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9

Ecology of Life Histories

9.1

Introduction.

Amongst the bewildering diversity of marine organisms run some basic patterns of life history that are correlated with the physical and biological nature of the habitat. The present chapter briefly reviews such patterns, interpreting wherever possible the significance of particular phenomena in terms of natural selection. In making these interpretations, it is necessary to keep in mind the counterbalancing benefits and costs associated with most adaptations. Energy or material committed to one function may be unavailable for another, and the development of a certain attribute may restrict the development of others. Each organism represents a compromise to the conflicting demands of simultaneous evolutionary problems. Excellence in one field usually costs poorer performance in another, with the result that different organisms outclass one another in different circumstances. It should also be borne in mind that observed characteristics are not necessarily interpretable just in terms of current selection pressures, but may represent states that were fixed historically in ancestral lineages, so implicating phylogeny (see Harvey & Pagel (1991) and Section 9.3.2.7).

Early attempts to rationalize data on life histories often used MacArthur and Wilson's concept of r - and K -selection (e.g. Pianka 1974), where r denotes the intrinsic (unlimited or exponential) per capita rate of increase and K the carrying capacity (asymptotic population size) of the logistic growth equation. In the logistic model, growth rates of populations at densities well below the carrying capacity are influenced largely by the variable r , whereas growth rates of populations at densities close to the carrying capacity are greatly influenced by K . Populations kept at, or repeatedly reduced to, low densities by physical or biotic environmental factors will be influenced by a different set of selective pressures (r -selection) from the set influencing more stable populations at high densities (K -selection). r -selected species correspond to opportunistic, early successional organisms in which rapid growth, early sexual maturity, high fecundity and great dispersal abilities are often advantageous. K -selected species correspond to late-successional organisms occupying more permanent habitats, in which competitive ability, resistance to predation, greater longevity, greater investment per offspring and the capacity to reproduce repeatedly in successive seasons are at a premium. r -selected features tend to be correlated with small body size and K -selected features with larger body size. As body size is inversely proportional to population growth rate and hence to the ratio of production to biomass, there is a trend of decreased population turnover rate and productivity from more r -selected to more K -selected species (Fig. 9.1). The ' rK continuum' has provided a framework upon which to build theories

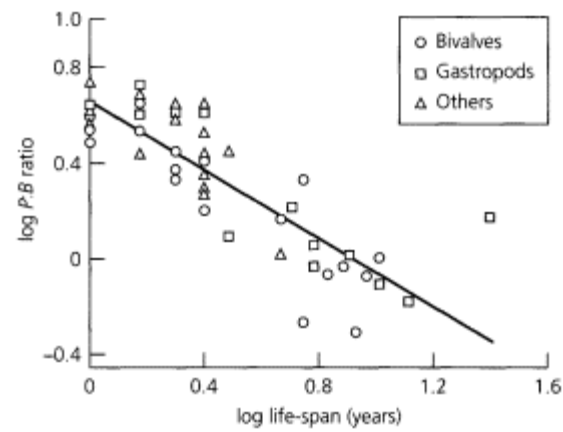


Fig. 9.1
The ratio of production (P) to biomass (B)
with increasing life-span and hence with
increasing body size. (After Robertson 1979.)

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of life history, but the need for modification has become increasingly apparent. Some of the organisms discussed below (e.g. heteromorphic algae, benthic invertebrates with planktonic larvae) will be seen to possess a mixture of *r*- and *K*-features, whereas other properties, such as resistance to physiological stress, are not covered adequately by the '*rK*' concept. The latter is evidently too restrictive and is gradually being replaced by more comprehensive schemes of classification as knowledge and understanding of life history ecology develops. For example, Grime (1979) included physiological stress along with population density, and Sibly & Calow (1986) offered a general scheme, encompassing *r*- and *K*-selection, based on gradients of juvenile growth rate and the ratio of juvenile to adult survivorship.

9.2

Algae and Higher Plants

9.2.1

Benthic Forms

Benthic vegetation extends to depths where the sea bed coincides with the lower limit of the photic zone. Representatives from the wide range of algal types, encompassing unicellular, filamentous, encrusting and foliose forms, are potentially able to colonize any kind of physical substratum. Because of their small size, rapid population growth and physiological robustness, unicellular and filamentous algae are able to survive under harsh or frequently disturbed conditions, such as the splash-zone of rocky shores, heavily grazed sublittoral rock surfaces or on the surfaces of mobile sediments. In more equable circumstances, foliose and encrusting macroalgae establish themselves on hard substrata, forming the dominant vegetation, e.g. intertidal fucoids or sublittoral kelps (Chapter 5).

Macroalgae are not so successful at colonizing sedimentary substrata. Fucoids and kelps may be found attached to shells or small stones and may continue growing even when detached from the substratum in very sheltered localities. Indeed, some members of the Fucales, such as certain morphs of *Ascophyllum nodosum* and the well-known oceanic rafts of *Sargassum* in tropical seas, can lead an entirely pelagic life. However, in general, angiosperms replace macroalgae as the dominant vegetation of shallow-water sediments, e.g. salt-marshes, sea-grass meadows, mangrove-swamps (Chapter 4). Features giving higher plants the ability to dominate terrestrial habitats also enable them to reinvade these aquatic habitats with equal success. Sophisticated skeletal and stomatal systems keep emergent vegetation erect and protected from desiccation while allowing efficient gaseous exchange. Roots and rhizomes provide anchorage, access to sedimentary nutrients and may serve as perennating organs protected from some of the physical hazards occurring above-ground. Angiosperm root-systems, however, are unable to cope effectively with hard surfaces, which therefore provide a competitive refuge for the macroalgae.

Macroalgae occur in an impressive variety of forms, but these can be grouped into several broad categories such as filamentous, membranous, finely branching, coarsely branching, calcareous and encrusting forms (Fig. 9.2a). Life cycles may involve very different growth forms, e.g. minute gametophytic and large sporophytic phases of kelps (Fig. 5.15a), or the frondose gametophytic and encrusting sporophytic phases of certain red algae (for a review of red algal life cycles, see Searles (1980)). Large physiological differences also occur among algae: some are quick growing but flimsy and short lived, others slow growing, robust and long lived; some contain bacteriocidal and herbivore-repellent chemicals; some are resistant to considerable physiological stress and others less so.

These features represent counterbalancing capacities for rapid growth, reproduction, environmental tolerance, resistance to predation and competition for resources (nutrients, space, light). Among the possible combinations of such properties, certain groupings are particularly

common, and many of these can be understood in terms of the type of habitat in which the algae are found. The role of physical and biological disturbances in determining community structure were discussed in Sections 5.1, 5.2 and 6.4, from which it is evident that there exists a continuum from frequently disturbed habitats, such as heavily grazed, rocky surfaces, to relatively undisturbed habitats, such as the fucoid zone on sheltered shores. Combinations of features expected to be advantageous in species exploiting young, temporally fluctuating communities of disturbed habitats (corresponding to an r -selected regime, Section 9.1)

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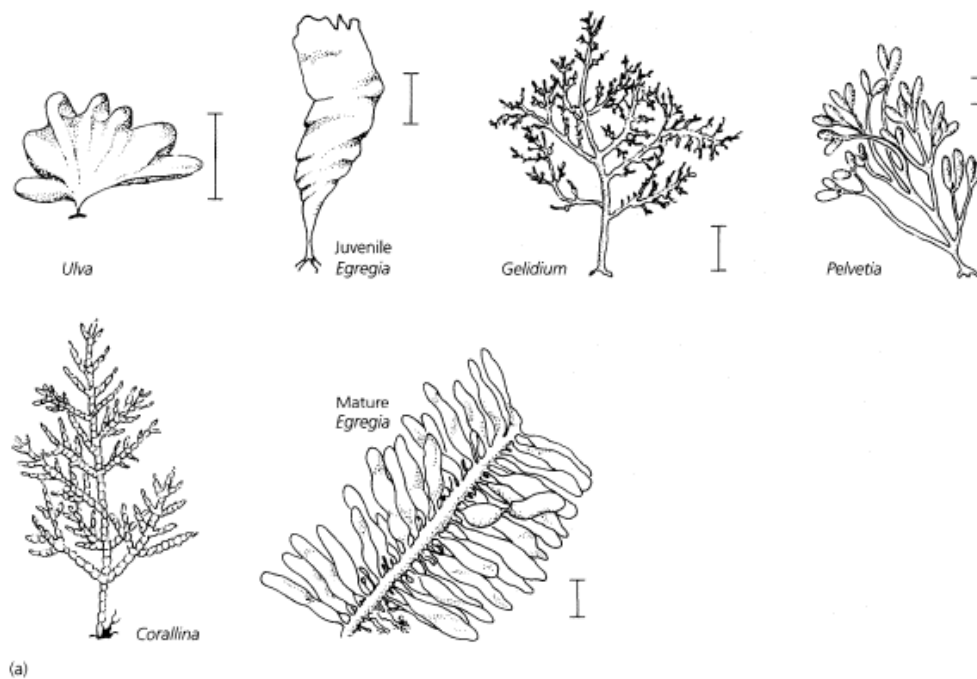


Fig. 9.2

(a) A range of algal morphologies. Scales represent 2 cm. The segment of *Egregia* is from a frond about 4 cm long.

