as well as those within a single species at different geographical sites. For example, along the West coast of North America most authors have reported a limited spawning period each year for *Mytilus edulis* in the late autumn or early winter months [October to February] (see Morris *et al.*, 1980 and Suchanek, 1981, for a review). This may be an adaptation for locating available settling sites (i.e. storm-generated patches of bare rock). In the same region, *M. californianus* appears to 'dribble' gametes throughout the year never spawning-out completely (Suchanek, 1981; Edwards, 1984). This may equally be related to its own continuously available settling sites (conspecific byssal threads). Alternatively, spawning periods of *M. edulis* from many different locations show tremendous temporal variability with spawning occurring at virtually any time of the year (Seed, 1976b). However, at each location there is reasonable agreement in spawning dates (see Seed, 1976b and Suchanek, 1981, for reviews).

The proximate cues involved in stimulating an actual spawning event are still not fully understood but may involve a combination of both endogenous and exogenous factors (Seed, 1976b). Temperature appears to be an extremely important cue both for initiating spawning as well as setting upper and lower thermal limits for reproduction. This is clearly evidenced from many species that initiate gametogenesis as sea temperatures are falling and then begin spawning as temperatures rise, or vice versa (see Engle and Loosanoff, 1944; Chipperfield, 1953; Sugiura, 1959; Lozada, 1968; Moore and Reish, 1969; Bayne, 1975; Seed, 1975; Kennedy, 1977). Spawning in *Mytilus californianus* may be influenced by absolute temperatures, whereas *M. edulis* may respond to more rapid changes in temperature (Lubet, 1959). Thermal limits may also be set by long-term average temperatures. Elvin and Gonor (1979) speculated that 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. These thermal limits can, in turn, ultimately influence geographical and latitudinal distributions (see especially Allen, 1955; Wells and Gray, 1960; Read and Cumming, 1967; Wilson and Hodgkin, 1967).

Another exogenous factor, often noted but not fully understood, is physical stimulation. For many years it has been known that *Mytilus edulis* will spawn in response to jarring, rattling or scraping the shell and/or pulling or cutting the byssal threads (Field, 1922; Young, 1942, 1945, 1946; Loosanoff and Davis, 1963; Brenko and Calabrese, 1969). These are precisely the same environmental cues as received during a winter storm, which also signal the presence of storm-generated patches of bare rock on which *M. edulis* can settle. This pattern correlates well with spawning and subsequent settlement events for this species observed on the West coast of North America. However, other physical or

biological correlates such as light levels (Elvin, 1976) or phytoplankton blooms (Griffiths, 1977) may be equally important. Currently, the relative contribution of each of these factors to spawning is unknown.

Interestingly, height on the shore seems to have little influence on the relative degree of gonad development and gametic production, although more gametes will be produced per individual from lower shore sites because the lower shore population is composed of larger individuals. While increased temperature and desiccation stress in upper shore zones produce higher metabolic costs, energy appears to be shunted away from growth (Baird and Drinnan, 1957; Baird, 1966; Seed, 1976b; Griffiths and Buffenstein, 1981), but not gametic output (see Seed, 1976b, for *Mytilus edulis* in England; Griffiths and Buffenstein, 1981, for *Choromytilus* in South Africa; Suchanek, 1981, for *M. californianus* in Washington, U.S.A.; Jordan and Valiela, 1982, for *Geukensia* in New England).

Seed (1976b) presented an excellent review of literature on spawning periods for *Mytilus edulis* and several other important mytilid species. Here I complement that list with information on works since that time that deal with reproductive cycles, spawning times, larval dispersal periods, settlement/recruitment times and/or growth rates for the common dominant mytilid species of the world (Table 6.2).

6.4.2 Larval dispersal and recruitment

Of all the environmental parameters influencing the abundance and distribution of adult rocky shore mussels we know least about life-spans, dispersal distances, predators or almost any other factors limiting mussel larvae. Because of the tremendous difficulty in following larval cohorts in the field (if such cohorts even remain as discrete entities), most larval life-spans have been determined either directly from laboratory cultures (Field, 1922; Bayne, 1965; de Schweinitz and Lutz, 1976) or inferred from the difference between the spawning date of a local population and subsequent recruitment dates into that same region (Kennedy, 1977; Griffiths, 1981a; Suchanek, 1981). This second approach is dangerous because it ignores the importance of immigration and emigration of larvae. For example, Kuenzler (1961a) found spawning in *Geukensia* during July and August, but significant recruitment only in March to June. It is highly unlikely that such larvae produced in mid-summer would either survive seven to eight months or remain in this localized region if they did survive. Much more likely is that the settling larvae either originated from a sub-population of the one under study, or from a different source entirely.

When the life-spans of mussel larvae have been estimated, they range in the order of two to four weeks (Nelson, 1928b; Bayne, 1964, 1965, 1976; de Schweinitz and Lutz, 1976), a period in which currents could easily wash the larvae into a different region. For what portion of that period a larva is 'competent' to settle (*sensu* Jackson and Strathmann, 1981), over what distances mussel larvae typically disperse, and what factors control immediate post-settlement survival are virtually unknown for nearly all mussel species, although Bayne (1964) and Seed (1969a,b) have presented a nearly complete picture for *M. edulis* in England. Only with concurrent investigations of spawning cycles, larval abundance and distribution patterns, and recruitment events can we make significant contributions to the understanding of complete mussel life history patterns.