are compared in Table 9.1 with those expected to be advantageous in species from mature, temporally constant communities from undisturbed habitats (similar to a *K*-selected regime). The counterbalancing benefits and costs ('trade-offs') associated with these features are listed in Table 9.2. To a large extent, theoretical expectations are borne out in nature. Thus, membranous forms such as *Ulva* and *Porphyra* are commonly the earliest colonizers of disturbed, rocky intertidal substrata, and if succession is allowed to proceed, the early colonists are replaced by more robust species (Fig. 9.2). Opportunistic species have higher net productivities than later colonists, which invest more material and energy into non-photosynthesizing structural or defensive materials. This trend is reflected by the ratio of productivity to total biomass (P/B), which decreases in the order of membranous, finely branching, coarsely branching and encrusting forms. The high net productivities of membranous algae such as *Ulva*, *Porphyra* and *Enteromorpha* are partly attributable to the extremely thin construction of the thallus and the large size of the cells, which result in relatively little self-shading by non-photosynthesizing materials. Late successional species grow more slowly and reproduce less profusely than opportunistic species, but their investment in non-photosynthesizing materials gains them greater life expectancy in at least three ways. First, non-photosynthesizing supporting tissue enables the algae to attain large sizes and to adopt overtopping growth forms that impart a competitive advantage over more delicate forms. The dominance of many sheltered, rocky shores by fucoids may be largely attributable to this factor. Secondly, the supporting tissue increases algal resistance to physical damage by waves, currents and scour. Thirdly, a tough

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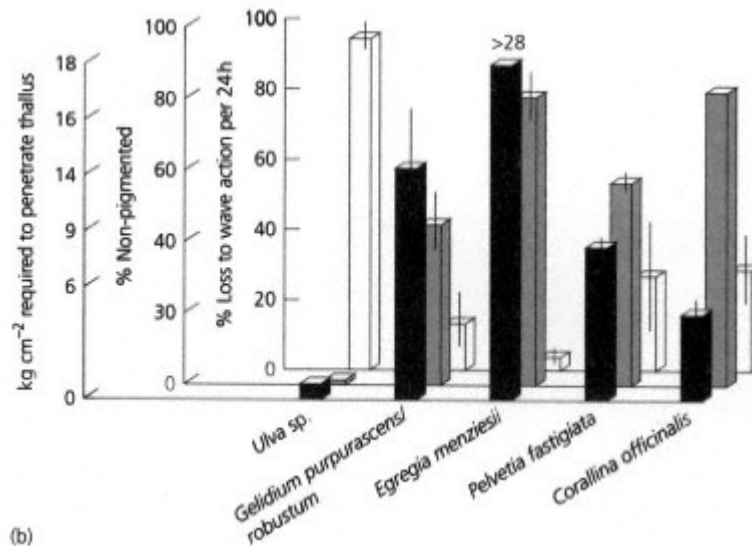
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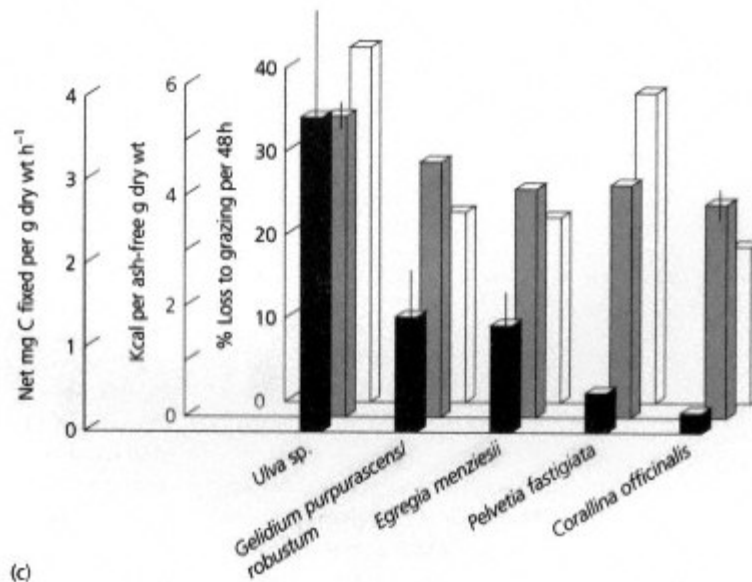
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(b)

Fig. 9.2
Contd

(b) Frond-toughness. Percentage of structural (non-photosynthetic) material in the frond, and resistance to wave shock among a series of Californian intertidal algae;



(c)

Fig. 9.2
Contd

(c) mean net primary productivities, energy contents, and palatabilities of the algal species as in (b). (After Littler & Littler 1980.)

epidermis, calcareous matrix, low energy content or presence of toxic chemicals reduce the acceptability to grazers.

Tolerance to physiological stress, such as desiccation and extremes of temperature or salinity, may or may not be associated with reduced productivity. High-shore furoids such as *Pelvetia canaliculata* are more resistant to desiccation, but are slower growing than lower-shore furoids (see Fig. 5.6). Some long-lived, slow-growing, encrusting algae such as *Hildenbrandia* are highly resistant to physiological stress (Section 5.1.4.2). On the other hand, opportunistic macroalgae such as *Ulva* and *Enteromorpha*, together with unicellular bluegreen and diatomaceous algae, are not only fast growing, but also are among the most resistant algae to physiological stress.

A number of red algae form epilithic, encrusting sporophytes that are long lived, apparently having evolved under selective pressures from intense

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Table 9.1 Hypothetical *a priori* survival strategies available to opportunistic macroalgae representative of stressed* communities vs. macroalgae characteristic of nonstressed** communities. (After Littler & Littler 1980.)

Opportunistic forms

1 Rapid colonizers on newly cleared surfaces

2 Ephemerals, annuals, or perennials with vegetative short- cuts to life history

3 Thallus form relatively simple (undifferentiated) and small with little biomass per thallus; high thallus area to volume ratio

4 Rapid growth potential and high net primary productivity per entire thallus; nearly all tissue is photosynthetic

5 High total reproductive capacity with nearly all cells potentially reproductive and many reproductive bodies with little energy invested in each propagule; released throughout the year

6 Calorific value high and uniform throughout the thallus

7 Different parts of life history have similar opportunistic strategies; isomorphic alternation; young thalli just smaller versions of old

8 Escape predation by nature of their temporal and spatial unpredictability or by rapid growth (satiating herbivores)

* Young or temporally fluctuating.

** Mature, temporally constant.

Late successional forms

1 Not rapid colonizers (present mostly in late seral stages) and invade pioneer communities on a predictable seasonal basis

2 More complex and longer life histories; reproduction optimally timed seasonally

3 Thallus form differentiated structurally and functionally with much structural tissue (large thalli high in biomass); low thallus area to volume ratio

4 Slow growth and low net productivity per entire thallus unit because of respiration of non-photosynthetic tissue and reduced protoplasm per algal unit

5 Low total reproductive capacity and specialized reproductive tissue with relatively high energy contained in individual propagules

6 Calorific value low in some structural components and distributed differentially in thallus parts. May store high- energy compounds for predictable harsh seasons

7 Different parts of life history may have evolved markedly different strategies; heteromorphic alternation; young thalli may possess strategies paralleling opportunistic forms

8 Reduce palatability to predators by complex structural and chemical defences

grazing and stressful physical conditions, e.g. wave action, sand scour. They also form short-lived, upright gametophytes that are faster growing but less robust than the sporophytes. When first describing these 'heteromorphic' forms, taxonomists mistook them for separate species, and although their identity is now recognized, the nomenclature is retained. For example, a common heteromorphic red alga on western North American rocky shores is the encrusting sporophyte known as *Petrocelis middendorffii*, which alternates with the foliose gametophyte known as *Gigartina papillata*. The sporophyte grows slowly, increasing in area by about 4% a year, or even shrinking in some years, but is generally long lived, an average-sized individual being anywhere from 25 to 90 years old. The gametophyte is probably annual, is more productive (0.64 vs. 0.09 mg C g⁻¹ per day) and is over twice as palatable to grazers as the sporophyte. Other algae, e.g. *Chondrus crispus* or *Corallina officinalis*, may have extensive crustose basal or holdfast systems from which grow erect thalli, and perhaps these algae invest differentially in the two structures according to environmental conditions. Among brown algae, kelps have heteromorphic life cycles (Fig. 5.15a), the tiny, ephemeral, opportunistic gametophytes alternating with the large, longer-lived sporophytes. However, even the sporophytes of some kelps may change morphologically as

they grow. The young sporophytes of *Egregia* spp. (Fig. 5.15b) are thin, membranous forms with high growth rates enabling them to recruit effectively during early successional stages, but with increasing age the sporophytes invest more energy and material into supporting tissues, thereby reducing productivity but at the same time increasing competitive

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Table 9.2 Hypothetical costs and benefits of the survival strategies proposed in Table 9.1 for opportunistic (inconspicuous) and late successional (conspicuous) species of macroalgae. (After Littler & Littler 1980.)

Opportunistic forms	Late successional forms
<i>Costs</i>	
1 Reproductive bodies have a high mortality	1 Slow growth, low net productivity per entire thallus unit results in long establishment times
2 Small and simple thalli are easily outcompeted for light by tall canopy formers	2 Low and infrequent output of reproductive bodies
3 Delicate thalli are more easily crowded out and damaged by less delicate forms	3 Low surface to volume ratios relatively ineffective for the uptake of low nutrient concentrations
4 Thallus is relatively accessible and susceptible to grazing	4 Overall mortality effects are more disastrous because of slow replacement times and overall lower densities
5 Delicate thalli are easily torn away by the shearing forces of waves and abraded by the sedimentary particles	5 Must commit a relatively large amount of energy and materials to protecting long-lived structures (energy that is thereby unavailable for growth and reproduction)
6 High surface to volume ratio results in greater desiccation when exposed to air	6 Specialized physiologically and thus tend to be stenotopic
7 Limited survival options because of less heterogeneity of life history phases	7 Respiration costs high because of the maintenance of structural tissues (especially unfavourable growth conditions)
<i>Benefits</i>	
1 High productivity and rapid growth permits rapid invasion of primary substrates	1 High quality of reproductive bodies (more energy per propagule) reduces mortality
2 High and continuous output of reproductive bodies	2 Differentiated structure (e.g. stipe) and large size increases competitive ability for light
3 High surface to volume ratio favours rapid uptake of nutrients	3 Structural specialization increases toughness and competitive ability for space
4 Rapid replacement of tissues can minimize predation and overcome mortality effects	4 Photosynthetic and reproductive structures are relatively inaccessible and resistant to grazing by epilithic herbivores
5 Escape from predation by nature of their temporal and spatial unpredictability	5 Resistant to physical stresses such as shearing and abrasion
6 Not physiologically specialized and tend to be more eurytopic	6 Low surface to volume ratio decreases water loss during exposure to air
	7 More available survival options due to complex (heteromorphic) life-history strategies
	8 Mechanisms for storing nutritive compounds, dropping costly parts, or shifting physiological patterns permit survival during unfavourable but predictable season

ability and physical robustness (Table 9.3). This shift in thallus form allows *Egregia* to compete effectively with opportunistic species for newly available space as well as to persist among late successional competitors for light and space.

The distribution of green, brown and red algae is very loosely related to depth. Green algae tend to be abundant intertidally, brown algae flourish both intertidally and sublittorally, and red algae are

most numerous sublittorally. This distributional sequence used to be interpreted as chromatic adaptation to prevailing light conditions. Blue and green light is least

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Table 9.3 Comparative values for juvenile and mature individuals of *Egregia menziesii* used to test the shifting-strategy hypothesis. (After Littler & Littler 1980.)

Thallus used	Net productivity (mg C fixed g ⁻¹ (dry wt h ⁻¹))	Toughness (kg cm ² to penetrate thallus)	Time of appearance on successional plots (months)
Juvenile	2.51 ± 0.13	3.60 ± 0.33	3.0
Mature	1.26 ± 0.52	> 28 (off scale)	10.0

absorbed by water, whereas longer wavelengths of red, orange and yellow light are strongly absorbed (see Sections 1.2 and 2.1). Phycobilins and carotenoids of complementary colour to underwater light absorb the latter more efficiently than chlorophyll, on to which they are able to pass the excitation energy for photosynthesis. These accessory pigments give brown and red algae their characteristic colour, which has therefore been regarded as adapted to changing light quality with increasing depth. Accumulating documentation of distributional exceptions and conflicting physiological data, however, throw increasing doubt on the general applicability of the chromatic adaptation hypothesis. For example, green algae survive at the expense of brown and red algae when heavily grazed by sea-urchins in deep sublittoral areas (Section 5.2.4.1). Chromatic adaptation could still be important in allowing the red algae to outcompete the green algae when undisturbed, or to survive under the canopy of tall brown algae that also flourish at these depths, but its role is far from clear. Physiological experiments, moreover, have shown algal morphology to be at least as important as colour in determining potential vertical distribution (Ramus *et al.* 1976), and the actual limits to range are probably set by such factors as desiccation, grazing, competition and availability of sites (Sections 5.1 and 5.2).

9.2.2

Phytoplankton

Phytoplankton is the most abundant pelagic algal life and is virtually ubiquitous in the surface waters of the seas. Floating rafts of macroalgae, such as *Sargassum*, are very restricted in geographical distribution and are confined to the airwater interface. By existing as small suspended particles, phytoplankton gains access to subsurface nutrient supplies through transportation by vertical mixing. Small size is advantageous in a planktonic existence for reasons considered in Chapter 2.

Shape is also important: flattened discs, long cylinders or filaments sink more slowly than spheres of similar volume. Spheres and discs absorb nutrients more rapidly per unit mass than long filaments of similar diameter when sinking at the same rate. Elaborations in the form of spines or hairs (Fig. 9.3) may reduce sinking rates in some instances, but because of the relatively high density of cell wall material, pronounced ornamentation could increase sinking rates in other cases. Large, spiny diatoms and dinoflagellates frequently contain oil droplets and large vacuoles that increase their buoyancy, and it would appear that the function of spines and other processes is frequently to deter zooplanktonic grazers such as copepods. Some diatoms are enclosed in gelatinous capsules of only very slight excess density. The gelatinous capsules may protect the diatoms from predation either by making them too big for zooplanktonic grazers to handle or by allowing them to pass unharmed through the guts of their predators. Chain-formation may decrease or increase sinking rate according to whether the aggregative surface area to volume ratio is increased or decreased (Fig. 9.3) and may deter some predators. Size and shape may therefore

represent an evolved compromise to the effects of sinking rate, efficiency of nutrient uptake, predation and possibly other factors (Hutchinson 1967).

Although planktonic algae exist as single cells or small cellular aggregates it is important to realize that the cells divide mitotically under favourable circumstances to produce clones of cells with identical genotypes. Each clone is genetically equivalent to the multicellular body of a nonclonal alga such as a fucoid or a kelp, and in this sense the clone is the genetic 'individual' and the component cells are spatially scattered modules of its 'soma' (for a discussion of clonal population ecology, see Harper (1977)). Advantages gained by dividing the body into a large number of detached modules include: (1) a high productivity facilitated by high ratios of absorptive surface area to cytoplasmic volume and of photosynthetic to structural materials; (2) the potential ability to disperse modules among

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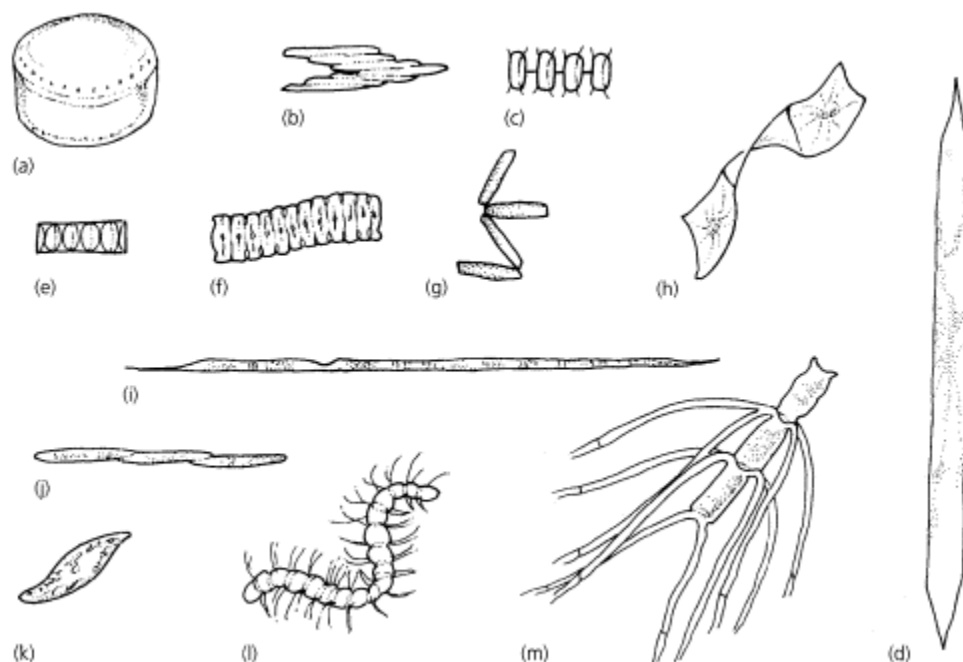


Fig. 9.3

Adaptive shapes and ornamentalations of planktonic algae: (a) *Coscinodiscus concinnus*; (b) *Bacillaria paradoxa*; (c) *Thalassiosira gravida*; (d) *Rhizosolenia styloformis*; (e) *Paralia sulcata*; (f) *Bellarochea malleus*; (g) *Thalassiothrix nitschioides*; (h) *Streptothecca thamensis*; (i) *Rhizosolenia hebetata*; (j) *Nitzschia seriata*; (k) *Gyrosigma* sp.; (l) *Chaetoceros curvisetus*; (m) *Chaetoceros convolutus*. (After Hardy 1962.)

different water masses, thereby increasing the chance of encountering favourable growing conditions; (3) the ability to quickly exploit localized resources by rapid (exponential) clonal growth; (4) lessening the probability of extinction of the genotype by spreading the risks of mortality among many independent modules.

9.3

Animals

Animals lead more varied lives than algae and higher plants, largely because of the more diverse sources of energy and nutrients that they exploit. The richness of life histories of marine animals could exceed the capacity of even a large textbook, but some important general features will be discussed here under the arbitrary headings of feeding and reproduction.

9.3.1

Feeding

9.3.1.1

Filter Feeders and Deposit Feeders.

Just as benthic algae and higher plants can acquire energy by remaining stationary and intercepting sunlight, so numerous animals can meet their energy requirements by remaining attached to the substratum and intercepting water-borne food particles: either planktonic organisms or particulate organic matter. Filter feeders sift food particles still in suspension, whereas deposit feeders gather food particles that have fallen out of suspension into the sediment.