Settlement and recruitment patterns for littoral mussels often show predictable annual trends, but occasionally they show massive settlements where the spatfall can vary by as much as one to three orders of magnitude (Suchanek, 1978; Hosomi, 1980; Griffiths, 1981a; Paine, pers. comm.). To my knowledge no long-term (≥ 10 yr) studies have been conducted on mytilid recruitment patterns to this end. At Tatoosh Island, 1972 and 1983 were massive recruitment years for *M. edulis* which resulted in the occupation of low littoral patches of cleared space in the *M. californianus* zone with up to 80% cover of *M. edulis*. Alternatively, some studies have even shown no recruitment, e.g. for five

TABLE 6.2

Information and references on reproductive cycles, spawning, recruitment and growth of mytilid mussels ('-' indicates no data found).

<i>Species</i>	<i>References</i>	<i>Size (mm) at first sexual maturity</i>	<i>Comments</i>
<i>Aulacomya ater</i>			
Africa:	Griffiths (1977) Griffiths and King (1979b)	15	Spawning almost anytime of year especially Aug./Sept. to Jan. or March
Chile:	Lozada <i>et al.</i> (1974)	-	settlement in Dec./Jan.
<i>Aulacomya maoriana</i>			
New Zealand:	Kennedy (1977)	-	gonads ripe from June to Sept., spawning and redevelopment, Aug. to Nov.
<i>Brachidontes variabilis</i>			
Australia:	Wilson and Hodgkin (1967)	-	ripe in January, brief spawning in late March/early April, settlement in April
<i>Choromytilus chorus</i>			
Chile:	Aracena <i>et al.</i> (1974) Yañez (1974)	-	settlement in April and Aug.-Sept.
<i>Choromytilus meridionalis</i>			
Africa:	Griffiths (1977, 1981a,b,d) Griffiths and Buffenstein (1981)	20	spawns most of year, especially July to Feb., greater reproductive output in littoral populations, recruitment all year
<i>Crenomytilus greyanus</i>			
Japan?:	Saito and Sakamoto (1951)	-	males develop in late Dec., females develop in early April, spawning in July and Aug.
U.S.S.R.:	Sadykhova (1970b)	-	spawns year-round with two peaks
<i>Geukensia demissa</i>			
North America (Atlantic):	Kuenzler (1961a,b) Bertness (1980) Jordan and Valiela (1982) Bertness and Grosholz (in prep.)	-	ripe in June/July spawn in July/Aug. or Aug./Sept. highest settlement March-June in the low littoral

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TABLE 6.2 *Cont'd*

<i>Species</i>	<i>References</i>	<i>Size (mm) at first sexual maturity</i>	<i>Comments</i>
<i>Modiolus modiolus</i>			
Europe:	Wiborg (1946) Seed and Brown (1975, 1977, 1978) Brown and Seed (1977)	30-40 40-50	spawning in March/April littorally: spawn in autumn and winter sublittorally: no annual spawning cycle spawning early spring/late summer
	Comely (1978)		
New England:	Witman (1984)	-	settlement sublittorally Sept./Oct.
<i>Mytilus californianus</i>			
North America (Pacific):	see Seed (1976b) and Suchanek (1981) for reviews and Nelson (1928b) Dehnel (1956) Harger (1970a) Paine (1974, 1976a) Elvin (1975) Jessee (1976) Petraitis (1978) Suchanek (1978) Elvin and Gonor (1979) Hines (1979a) Paine and Levin (1981) Kelley <i>et al.</i> (1982) Trevelyan and Chang (1983) Edwards (1984) Petersen (1984a,b)	15	spawns and settles year-round, sometimes with peaks in spring and autumn larval life span c. 3 weeks
<i>Mytilus edulis</i>			
World-wide:	see Seed (1976b) for review	-	variable spawning times dependent on geographic location, larval life span 15-30 days with settlement possible up to 40 days
Europe:	Kautsky (1982) Lowe <i>et al.</i> (1982)		
North America:	see Suchanek (1981) for review and Suchanek (1978) Newell <i>et al.</i> (1982) Edwards (1984)	- - -	spawning from July (May?)-Nov. with a peak in Sept. and Oct.

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TABLE 6.2 *Cont'd*

<i>Species</i>	<i>References</i>	<i>Size (mm) at first sexual maturity</i>	<i>Comments</i>
<i>Mytilus edulis aoteanus</i>			
New Zealand:	Pike (1971) Kennedy (1977)	- -	maturation Feb.-July, gonads ripe from Jan.-Sept., spawning from Aug. (July?)-March
<i>Mytilus edulis chilensis</i>			
Chile:	Padilla (1973) Yañez (1974)	- -	settlement in spring and summer settlement in summer
<i>Mytilus edulis diegensis</i>			
North America (Pacific) (California only):	Coe (1945, 1946)	-	spawns year-round, especially March-June and early winter
<i>Mytilus edulis planulatus</i>			
Australia:	Allen (1955) Wisely (1964) Wilson and Hodgkin (1967)	- - 30	settlement June/July to Dec. spawns June to mid-Aug. ripe and spawning Apr.-July and Sept., spawning April and July/August and Sept.-Nov., settlement June and Aug.-Nov.
<i>Mytilus edulis platensis</i>			
Argentina:	see Seed (1976b) Moreno <i>et al.</i> (1971)	-	spawns in early spring
<i>Mytilus galloprovincialis</i>			
Japan:	Hosomi (1980)	-	recruitment mostly in summer
Europe:	see Seed (1976b) for review and Seed (1978)	- -	variable spawning times dependent on location spawning Aug.-March/April
<i>Mytilus smaragdinus</i>			
Philippines:	see Seed (1976b) Obusan and Urbano (1968) and Barkati and Ahmed (1974) Tan (1975b) Nagabhushanam and Mane (1978) Shetty (1981)	- -	spawns year-round with peaks in May and November