Filter feeders are represented among diverse phyla (Fig. 9.4 and Plates 23 and 24, facing p. 208), being most numerous where currents bring food particles from large catchment areas. Many filter feeders employ ciliary tracts or sticky mucus, or both, to trap food particles and transport them to the mouth. Arthropods lack cilia and use meshes constructed from interlocking hairs and bristles (Fig. 9.4g). The filtration device is either external, as with the radially symmetrical crown of tentacles or bristles of coelenterates, bryozoans, phoronids, polychaetes, arthropods, echinoderms and hemichordates, or internal, as with the choanocyte chambers of sponges, lamellae of

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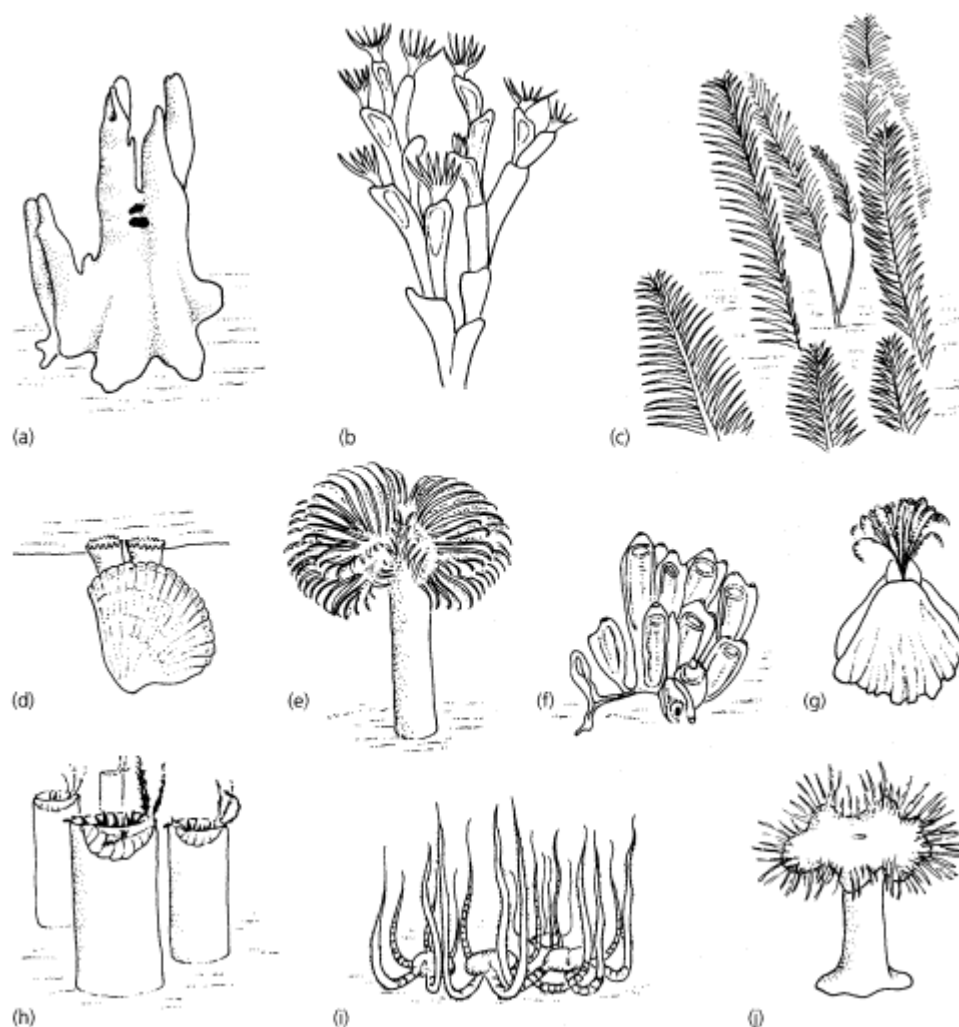


Fig. 9.4

Filter-feeding benthic animals: (a) the sponge *Amphilectus*; (b) the bryozoan *Bugula*; (c) the hydroid *Algaophenia* with its flat surface at right angles to the prevailing current; (d) the bivalve *Cerastoderma edule*; (e) the polychaete *Bispira volutacornis*; (f) the tunicate *Clavellina lepadiformis*; (g) the barnacle *Semibalanus balanoides*; (h) the amphipod *Haploops tubicola*; (i) the brittlestar *Ophiothrix fragilis*; (j) the anemone *Metridium senile*. (After Hughes 1980b.)

bivalves, lophophores of brachiopods and pharyngeal chambers of tunicates. Radially symmetrical discs, cups or fans formed by tentacles or intermeshing bristles optimize combinations of surface area, mechanical strength, metabolic operational costs and trapping efficiency. The last may also be increased by adjusting the orientation of the filter so that it always faces the water currents. This may involve movement of the animal, as in barnacles and polychaetes, or a modification of colonial growth as in feather- or leaf-shaped hydroids, bryozoans and gorgonians that grow with their broad surfaces at right angles to the current (Fig. 9.4c).

Cnidarians, through their possession of stinging nematocysts, are potentially able to catch large prey in addition to small suspended particles. Some anemones, such as the western North American *Anthopleura elegantissima*, which subsists largely on dislodged mussels, can cope with prey almost as large as themselves. Other filter feeders, e.g. stony

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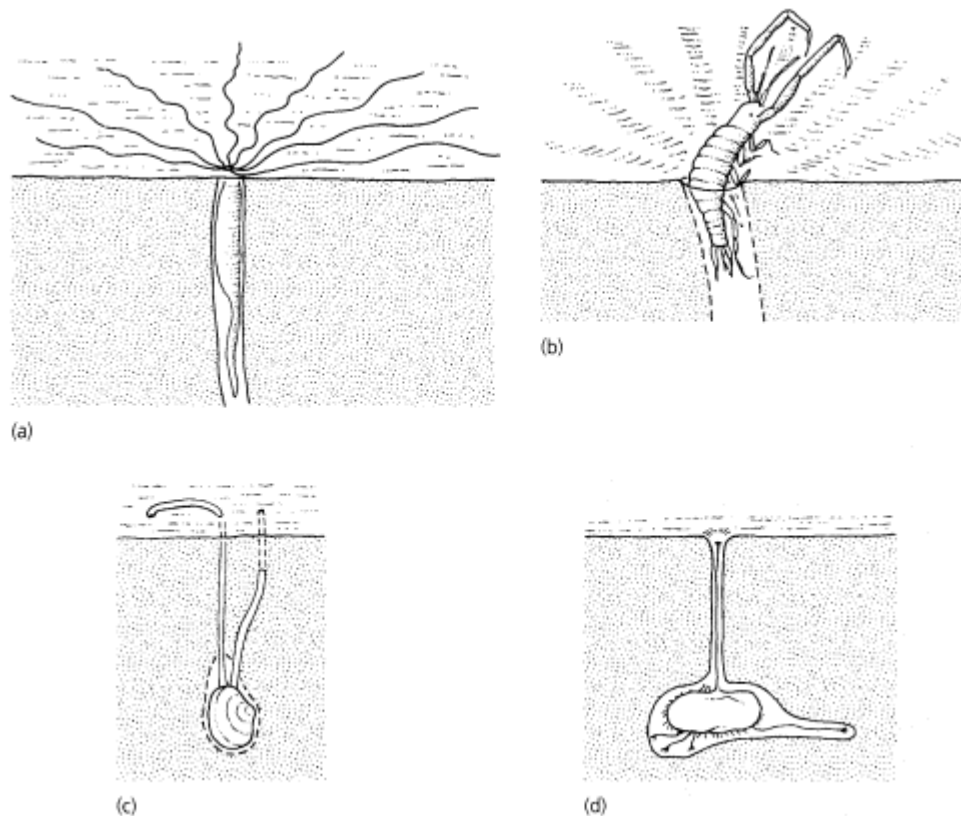


Fig. 9.5
Deposit feeders: (a) the polychaete *Amphitrite*; (b) the amphipod *Corophium volutator*; (c) the bivalve *Scrobicularia plana*; (d) the burrowing urchin *Echinocardium cordatum*. (After Hughes 1980b.)

corals, soft corals, giant clams (*Tridacna*) and certain ascidians living in shallow, sunlit waters, rely to a greater or lesser extent on the photosynthates of symbiotic zooxanthellae (dinoflagellates, or in the case of tunicates, bluegreen algae) as a source of energy (Section 6.10.1).

Deposit feeders also form a diverse taxonomic assemblage (Fig. 9.5 and Plates 25 and 26, facing p. 208). Whereas filter feeders tend to live on hard substrata or in sediments where there is little silt to clog the delicate filtering mechanisms, deposit feeders are able to cope with silty sediments, which they ingest to extract the micro-organisms associated with detrital or mineral particles. Because deposit feeders need to process copious quantities of sediment to extract sufficient food and because they also tend to live in unstable substrata, they are generally more mobile than filter feeders, showing greater morphological adaptation for locomotion and lacking the radial symmetry and colonial existence of many filter feeders.

9.3.1.2 Predators

In an ecological context, herbivory and carnivory can be regarded as types of predation, the only essential difference being the trophic level of the prey. Predators may consume entire prey organisms, as with fish eating zooplankton or dogwhelks eating barnacles, or they may consume only part of the prey organism without killing it, as with herbivorous grazers of benthic macroalgae or carnivorous grazers of sedentary colonial animals. Both grazers and non-grazers

show a wide range of feeding behaviour from extreme dietary specialization to extreme generalism. Dietary specialization is more appropriate where specific prey are predictably abundant. Such is often the case with prey that have defence

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mechanisms effective against predators, resulting in low overall predation pressure. Examples are plentiful among sedentary animals. Sponges are pervaded by spicules that not only make sponge tissue unpalatable to many predators, but also lower its energetic value as food. In tropical to warm temperate regions where grazing fish are numerous, sponges living on open surfaces contain toxic chemicals that repel fish; for example, in the Red Sea, the sponge *Latrunculia magnifica* contains a cholinesterase inhibitor. In the same regions, sponges occupying protective microhabitats within crevices or beneath ledges do not possess toxins, which presumably are manufactured at some cost. Cnidarians are charged with stinging nematocysts that are defensive as well as offensive in function. The sea anemone *Anemonia sulcata* also contains toxic polypeptides that are lethal when experimentally injected into fish and crustaceans, and which presumably repel predators in nature. Organisms protected from the majority of predators present a potentially rich food source for any animals that develop means of breaking through the defence mechanisms. Not surprisingly therefore, virtually all plants and animals armed with antipredation devices are exploited by a few coevolved predators, specialized to deal with these defences. Certain nudibranches and cowries specialize on sponges; for example, the nudibranch *Archidoris pseudoargus* feeds entirely upon the sponge *Halichondria panacea*, and the nudibranch *Aeolidia papillosa* feeds on sea anemones.