THE ECOLOGY OF ROCKY COASTS

TABLE 6.2 *Cont'd*

<i>Species</i>	<i>References</i>	<i>Size (mm) at first sexual maturity</i>	<i>Comments</i>
<i>Perna canaliculus</i>			
New Zealand:	Havinga (1956)	-	-
	Greenway (1969a,b, 1975)	70	settlement in February and May
	Pike (1971)	-	spawns in summer and August
	Luckens (1976)	30-40	spawns in spring and summer
	Kennedy (1977)	-	settlement occurs year-round
	Hickman and Illingworth (1980)	-	-
<i>Perna perna</i>			
Venezuela:	Carvajal (1969)	-	spawning and larvae abundant in Dec.-Jan., March, June-July
Brazil:	Lunetta (1969)	-	spawning year-round, especially in April-June and Sept.
	Velez and Epifanio (1981)	-	-
<i>Perumytilus purpuratus</i>			
Argentina:	Penchaszadeh (1973)	-	settlement in late spring/early summer
Chile:	Lozada and Reyes (1981)	8-12	spawns year-round, both sexes develop and spawn simultaneously
<i>Septifer bilocularis</i>			
Australia:	Wilson and Hodgkin (1967)	-	ripe December to April, brief spawning in mid-April
<i>Xenostrobus pulex</i>			
Australia:	Wilson and Hodgkin (1967)	-	spawning Aug./Sept. and Oct./Jan., settlement in Sept.
	Luckens (1976)	8-10	spawns Aug.-Jan., settlement in low littoral-all year, settlement in high littoral-variable

years on littoral (Brown and Seed, 1977) and two years on sublittoral (Comely, 1978) *Modiolus modiolus* beds.

Planktonic mussel larvae may suffer as much as 99% mortality (Bayne, 1976). The most important factors that affect this mortality and, conversely, larval recruitment success are (i) suitable environmental conditions, (ii) adequate food supply, (iii) predation, (iv) accidental ingestion by filter-feeding invertebrates, and (v) location of a suitable settling substratum (Hancock, 1973; Bayne, 1976). To date we have some information on environmental factors critical to mussel larvae, especially temperature (Thorson, 1950 and see Bayne, 1976, for review). Virtually nothing is known about larval mytilid food supplies, although Bayne (1965, 1976) suggested that death due to starvation is highly unlikely. General categories of natural predators on mussel larvae are well known (see Mileikovsky (1974) and Bayne (1976) for reviews), but I know of no detailed works for any species. Accidental ingestion and mortality due to filter-feeding invertebrates has received considerable attention (Thorson, 1946, 1966; Bayne, 1964; Hancock, 1973; Mileikovsky, 1974). These reports show that mussel larvae can be bound in pseudofaeces or ingested and passed, sometimes alive (Mileikovsky, 1974), through the digestive tract of a filter-feeder, even a conspecific.

Information concerning suitable settling substrata, including data from laboratory tests (Trevelyan and Chang, 1983; Petersen, 1984b), indicates that considerable species-substratum specificity exists between different mytilid larvae, although this may be less acute in the field (Thorson, 1966; Petraitis, 1978). *M. edulis* has been shown to settle on a wide variety of filamentous substrata: byssal threads of their own species (Seed, 1969a; Dayton, 1971; Petraitis, 1978), filamentous algae (Colman, 1940; DeBlok and Geelen, 1958; Bayne, 1964; Seed, 1969a; Suchanek, 1978; Petersen, 1984a,b), and on sticks or filamentous ropes used in the mytiliculture industry (Korringa, 1976; Mason, 1976; Lutz, 1977, 1980). *Modiolus modiolus* larvae prefer adult conspecific periostracal 'hairs' (Brown and Seed, 1977; Comely, 1978). In Washington, where *Mytilus edulis* and *M. californianus* co-occur, plantigrades of the latter species are more often attracted to adult conspecific byssal threads (Petraitis, 1978; Suchanek, 1978, 1981), although this specificity was questioned by Petersen (1984a,b). Results of these types, involving two closely related sympatric species producing larvae in the same region at the same time, if they are to be meaningful, depend totally upon the investigators' abilities to identify pediveligers correctly to the species level, or to grow them successfully to an identifiable stage. In these cases the use of electrophoresis could aid in discriminating between closely related pediveligers unidentifiable by morphology alone.

Evidence also suggests that some mussels may rely heavily upon earlier ecological (possibly successional) stages for recruitment. Enhanced mussel settlement has been noted in the presence of the hydroid *Tubularia* (Lambert, 1939) and various species of barnacles (Obusan and Urbano, 1968; Tham *et al.*, 1973; Luckens, 1976; Mason, 1976; Menge, 1976; Suchanek and Duggins, in prep.). The significance of this phenomenon to mussel community development remains unknown.