Generalist predators can be expected to contract or expand their diets according to the relative abundances of more or less preferable prey. The western North American starfish *Pisaster ochraceus* prefers mussels but will also feed on barnacles and then gastropods as the preferred prey become scarce. Dietary preferences sometimes reflect the profitabilities of different prey. Profitability will be a complex function of the likelihood of capture, yield of food material and the time and effort needed to handle the prey. In other instances, dietary preferences may reflect the limited time available for foraging or the need to minimize the time spent foraging, during which the predator may itself be at risk to predation or to other mortality factors.

Predators can be classified as searchers, pursuers and ambushers (Fig. 9.6). Searchers (Plate 27, facing p. 208) spend most of their foraging time locating prey which, once encountered, are caught and eaten relatively quickly; these predators will tend to be generalists, feeding opportunistically on any easily caught prey. Pursuers (Plate 28, facing p. 208) feed on prey that take a relatively long time to catch and subdue, so that a large proportion of the foraging time is spent pursuing individual prey; these predators will tend to specialize on prey with high profitabilities, perhaps becoming morphologically adapted to capturing particular prey efficiently. Ambushers wait for prey to come close enough to be caught by surprise or by blundering into a trapping mechanism; these predators do not actively search for prey or pursue them, but some considerable time may be spent subduing and digesting very large prey. Ambushers cannot determine which prey shall be encountered and so will tend to accept all capturable prey, sometimes being able to tackle prey as large as or even larger than themselves.

As with most biological classifications, this categorization of predators is arbitrary and many animals will have intermediate predatory behaviour or may even switch from one category to another according to circumstances. The shore crab, *Carcinus maenas*, is a most opportunistic feeder as it migrates with the tide to forage on the shore (Fig. 9.6a). When feeding among an abundance of mussels, however, *Carcinus* displays a surprising ability to modify its predation technique to deal specifically with mussels and tends to choose the most profitable mussel sizes (Fig. 9.7). The dogwhelk, *Nucella lapillus*, feeds almost entirely on barnacles and small- to medium-sized mussels. Although these sedentary prey are not pursued, dogwhelks spend a very long time handling them (over 10 h to drill and over 15 h to consume a medium-sized mussel) and because of this, dogwhelks fit into the 'pursuer' category. However, like most predators, dogwhelks will feed opportunistically on any moribund prey, such as a freshly killed fish. Ambushers are often morphologically constrained to adopt the one predation method. Anemones such as *Anthopleura elegantissima* or *Actinia equina* that feed on macroscopic food are unable to

pursue prey, but their stinging nematocysts and numerous tentacles enable them to subdue large prey which slip through the wide pharynx, lubricated with mucus, into the distensible sack-like stomach. Deep-sea fish such as gulper eels (Fig. 9.6f) and angler-fish are ambushers *par excellence*. At these great depths prey are scarce indeed (see

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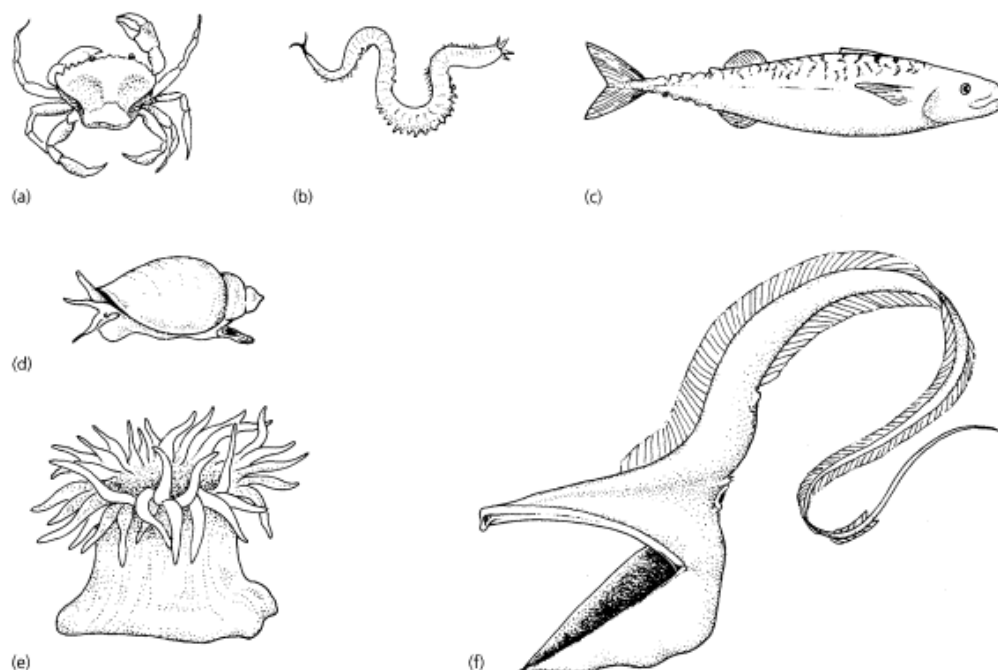


Fig. 9.6

Kinds of predators. Searchers: (a) crab, *Carcinus maenas*; (b) polychaete, *Nereis* sp. Pursuers: (c) mackerel, *Scomber scombrus*; (d) dogwhelk, *Nucella lapillus*. Ambushers: (e) anemone, *Actinia equina*; (f) deep-sea gulper, *Eupharynx pelecyanoides*. (a and c after Hughes 1980b; d and e after Hughes 1980a; f after Briggs 1974.)

Section 1.3), so that pursuit and selective feeding would be uneconomical. Gulper eels, angler-fish and others have become little more than suspended traps, most of the body muscles and skeleton having atrophied except for the jaw apparatus, so that sustained searching or pursuing would be impossible. The mouth has an enormous gape and in some cases can even be unhinged, and the stomach is hugely distensible so that prey considerably larger than the predator can be swallowed.

Copepods, which account for a large proportion of the zooplankton, are important filter feeders on phytoplankton (chapter 2) and as with all arthropods, the filter is constructed from intermeshing bristles borne on modified limbs. Size selection of algal cells occurs as a mechanical consequence of the mesh diameter of the filter, but whether mesh size can be modified according to the availability of different algal types remains in debate. Algal quality also is important in addition to size. *Acartia clausi* avoids the dinoflagellate *Ceratium tripos*, which is armoured with cellulose plates, but accepts unarmoured larger and smaller algae. Copepods are sometimes able to grasp individual items with the mandibles. *Acartia tonsa* can use the grasping mechanism to prey upon nauplii of other copepods while simultaneously filtering algal cells.

9.3.2

Reproduction and Dispersal

9.3.2.1

Asexual Vs. Sexual Reproduction

Asexual reproduction occurs among most phyla and may take place by two fundamentally different processes. First, embryos may develop parthenogenetically from unfertilized eggs and secondly, the body may divide as it grows. Parthenogenesis has evolved

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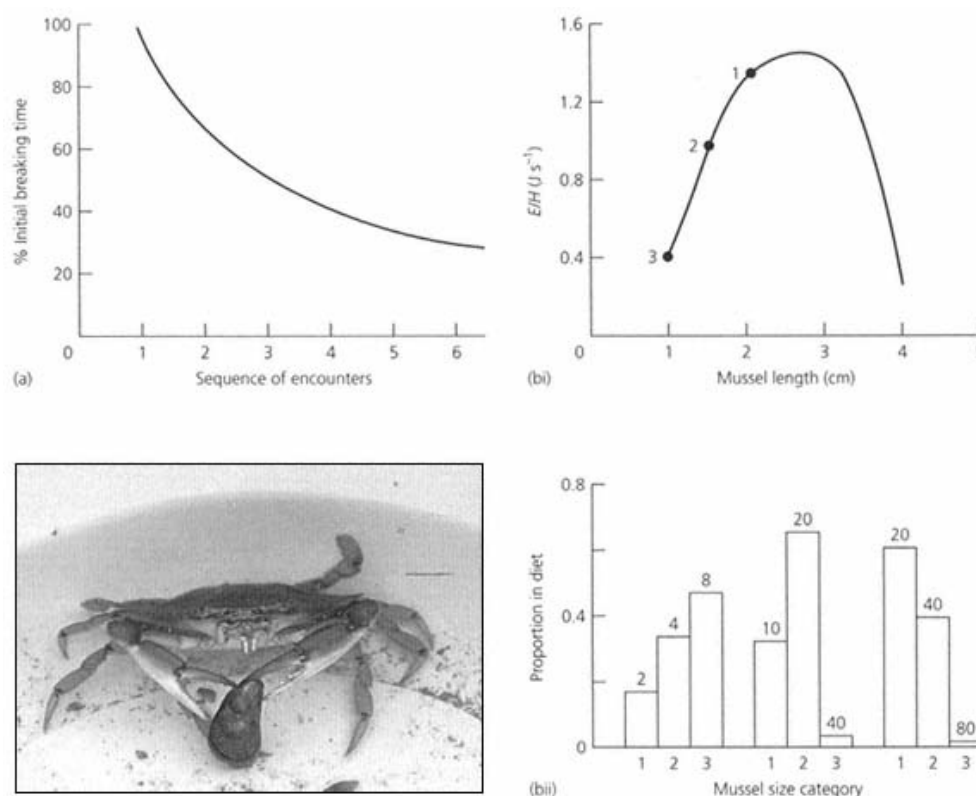


Fig. 9.7

(a) The time taken by the crab *Carcinus maenas* to open a mussel, *Mytilus edulis*, decreases as the crab becomes more experienced at handling the prey. (After Cunningham & Hughes 1984.) (bi) The profitability (energy yield per handling time) of mussels to foraging crabs peaks at intermediate mussel size; and the blue crab, *Callinectes sapidus*, opening a marsh mussel, *Geukensia demissa*. (bii) The diet of shore crabs fed on three sizes of mussels where the profitability is $1 > 2 > 3$. Numbers offered appear over the histograms. As the most profitable mussels became more abundant the crabs fed disproportionately upon them. (After Townsend & Hughes 1981.)