6.4.3 Growth

For an in-depth discussion of growth in mussel larvae and adults see Bayne (1976) and Seed (1976b), respectively. In addition, attention is drawn especially to the following works on *Aulacomya ater* (Lozada *et al.*, 1974; Griffiths and King, 1979a,b; Griffiths, 1980a), *Choromytilus chorus* (Molina) (Aracena *et al.*, 1974), *Choromytilus meridionalis* (Griffiths, 1980a, 1981a,b,c,d; Griffiths and Buffenstein, 1981), *Geukensia demissa* (Kuenzler, 1961a,b; Lent, 1967; Bertness, 1980; Lutz and Castagna, 1980; Seed, 1980b; Jordan and Valiela, 1982; Bertness and Grosholz, in prep.), *Modiolus modiolus* (Seed and Brown, 1975, 1978; Brown *et al.*, 1976; de Schweinitz and Lutz, 1976; Brown and Seed, 1977; Comely, 1978), *Mytilus californianus* (Paine, 1976a; Elvin and Gonor, 1979; Suchanek, 1981; Trevelyan and Chang, 1983), *Mytilus edulis* (Lutz, 1976; Tsuchiya, 1980, 1982; Suchanek, 1981),

Mytilus galloprovincialis Lamarck (Seed, 1978b; Hosomi, 1980), *Perna canaliculus* (Luckens, 1976), and *Xenostrobus pulex* (Lamarck) (Luckens, 1976).

6.4.4 Physical and biological factors causing mortality in adults

a) Physical factors

In addition to the effects of temperature and desiccation mentioned above, factors associated with harsh winter conditions (i.e. ice, storm-generated waves and wave-driven logs) are the foremost physical factors causing mussel mortality. In salt marshes of New England, ice-rafting can remove large regions of vegetation and attached fauna, including populations of *Geukensia demissa* (Bertness and Grosholz, in prep.), although quantitative data on such mussel mortality have not been published. Ice-crushing or scouring can also cause severe mortality for *Mytilus edulis* populations in Boreal regions such as Baffin Island (Stephenson and Stephenson, 1972) and Glacier Bay, Alaska (pers. obs.).

Storm-generated waves and/or wave-driven logs cause dramatic mortality for rocky shore mussels. At Tatoosh Island, an extremely wave-exposed site, storm-related events caused the disruption of up to 65% of the area of some *Mytilus californianus* beds, leaving patches of bare space as large as 38m², with much greater size and frequency of patch initiation occurring during winter months and at sites exposed to more wave action (Levin and Paine, 1974; Paine and Levin, 1981). This disturbance rate varied over six winters of study from 0.4 to 5.4% of the mussels removed per month. Initial patch size may later enlarge from wave shock up to c. 5000% (Dayton, 1971), most likely as a result of weaker byssal thread attachments in the interior portions of these mussel beds than at the edges (Witman and Suchanek, 1984). Subsequent processes that are involved in the 'healing' of such patches are described in the following section.

Other studies on this system, where *Mytilus edulis* and *M. californianus* occur sympatrically, have indicated that greater levels of disturbance should occur when more *M. edulis* are present because the former species cannot attach itself effectively at sites with high wave exposure (Harger, 1968, 1970c; Harger and Landenberger, 1971). Harger extended this argument further to explain the absence of *M. edulis* from exposed Californian sites where *M. californianus* is dominant. However, as mentioned previously, *M. edulis* is abundant in some of the most wave-exposed sites known (Tatoosh Island, Washington and Torch Bay, Alaska). Further, Harger also suggested that, although *M. californianus* can attach strongly, it does not crawl as effectively as *M. edulis* and suffers burial and mortality from excessive siltation in protected embayments, eliminating it from those habitats. An alternative explanation was presented by Petraitis (1978) who showed that *M. californianus* larvae were lacking in protected bays where *M. edulis* was dominant.

Other *Mytilus*-dominated systems display similar winter disturbance phenomena. Menge (1976) and Lubchenco and Menge (1978) related wave shock to the organizational states of New England rocky shore communities where *M. edulis* was present, but did not quantify the levels of disturbance on *M. edulis*. In fact, their most exposed sites had the greatest cover of *M. edulis*, a result of the ineffectiveness of predators on *Mytilus* under such conditions.

b) Biological factors

Competition. Because mussels are effective and dominant competitors for space on horizontal or gently sloping substrata, only rarely do we see other species displacing them under these conditions at mid- to low-shore sites. However, occasionally, when two or more mytilid species live sympatrically (as do *Mytilus edulis* and *M. californianus* in Washington), interspecific competition can result in the partial exclusion of one species (in this case *M. edulis*). This competitive superiority results in the

sharp lower limit of *M. edulis* beds on the high-shore (see above under *Lower Limits*). Whether this exclusion in Washington is the result of crushing by the larger, thicker-shelled *M. californianus* (proposed by Harger, 1970c, 1972b) or of its superior predator-detering mechanisms, remains unknown. Another example of mortality from interspecific competition derives from the field manipulations of Paine (1971) where the low-shore kelp *Durvillea* in New Zealand seemed to exclude *Perna canaliculus* from this zone (see above under *Lower Limits*).