recurrently, and continues to do so in many independent lines, especially in those occupying terrestrial and freshwater habitats. Some parthenogenetic lines have lost the ability to reproduce sexually, and although benefiting in the short term from a higher potential rate of increase than sexual relatives (by omitting males that cannot give birth), these parthenogenetic animals lack the evolutionary potential associated with sex and so are much more prone to extinction than sexual lines. Other animals incorporate both parthenogenetic and sexual phases into their life cycles. Cyclical parthenogens usually reproduce sexually when growing conditions begin to deteriorate. The parents die and the progeny endure the ensuing harsh periods as dormant zygotes, or early embryos, protected within resistant capsules. When favourable growing conditions return, each embryo develops into a parthenogenetic female. This female reproduces parthenogenetically throughout the favourable growing period, forming a clone of genetically identical modules. Such a life cycle is similar to that of many unicellular algae (Section 9.2.2) and is associated with similar advantages, i.e. the maintenance of a favourable surface area to volume ratio by splitting the 'body' into modules, the ability to disperse modules over a wide area in search

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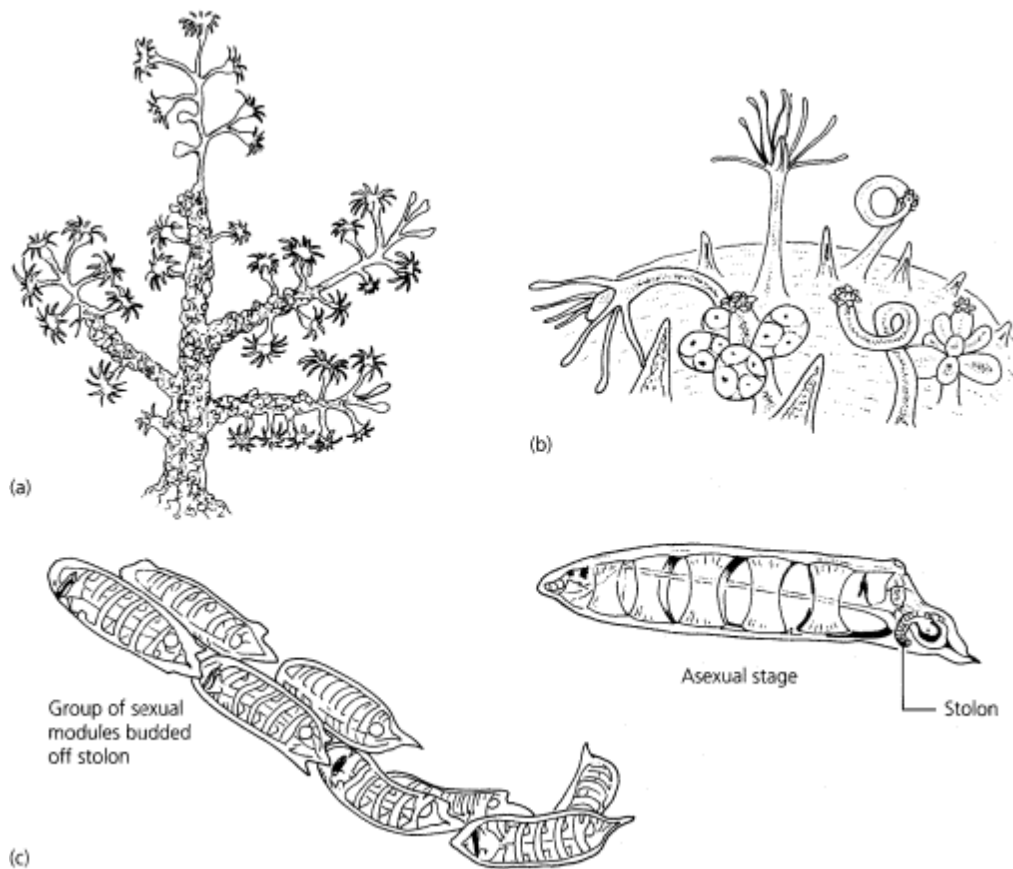


Fig. 9.8

Clonal animals. (a) When modules (zooids) of a growing clone remain united they form a colony, which is usually a benthic sedentary form as in this example of the hydroid *Bougainvillia*. (b) The clonal modules are genetically identical but may become specialized for different functions as in *Hydractinia echinata* with feeding (long tentacles), defensive (cluster of knob-like tentacles) and reproductive (large vesicles, left and right of the colony) zooids. (c) Modules of a growing clone may become detached as with most pelagic tunicates. Depicted is the salp *Iasis* (*Salpa*) *zonaria*, which alternates between an asexual, clone-forming stage and a sexual, outbreeding stage. The asexual stage buds off chains of modules from a stolon. The modules remain attached in groups for a while, during which time they are functional females. After giving birth to a single asexual young, each female module changes sex and becomes detached from the others, shedding sperm into the sea-water and perhaps fertilizing another clone. (After Hardy 1962.)

of unpredictably located patches of resource, the rapid exploitation of local patches of resource, and the lessening of the probability of extinction of the genotype by spreading the risk of mortality among many independent modules. Cyclical parthenogens include aphids, rotifers and cladocerans, but whereas rotifers and cladocerans are common in fresh water, they are relatively scarce in the sea, being overshadowed by copepods. Why neither marine nor fresh water copepods have developed any parthenogenetic lines remains a tantalizing, unanswered question.

Asexual reproduction by budding or fission of the body does not involve gametogenesis and is therefore different from parthenogenesis. Both processes, however, result in the formation of a clone of genetically identical modules. Budding or fission is common among many invertebrate phyla and the resulting clonal modules may remain attached to each other to form colonies, e.g.

colonial hydroids, zooanthids, corals, bryozoans and colonial tunicates (Fig. 9.8a), or they may become detached to form a clone of aggregated or dispersed modules, e.g.

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solitary hydroids, scyphozoans, anemones, certain polychaetes and most pelagic tunicates (Fig. 9.8c). Division of the growing body into a clone of modules has several advantages. If the modules are dispersed the clone gains similar advantages to those of parthenogenetic animals. *Thalia democratica*, for example, is a warm-water, pelagic tunicate that completes the alternation of asexual budding and sexual reproduction within 2 days. It has about the shortest generation time of any metazoan and is thus well able to exploit local phytoplankton blooms (Heron 1972). If the modules form an aggregation or an organically united colony, the dispersal ability of the clone is severely reduced, but several other advantages remain that are of great significance among sedentary animals. First, filter-feeding devices such as the tentacular crowns of coelenterates, bryozoans and polychaetes work efficiently only below a certain size. Modular iteration preserves the optimal size of the feeding apparatus while allowing a continued increase in biomass. Secondly, modules can become specialized for different functions. Such 'division of labour' is seen most often in organically united colonies, e.g. the hydroid *Hydractinia echinata*, in which different polyps are specialized for feeding, reproduction and defence (Fig. 9.8b), but may occur in modular aggregations, as with the anemone *Anthopleura elegantissima* in which peripheral polyps forgo sexual reproduction and use the energy to defend the reproductive polyps within. Division of labour and co-operation among modules of a clone are not altruistic, as only a single genotype is involved, but are analogous to the division of labour among the organs of a non-clonal animal. Thirdly, a very flexible growth form is achieved, which can be modified to suit local conditions, e.g. topography of the substratum, direction of prevailing currents (Fig. 9.4c), or presence of other organisms. Fourthly, sedentary animals are at risk of predation by carnivorous grazers. Modules escaping predation can sustain damaged clone-mates until these are regenerated or replaced. Fifthly, the ability to compete for and retain space on the substratum is increased by the collective effort of the modules. Reviews of clonal biology have been given by Jackson *et al.* (1985), Harper *et al.* (1986) and Hughes (1989).

Among the great variety of forms exhibited by sedentary modular colonies, Jackson (1979) recognized six basic shapes: runners (linear or branching encrustations), sheets (two-dimensional encrustations), mounds (massive, three-dimensional encrustations), plates (foliose projections from the substratum), vines (linear or branching, semi-erect forms with restricted zones of attachment) and trees (erect, usually branching projections) (Fig. 9.9). Runners and vines are the most opportunistic forms, advancing quickly in a linear fashion to make temporary use of unoccupied space before being outcompeted by other growth forms that show increasing commitments to survival within their own areas of settlement (sheets < mounds < plates < trees). For example, the bryozoan *Electra pilosa* adopts the runner growth form and opportunistically colonizes unoccupied patches on the surface of *Fucus spiralis*, but is eventually overgrown by *Alcyonidium hirsutum* and *Flustrellidra hispida*, which grow more slowly in any single direction but also advance two-dimensionally to form sheets over the substratum (Section 5.1.7.6). When two similar growth forms meet, the competitive outcome may depend on subtle factors such as whether two growing edges meet or whether one growing edge impinges on a non-growing edge.

Sometimes, colonies react allelochemically to competitors. When different, and therefore genetically distinct, clones of the sponge *Hymeniacidon* grow into contact, they produce a substance that interferes with cellular adhesion. By means of this chemical warfare, one colony usually dominates the other, in a fashion reminiscent of the competitive hierarchies by mesenterial digestion found among corals (Section 6.4.1). Allelochemical interactions are common among sponges, bryozoans and tunicates inhabiting crevices, caves and shaded overhangs on coral reefs. Coexistence among these animals apparently is facilitated by the presence of competitive loops rather than hierarchies. For example, species A might overgrow species B which might overgrow species C, but species C is able to suppress species A by an allelochemical interaction. The occurrence of competitive loops in a community of potential competitors forms what Buss & Jackson (1979) called a competitive network, the complexity of which increases with the frequency of loop formation. Among the inhabitants of cryptic coral reef habitats, competitive

loops are common and often permanent, whereas among the epiphytes of *Fucus serratus* they are infrequent and temporary (Section 5.1.7.6), and are probably absent among corals.