On more vertical faces in Washington the gooseneck barnacle *Pollicipes polymerus* Sowerby effectively outcompetes both *Mytilus* species (Paine, 1974). Although the mechanism for this is unknown, it may be related either to the relatively greater attachment strengths of *Pollicipes* on more vertical slopes, or to the inherent behavioural tendency of *M. californianus* to move downward. This lack of competitive superiority by mussels on vertical surfaces is true for *M. edulis* in New England as well (Menge, 1976).

Intraspecific competition can also cause mortality as a result of overcrowding which results in either (i) diminished food intake (Stiven and Kuenzler, 1979; Bertness, 1980), or (ii) subsequent instability of the mussel matrix and detachment by strong wave action (Seed, 1976b; Griffiths, 1981a).

Predation. Predation is undoubtedly one of the most significant and well-known sources of mortality for mussels. Typical predators include gastropods, sea stars, crabs and birds, with sea urchins, lobsters, fish and some mammals being less well-known. Until the last decade, our understanding of how predators affect mussel populations was derived almost entirely from studies on *Mytilus edulis*, with the exception of Paine's work (1966, 1969a) on *M. californianus* in Washington and his later work (1971) on *Perna canaliculus* in New Zealand. Since that time many excellent studies have helped to improve our understanding of world-wide patterns of predation on mytilid populations.

Seed (1976b) reviewed the most significant predators on *M. edulis* and gave some information on other mussel species. Additional works on *M. edulis* include those of Field (1922) who listed several other predators including the naticid gastropods *Lunatia heros* (Say) and *Polinices* (= *Neverita*) *duplicata* (Say), herring gulls, night herons, crows, ducks, killifish, cunners, scaups, tautogs, squeteagues, flounders, cod and eels, as well as the gray rat *Rattus norvegicus norvegicus* (Berkenhaut) and the muskrat *Ondatra zibethica* (L.). More recent studies on the Atlantic coast of North America deal directly with the dog whelk *Nucella* (= *Thais*) *lapillus* (L.) (Menge, 1976, 1978a,b, 1983; Menge and Sutherland, 1976; Lubchenco and Menge, 1978), the oyster drill *Urosalpinx cinerea* (Say) (Peterson, 1979), the sea stars *Asterias forbesi* (Desor) and *A. vulgaris* Verrill (Lubchenco and Menge, 1978; Menge, 1979, 1983; Peterson, 1979), and the crabs *Cancer borealis* Stimpson, *C. irroratus* Say, *Carcinus maenas* (L.) (Menge, 1983) and *Callinectes sapidus* Rathbun and *Neopanope sayi* (Smith) (Peterson, 1979). Further studies on *M. edulis* in Europe include work on predator preference, the mechanics of shell crushing, and energy maximization by the shore crab *Carcinus maenas* (Seed and Brown, 1975; Elnor, 1978; Elnor and Hughes, 1978). On the Pacific coast of North America similar groups of predators have been identified for *Mytilus edulis*: the gastropods *Nucella canaliculata* (Duclos), *N. emarginata* (Deshayes), *N. lamellosa* (Gmelin), and *N. lima* (Martyn), the sea stars *Evasterias troschelii* (Stimpson), *Leptasterias hexactis* (Stimpson), *Pisaster ochraceus* Brandt and *Pycnopodia helianthoides* (Brandt) (Suchanek, 1978, in prep.; Paine, 1980), and a number of shorebirds (scoters, surfbirds, crows and gulls).

On the East coast of North America, recent studies have shown few predators on adult *Geukensia demissa* living in mid- to high-littoral sites in salt marshes, although small mussels may be especially susceptible to predation by the crab *Callinectes sapidus* (Peterson, 1979; Hughes and Seed, 1981; Bertness and Grosholz, in prep.), and/or *Panopeus herbstii* H. Milne Edwards (Seed, 1980a). Through a series of laboratory feeding experiments on a closely related sublittoral mytilid in Europe (*Modiolus modiolus*) Seed and Brown (1975, 1978) showed similar trends for selection of small mussels by a suite

of predators (the sea star *Asterias rubens* L. and the crabs *Cancer pagurus* L., *Carcinus maenas*, *Pagurus* (= *Eupagurus*) sp. and *Liocarcinus* (= *Portunus*) sp.).

In Chile, work by Paine and Palmer (1978) has identified the clingfish *Sicyases sanguineus* Müller and Troschel as a significant rocky shore predator on both *Perumytilus purpuratus* and *Semimytilus algosus* (Gould). Further work in Chile by Paine *et al.* (1985) has shown that the sea star *Heliaster helianthus* (Lamarck) exerts strict control on *P. purpuratus* populations (see above under *Lower Limits*).

A flurry of recent work on sublittoral *Aulacomya ater* and *Choromytilus meridionalis* in South Africa has shown that their major predator, the rock lobster *Jasus lalandii* (H. Milne-Edwards), consumes smaller size-classes and greater numbers of *C. meridionalis*, resulting in domination of kelp bed sites by *A. ater* (Pollock, 1979; Pollock *et al.*, 1979; Griffiths and Seiderer, 1980; Griffiths, 1981a,c; Seiderer *et al.*, 1982). Other predators on these mussels, especially *C. meridionalis*, include the gastropods *Natica tecta* Anton (Griffiths, 1981a,c; Penney and Griffiths, 1984) and *Nucella cingulata* (L.) (Penney and Griffiths, 1984; Wickens and Griffiths, in press), the sea star *Marthasterias glacialis* (L.) (Branch, 1978; Griffiths, 1981a; Penney and Griffiths, 1984), the kelp gull *Larus dominicanus* Lichtenstein, the oystercatcher *Haematopus moquini* Bonaparte and the musselcracker fishes *Cymatoceps nasutus* (Castlenau) and *Sparadon durbanensis* (Castlenau) (Griffiths, 1981a; Penny and Griffiths, 1984).

In New Zealand, Luckens (1976) has identified several predators on the littoral mytilids *Perna canaliculus* and *Xenostrobus pulex*, although no quantitative data were given on their relative importance in controlling the mussel populations. These predators included the gastropods *Thais orbita* (Gmelin) (= *Dicathais scalaris* (Menke)) and *Lepsiella scobina* (Quay and Gaimard) for both mussel species and the rock cod *Acanthoclinus quadridactylus* (Bloch and Schneider) on *X. pulex*.

One of the reasons that certain mussel species can coexist with their predators is that they have 'escaped' to a size too large to be opened or drilled. Dayton (1971) inferred such size-limited predation for *Nucella* and Paine (1976a) demonstrated this clearly for *Pisaster* on *Mytilus californianus* in Washington. Similar results have been shown for crab predation on sublittoral *Modiolus modiolus* in England (Seed and Brown, 1978) and for sublittoral *Aulacomya ater* and *Choromytilus meridionalis* in South Africa for a number of predators (Pollock, 1979; Pollock *et al.*, 1979; Griffiths and Seiderer, 1980; Griffiths, 1981c; Penney and Griffiths, 1984).

Boring and fouling organisms. Seed (1976b) reviewed the literature on boring organisms such as the sponge *Cliona* and other parasites that affect mussels by degrading either the shell or tissues. *Cliona* is found occasionally on *Mytilus californianus* shells in Washington, but none appeared to cause mortality (Suchanek, 1979 and pers. obs.).

Fouling organisms are now being recognized as significant sources of mortality for mussel populations, both littorally and sublittorally. In Washington, the brown alga *Postelsia palmaeformis* Ruprecht can and does overgrow the valves of *Mytilus californianus* and, after the plants grow to 10cm, they are capable of dislodging some of their hosts (Dayton, 1971; Paine, 1979). In fact, over 25 species of algae and over 64 species of invertebrates foul the shells of *M. californianus* and can produce potentially detrimental effects (Suchanek, 1979, in prep.). Mortality from fouling can occur in two ways: (i) overgrowth of the valve openings causing restriction or total blockage of the feeding currents resulting in starvation (e.g. by sponges or barnacles) and (ii) dislodgement as a result of increased weight or shearing stresses encountered during winter storms (e.g. by algae or barnacles). I know of no published works for the first scenario. However, a survey of *M. californianus* shells washed ashore onto Shi Shi Beach, Washington, after winter storms revealed that 79% were either heavily fouled, or inexorably bound by byssus to a mass of mussels that were fouled, by algae or barnacles (Witman and Suchanek, 1984). Further, data from field measurements and laboratory experiments showed that

mussels that were overgrown by kelp encountered flow-induced forces 2 to 6 times greater than unfouled mussels (Witman and Suchanek, 1984).

Sublittoral mussel beds provide additional evidence for mortality from kelp fouling. After 11 months of monitoring marked *Modiolus* in New England, Witman (1984) found that 84% of fouled mussels and 0% of unfouled mussels were dislodged, showing that fouling negatively affects mussel survival. Without causing mortality outright, fouling organisms can also simply lower the fitness of mussels by reducing body tissue and/or gametic development. This has been documented for sublittoral populations of *Mytilus californianus* (Paine, 1976b) as well as for sublittoral *Modiolus modiolus* (Witman, 1984). The mechanism responsible for such lowered fitness is most likely to be related to lowered food intake for the sublittoral *Mytilus californianus* and to the greater expenditure of energy on maintenance and production of more byssal threads for secure attachment instead of gametic output or growth for *Modiolus modiolus*.

6.4.5 Recovery from disturbance

For mussel populations recovering from the disturbance events documented above, both the recovery rates and the types of recovery processes involved can vary considerably. Factors that seem to be especially critical to the rate (and details) of mussel bed recovery are: disturbance patch size, disturbance season, height on the shore, angle of substratum, thickness of mussel bed and larval recruitment. When *Mytilus californianus* populations are artificially or naturally disrupted, a series of moderately predictable events leads to the eventual return of this competitive dominant, beginning with diatoms and filamentous algae (Hewatt, 1935) and a series of macroalgae (Dayton, 1971). Work by R.T. Paine and colleagues (Levin and Paine, 1974, 1975; Suchanek, 1978, 1981, in prep.; Paine and Levin, 1981; Paine, 1984) showed that recovery is deterministic. Certain species which are competitively subordinate to *M. californianus* can colonize initially if the season of disturbance corresponds to their recruitment periods (e.g. in winter the barnacles *Pollicipes polymerus* and *Semibalanus cariosus* Pallas, the brown alga *Hedophyllum sessile* (C. Ag.) and *Mytilus edulis*). These species, however, are eventually outcompeted with the system returning to the competitive dominant within seven to ten years in the mid-shore (Paine and Levin, 1981).