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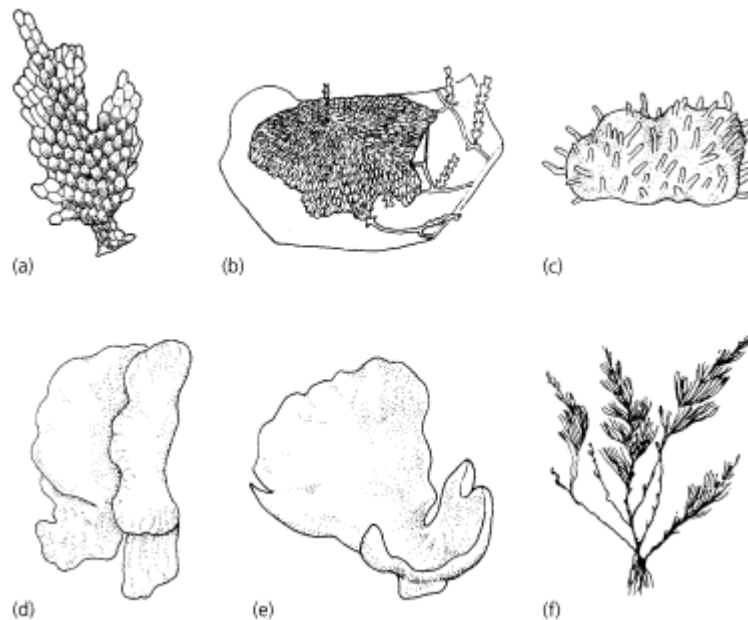


Fig. 9.9

Growth forms of sedentary modular colonies. (a) Runner: bryozoan *Electra pilosa*. (b) Sheet: bryozoan *Alcyonidium polyoum*, overgrowing vine: hydroid *Dynamena pumila* (after Stebbing 1973). (c) Mound: sponge *Polymastia* sp. (after Bowerbank 1874). (d) Vertical plate: sponge *Phakellia robusta*. (e) Horizontal plate: sponge *P. ventilabrum* (after Bowerbank 1874). (f) Tree: bryozoan *Bugula plumosa* (after Ryland 1962).

9.3.2.2

Larval Life

Sexual reproduction in most marine animals results in the formation of larvae that persist for varying lengths of time before metamorphosing into the pre-adult stage. The range of larval sizes is narrow, invertebrate larvae being about 0.51.5 mm in overall diameter and fish larvae perhaps an order of magnitude larger. Various modes of larval life are possible. Larvae may be pelagic (planktonic) or non-pelagic (benthic), feeding (planktotrophic) or non-feeding (lecithotrophic), brooded or non-brooded, and intermediate or mixed modes also occur. It is difficult to generalize about the relative advantages of the different modes of larval life because many interacting selective forces may be involved, and because the experimental testing of ideas is hindered by the difficulty of measuring larval survivorship and dispersal in the field. At present it is possible only to list plausible hypotheses. Before doing so, it will be helpful to consider some general biological relationships.

1 The larger the egg the longer is the embryonic development time from fertilization to hatching (Fig. 9.10). There may be two contributing factors to this correlation. First, larger eggs contain more yolk, which retards cleavage; some animals reduce this effect by providing extra-embryonic yolk supplies to the embryos, e.g. the non-developing 'nurse eggs' contained within the egg capsules of dogwhelks (*Nucella lapillus*). Secondly, the longer the prehatching development time, the more advanced is the developmental stage at hatching. Animals requiring developmentally more advanced hatchlings must therefore provide the eggs with more yolk, thereby making them

larger. The largest eggs have sufficient yolk to nourish the embryo through to metamorphosis before hatching (direct development), whereas the smallest eggs contain yolk sufficient only for limited embryonic development, so that the hatching larvae must spend some time feeding in the plankton (planktotrophic) to complete their development. Eggs of intermediate size hatch into 'lecithotrophic' larvae, endowed with sufficient yolk to sustain them during their brief motile existence and to enable them to complete metamorphosis. Postlarval juveniles hatching from larger eggs with direct development are slightly more advanced or larger than newly metamorphosed postlarvae from smaller eggs with lecithotrophic development. Among direct developing eggs, larger eggs produce larger hatchlings.

2 Because the energy available to a parent for egg production is limited, the larger the egg the smaller is the clutch size (Fig. 9.11a).

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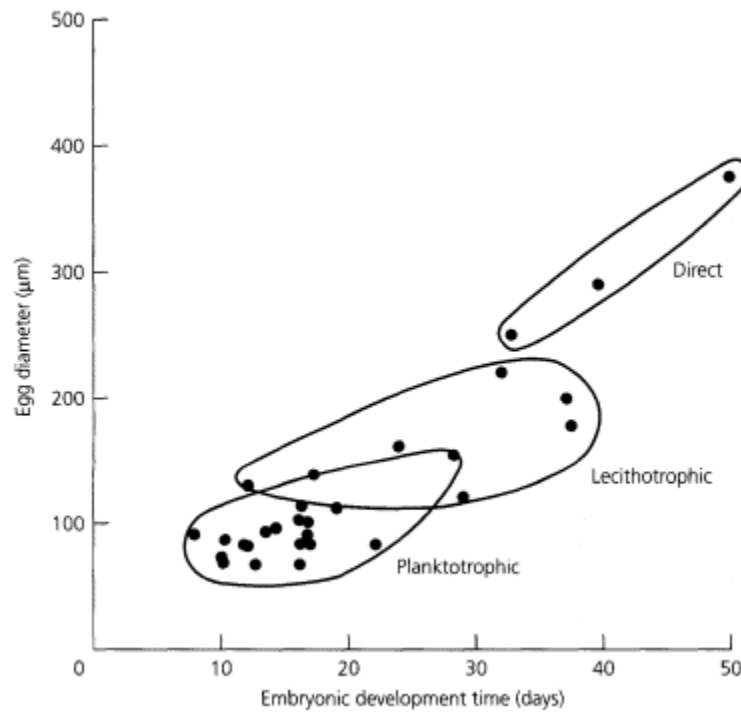


Fig. 9.10

The time taken by nudibranch eggs to develop and hatch as veligers from the egg capsules increases in larger eggs. (After Todd & Doyle 1981.)

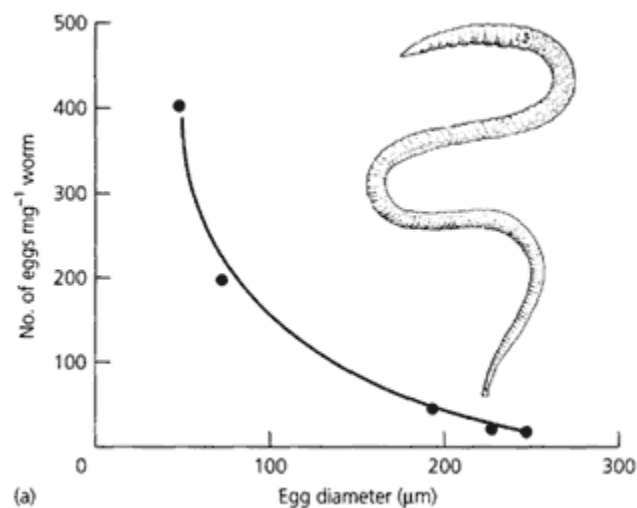


Fig. 9.11

(a) The fecundity of polychaetes within the *Capitella capitata* species-complex decreases as larger eggs are produced.

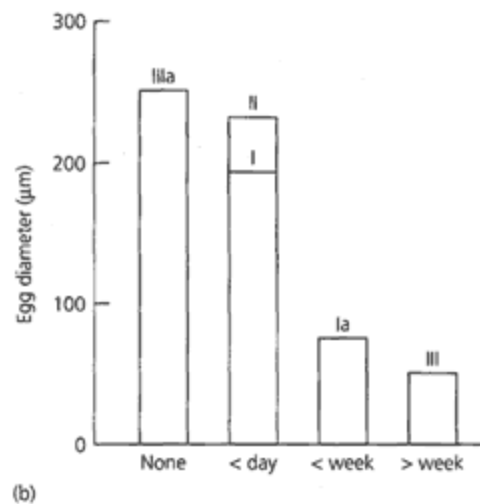


Fig. 9.11

(b) Egg size, and hence the amount of yolk reserve, is negatively correlated with the time that larvae spend in the plankton. *Capitella* species IIIa has direct development without a pelagic phase; species I, Ia and II have lecithotrophic larvae with short pelagic phases; and species III has planktotrophic larvae with a longer pelagic phase. (After Grassle & Grassle 1977.)

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Table 9.4a Maximum time of survival in days at an assumed oxygen consumption of 5 ml g⁻¹ (dry wt) h⁻¹. (After Crisp 1976.)

Source of energy	Percentage of tissue weight devoted to energy store				
	5	10	25	50	75
Lipid	0.8	1.7	4.2	8.3	12.5
Protein	0.5	1.0	2.5	5.0	7.5
Carbohydrate	0.3	0.7	1.7	3.3	5.0
Metabolic rate of non-storage tissue ml O ₂ g ⁻¹ h ⁻¹	5.3	5.6	6.7	10.0	15.0

Table based on $t + \frac{q \times x}{24 \times r}$ days

where q is oxygen requirement in ml g⁻¹ of metabolite, x is fraction of body tissue devoted to reserves and r is respiration rate in ml g⁻¹ h⁻¹.

Table 9.4b Oceanic diffusion. (After Crisp 1978.)