The size of disturbance affecting a *Mytilus californianus* bed is also a critical element in the recolonization process. In small disturbance patches 'healing' may be achieved by mussels leaning over, especially when adjacent mussel beds are thick and disturbance patches are moderately small (Paine and Levin, 1981; Suchanek and Duggins, in prep.). Grazers such as limpets and chitons that live in the interstices of the mussel bed also graze out to a predictable distance from the perimeter of the bed into smaller disturbance patches. Their grazing distances have been measured at c. 25–30cm from the perimeter of a bed, and often result in a barren halo or 'browse zone' adjacent to the bed (Dayton, 1971; Suchanek, 1978). When disturbance patches have areas less than a critical size (c. 2500cm² for circular patches; i.e. < 25–30cm radius) the entire primary substratum of the patch is grazed heavily. Patches larger than this (at least in their central portions) will undergo the predictable sequence of colonization mentioned above, with adult mussels rolling in and re-attaching and larval mussels later recruiting from the plankton at a mean patch age of c. 26 months and reclaiming primary substratum at a rate of 2.0–2.5%·mo⁻¹ (Paine and Levin, 1981).

Height on the shore also has a dramatic effect on rates of recovery. Recovery ('healing') of artificially induced 0.10m² disturbance patches in *Mytilus californianus* beds was very rapid in the low-shore (sometimes within 6–12 months), intermediate in mid-shore (1–2 years) and extremely slow in high-shore patches (some not recovering after 10 years) (Suchanek and Duggins, in prep.). These rates, however, were also highly correlated with the thickness of the mussel beds at these sites. Exposure may also be important as sites more protected from wave action (e.g. Shi Shi) had considerably longer

recovery rates than those at more exposed locations (e.g. Tatoosh Island). Similar slow recovery rates have been noted in disturbance patches in *M. edulis* beds in Alaskan rocky shore sites (Suchanek and Duggins, in prep.).

Mussel recovery may also be enhanced by the presence of prior barnacle cover. In one New England site Menge (1976) found that *Mytilus edulis* recolonized 90% of barnacle-covered substrata in seven months, but 0% where no barnacles occurred. Similar trends have been found in Torch Bay, Alaska where recolonization of *M. edulis* on smooth, barnacle-free substrata was suppressed for over seven years (Suchanek and Duggins, in prep.).

In sublittoral habitats in New England, Witman (1984) found similarly slow recovery patterns for *Modiolus modiolus*. In a series of artificially cleared 115cm² patches in *M. modiolus* beds, after 24 months none was recolonized by mussels but 47% were recolonized by laminarian kelps (Witman, pers. comm.). However, it is uncertain what longer term patterns may be revealed in this system.

6.5 Mussels as Habitat Structure for Associated Organisms

As structurally complex entities, mussel beds provide refuge and habitat for a wide diversity of associated organisms. Although the diverse nature of some of these associations has been known for many years (Hewatt, 1935), until recently quantification of the member species and development of this community - along with any documentation of their importance to community dynamics - has been non-existent. Such associated communities have been noted for *Aulacomya ater* (Lawrence and McClintock, in prep.), *Brachidontes rodriguezii* D'Orb. (Penchazadeh, 1973), *Brachidontes rostratus* (Dunk.) (Bennett and Pope, 1953; Stephenson and Stephenson, 1972), *Modiolus modiolus* (Brown and Seed, 1977; Comely, 1978; Witman, 1984), *Mytilus californianus* (Hewatt, 1935; Ricketts and Calvin, 1939; Kanter, 1978; Suchanek, 1979, 1980, in prep.; Paine and Suchanek, 1983), *Mytilus edulis* (Nixon *et al.*, 1971; Tsuchiya, 1979; Tsuchiya and Nishihira, in prep.; Suchanek, unpubl. data), *Perumytilus purpuratus* (Ramirez, 1965; Suchanek, unpubl. data), and *Septifer bilocularis* (Jackson, 1976).

A mussel bed community consists of three major components: the mussel matrix, a diverse assemblage of associated organisms, and accumulated detritus at the base of the mussel bed. The mussel matrix is structurally more complex than the surrounding substratum, which, as in many other biological systems (e.g. aquatic, marine and terrestrial; see respectively Allan, 1975; Kohn and Leviten, 1976; MacArthur, 1964), leads to increased species richness. Increasing the thickness of the matrix (i) decreases the influence of wave action, temperature, and sunlight at the base of the bed and (ii) increases relative humidity and sedimentation. For *Mytilus edulis* this matrix can reach a thickness of 10cm (Nixon *et al.*, 1971); for *M. californianus* the matrix is often 5 or 6 mussel layers deep and can reach a thickness of c. 35cm (Suchanek, in prep.).

Associated organisms can be classified into three typical categories: epibiota (the fauna and flora that grow on, or bore into, the mussel shells), mobile fauna (those organisms that move freely throughout the mussel matrix), and infauna (those animals that are restricted to, and often dependent upon, the organic detritus and shell debris that accumulates at the base of the mussel bed matrix). There may be some overlap between categories. Together, these organisms comprise a community conveniently defined by the physical limits of the mussel matrix, with all trophic levels represented (except for external sources of zooplankton and phytoplankton). There is, of course, interaction and energy flow between other systems and/or populations of organisms such as fishes, birds, and a certain amount of migration by mobile animals that move out of the mussel matrix, for example, at high tide. Witman (1984) found that 22% of the species in a sublittoral *Modiolus* community were restricted to the mussel matrix.

Accumulated detritus contains faeces and pseudofaeces, other organic detritus, and inorganic

components such as shell debris, sea urchin spines and sediment. In 22cm thick *Mytilus californianus* beds in Washington, the dry weight of detritus can reach $65 \text{ kg} \cdot \text{m}^{-2}$ (Suchanek, in prep.). Comparable values for a 10cm thick *M. edulis* bed in Rhode Island are $14.4 \text{ kg} \cdot \text{m}^{-2}$, with an organic content of 3.86% (Nixon *et al.*, 1971).

Species richness of associated organisms has been documented for the *Mytilus californianus* community (over 303 taxa - Suchanek, 1979, 1980, in prep.), the *Modiolus modiolus* community (90 taxa - Brown and Seed, 1977; 23 taxa - Witman, 1984), and the *M. edulis* community (69 taxa - Tsuchiya and Nishihira, in prep. b). Both species richness and diversity indices are correlated with age and structural complexity of the mussel matrix (Suchanek, 1979, in prep.; Tsuchiya and Nishihira, in prep. a, b). Species richness is also correlated with height on the shore. Through a series of field experiments using artificial mussels in varying degrees of structural complexity, Suchanek (1979, in prep.) showed that the physical structure of the matrix was the most important factor promoting species diversity (H' = Shannon-Weiner index), but not necessarily species richness (S = total number of species) at both high- and low-shore sites. Within one year these artificial mussels attracted an associated community equivalent to real mussel beds of comparable structural complexity.

6.6 Mutualism and the Rôle of Associated Grazers

Mytilus edulis has the inherent ability to clean fouling organisms from its shell by use of a prehensile foot (Theisen, 1972). This adaptation has not been shown for any other mytilid. As a result shells of *M. edulis* contrast sharply with other species of mussels from naturally occurring populations by the distinct absence of potentially harmful fouling organisms (Suchanek, in prep.). When barnacles or kelp severely foul mussel shells, mortality is a well documented result (see above). One mechanism that protects mussels from overfouling and subsequent mortality is the constant action of mobile grazers such as limpets, chitons and/or sea urchins within the mussel matrix (Suchanek, 1979, in prep.; Witman, 1984).

The mussel matrix provides increased protection for these mobile grazers from predation and/or desiccation. In the littoral *Mytilus californianus* system birds such as oystercatchers, surfbirds, sandpipers, turnstones, wandering tattlers, crows and gulls forage extensively for limpets and chitons at low tide (Suchanek, in prep.). In the sublittoral *Modiolus modiolus* system, fish (cunners) and invertebrates (crabs and lobsters) are the major predators on grazing sea urchins that seek refuge in these mussel beds (Witman, 1984). Clearly, mussels benefit also from this association because the grazers continually remove potentially harmful fouling organisms (see above). Thus, mutual benefit is derived by increasing the fitness both of mussels and associated grazers when they co-occur.

This grazer-related benefit to mussels has been confirmed experimentally both littorally and sublittorally. By removing associated grazers from isolated littoral *M. californianus* beds, Suchanek (1979, in prep.) documented the disappearance of the grazing halo around such beds and the development of a heavy fouling of barnacles and algae on the mussels. Witman (1984) similarly removed sea urchin grazers from sublittoral *Modiolus modiolus* beds and documented a thirty-fold increase in kelp-induced dislodgement of mussels from urchin-free areas, i.e. without grazers, compared with control sites.

These data strongly indicate that a mutualistic relationship exists between grazers and mussels. Grazers in both systems also occur in habitats other than the mussel beds, making this a facultative, rather than an obligate mutualism (*sensu* Boucher *et al.*, 1982).

6.7 Conclusions

Mytilid mussels seem to outcompete most other rocky shore species in exposed or semi-exposed temperate zone habitats throughout the world. A strong but flexible attachment mechanism (byssal threads) has enabled them to exploit rocky substrata, especially littoral sites where wave action is

intense. Littoral mussels usually exist in discrete and predictably stable zones. The upper limits of these zones appear to be controlled by physical factors such as temperature (heat or freezing) and/or desiccation. Lower limits seem to be more under the biological control of intra- or interspecific competition or predation by a wide variety of taxa, both invertebrate and, less commonly, vertebrate.

Reproductive cycles, spawning, and recruitment phenomena for mussels are variable, but are usually consistent for any one species within a particular geographical region. Although we know little about the details of larval life histories, the planktotrophic veliger larvae of some mytilid mussels have life spans of two to four weeks.

Dominant mussel beds are often disrupted during winter storms, more so at increasingly wave-exposed sites. Subsequent recovery to full mussel cover usually proceeds through a predictable sequence of events. Recovery speed is dependent upon many parameters including disturbance season, initial size of disturbance, height on the shore, angle of the substratum, thickness of adjacent mussel bed, and stochastic events of local mussel recruitment (by both larvae and adults).

Mussel beds provide habitat structure for a wide diversity of associated organisms. The species richness of these associates appears to be correlated with both mussel-bed age and especially the structural complexity of the physical mussel matrix. In one littoral and one sublittoral mussel system, a facultative mutualism has been shown to exist between some of the associated grazers and the mussels. Grazers benefit by gaining protection from predators within the mussel matrix. Mussels also benefit from the continual grazing activities of the grazers which remove fouling algae and barnacles that could dislodge mussels during periods of increased wave action, causing mortality.