Pelagic life	Log ₁₀ (probable distance transported in cm)	Order of magnitude	Whether likely to be exceeded by tidal currents
36 h	4	100 m	Yes
12 days	5	1 km	Yes
714 days	6	10 km	?
14 days ³	7	100 km	No
months			
1 year	8	1000 km	No

It follows from 1 and 2 that planktotrophic larvae are produced in greater quantities per brood than lecithotrophic larvae which are, in turn, produced in greater quantities than direct developing larvae.

3 Released larvae are at constant risk to predation, and if pelagic, also to transportation by currents into unfavourable areas. The cumulative risk of mortality therefore increases exponentially with increased duration of the mobile phase.

4 Dispersal ability increases with increased duration of the mobile phase. This relationship is not simple, however, because in nearshore waters tidal currents are usually stronger than residual currents, with the result that the average distance transported would increase to a first maximum after 6 h in the plankton, beyond which it would increase only very slowly. Hence a pelagic phase exceeding 6 h duration would achieve little additional dispersal while greatly increasing the cumulative risk of mortality. Significantly increased dispersal would only be achieved by greatly prolonging the pelagic phase so that larvae could be transported long distances by non-tidal currents (see Crisp 1976).

With these generalizations in mind, some guesses can be made about the ecological significance of various modes of larval development.

Dispersal Hypothesis

Animals with limited powers of postlarval dispersal, e.g. most benthic invertebrates, must rely on pelagic eggs and/or mobile larvae for dispersal. As with seeds transported by the wind, the small size of larvae enables them to use passive transportation (by water currents) as an energetically

cheap means of dispersal. Also like seeds, larvae have some capacity to delay metamorphosis until a suitable settlement site is encountered. Among non-feeding larvae, energy reserves dictate that metamorphosis can be delayed only for a short while (Table 9.4) (this restriction is much less severe in cold, polar regions where metabolic rate is reduced; see Environmental constraints), after which settlement becomes more indiscriminate and usually proves fatal. Feeding larvae can delay settlement

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for longer, but never as long as many seeds, which can remain dormant and viable for several years. Larvae on the other hand have the additional feature of small-scale locomotive powers, so that the encountering of suitable places for settlement and metamorphosis is less haphazard than with seeds.

Increased dispersal ability is achieved at the cost of increased larval mortality (see 3 above). Longdistance dispersal therefore has a reasonable chance of success only if very large numbers of larvae are released, and because of energetic constraints (see 2 above), these must be planktotrophic. As long as food is available to them, planktotrophic larvae theoretically could spend any amount of time drifting and, indeed, some Pacific echinoderm larvae spend as much as 36 weeks in the plankton, giving them sufficient time to traverse the ocean in favourable currents. If long-distance dispersal is unnecessary, an animal could gain by producing fewer larger eggs, each of which has a greater chance of surviving to metamorphosis, a trend which reaches its peak with direct development and elimination of the mobile larval stage. The optimal dispersal ability will depend on the spatial distribution and degree of permanence of suitable sites for colonization. If these are unpredictably located, then long-distance dispersal may be advantageous, whereas if they are predictably located nearby, then more limited dispersal will suffice and greater larval survivorship will be more advantageous. Also, predictably located settlement sites are more likely to be encountered by larvae than unpredictably located sites, so that competition among larvae and postlarvae may be more severe in the former than in the latter. Competitive ability will increase with advanced embryonic development or with larger size, so that increased egg size and associated reduced clutch size may be expected among animals successfully exploiting predictably located settlement sites. It is becoming increasingly apparent that larval recruitment tends to be local, often close to the parent, and that many benthic colonial species release larvae when tidal currents are minimal, or have larval behaviour which favours local settlement.

Some support for the dispersal hypothesis is to be found in the reproductive modes of sibling species of polychaete comprising the *Capitella capitata* species-complex. These sibling species are morphologically so similar that their identities were only ascertained when their isozymes were examined electrophoretically by Grassle & Grassle (1977). Their morphological similarity and recent common ancestry makes these polychaetes ideal subjects for comparing variations in reproductive mode, because the influences of morphological and phylogenetic constraints can be discounted. Among the sibling species of *Capitella*, decreasing egg size is correlated with increasing clutch size, with increasing duration of the pelagic phase and hence with increasing powers of dispersal (Fig. 9.11b). Species IIIa has non-pelagic (benthic) larvae with very limited dispersal potential, species I and II have non-feeding (lecithotrophic), pelagic larvae, and the remainder have feeding (planktotrophic) larvae that remain in the plankton for several days (species Ia) to 2 weeks (species III) and are capable of long-distance dispersal. All the *Capitella* species can be regarded as opportunistic (Section 9.1), typically colonizing fine sediments that have been denuded of competitively superior species by environmental disturbance such as pollution. Some of the *Capitella* species, however, behave more opportunistically than others. Species I, II and IIIa are the most opportunistic, settling soon after hatching as relatively advanced larvae. Larval survivorship is high and these species can rapidly colonize local areas after disturbance has eliminated competitors. The continued existence of species I, II and IIIa depends on the frequent occurrence of disturbed patches of habitat, which they are ready to exploit at any time by virtue of their continued reproduction throughout the year. Species Ia and III occur in less variable subtidal habitats and because of the longer pelagic phase, they are slower to colonize new habitats than the more opportunistic species. The relatively wide larval dispersal of species Ia and III, however, enables them to select potentially more favourable habitats, which will be rarer and less predictably located than the frequent local disturbances exploited by species I, II and IIIa. The persistence, however, of invertebrate species with direct development along with others possessing a pelagic larval phase in the Antarctic, where ice scour repeatedly decimates shallow

benthic populations, shows that larval dispersal is not a prerequisite for coping with disturbed habitats.

A serious problem with the dispersal hypothesis is that the successful establishment of an individual

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following dispersal depends to a great extent on colonizing ability and this may be uncorrelated, or even negatively correlated with dispersability. The production of planktotrophic or lecithotrophic larvae, or the brooding of young may represent the action of various selection pressures, some of which are discussed below, or may simply be inherited from distantly ancestral lineages without any relation to present conditions. If so, dispersability is merely a secondary consequence of developmental mode.

Moreover, the highest levels of dispersability, conferred by planktotrophic development, may hinder colonization of isolated habitats that do not lie in major pathways of larval transportation. This is because planktotrophic larvae of a new colonist are likely to be carried away by currents, leaving the parent in reproductive isolation. On the other hand, brooded young, or even lecithotrophic larvae, will tend to remain in the parental habitat, potentially establishing a reproductive population. This principle may explain the absence of the planktotrophic *Littorina littorea* from Rockall and the successful colonization of this small, offshore island by the ovoviviparous *Littorina saxatilis* (Johannesson 1988). The relationship between developmental mode and geographical distribution is discussed further in Section 10.3.1.

Size-Threshold Hypothesis.

Some researchers have postulated that to produce sufficient numbers of lecithotrophic or direct developing larvae, an animal must attain a threshold size, at which the body will contain sufficient energy reserves to manufacture the large eggs. Below the threshold, the body contains insufficient stored energy to make lecithotrophy or direct development worth while, because the resulting clutch sizes would be too small. Todd and Doyle used this hypothesis to explain lecithotrophy in the larger nudibranch *Adalaria proxima* and planktotrophy in the smaller nudibranch *Onchidoris muricata*.

Conversely, others have postulated that planktotrophy will not be feasible below a threshold body size because, even though the eggs are small, restricted bodily energy reserves could not produce enough of them to compensate for the larval mortality incurred by a long pelagic phase. Tiny bivalves belonging to such genera as *Gemma* and *Mysella*, which live in shallow-water sediments, or *Lasaea* and *Turtonia*, which inhabit small intertidal crevices, all brood their embryos and release them at the post-larval stage. *Lasaea rubra*, for example, incubates 1222 embryos in its suprabranchial chambers and releases them as 0.50.6 mm juveniles, even though the parent is itself only 23 mm in length. Perhaps, with such small energy reserves, the potential clutch size of these tiny animals is so restricted that larval mortality must be avoided altogether. This also may be the case among meiofaunal animals, ranging from 50 μ m to 3 mm in length and adapted to life in the interstices of sedimentary particles. Ninety-eight per cent of interstitial species lack pelagic larvae and many brood their young to an advanced developmental stage, whereas others protect their eggs in sticky cocoons that readily adhere to sand grains. Clutch sizes are correspondingly small, two to three eggs being normal and seldom exceeding 10. An exception 'proving the rule' is to be found among tubicolous polychaetes in the genus *Dodecaceria*. Most species form clones by fission and although each worm is diminutive, producing only a few small eggs, its larvae are planktotrophic. But as all clonemates share the same genome, they are collectively equivalent to one individual of an aclonal species, and together they produce multitudes of larvae.

Energy-Subsidy Hypothesis

The plankton is a food resource used by animals ranging from small invertebrates to the largest vertebrate (Chapter 2). During phytoplankton blooms this food resource is particularly rich and it is conceivable that it may pay some species to exploit the plankton not only as food for themselves but also as food for their progeny, thereby subsidizing the energetic cost of reproduction. Fecundity would be increased because the parent need make only a small energetic

investment per larva (Fig. 9.11b). Larval growth, and hence chance of successful recruitment, would be enhanced when planktonic food is particularly abundant, allowing the parent to increase its reproductive value in years with a good bloom. The converse, however, would be true in years with a poor bloom, and it has not yet been demonstrated that there is a net gain in energy as a result of feeding in the plankton. It is certain that the spawning of some animals is timed so that their larvae can exploit the phytoplankton bloom. For example, increased

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phytoplankton concentration in the spring triggers spawning in the chiton *Tonicella lineata* on western North American shores.

Food-Niche Hypothesis

It has been suggested that by exploiting a different food resource, planktotrophic larvae avoid competition with the parental generation or with meiofaunal species similar in size to the macrofaunal larvae (Warwick 1989), but such competition could equally be avoided by the production of non-feeding larvae. Feeding larvae may need to forage in the plankton to encounter suitably small food organisms, but again this constraint could be avoided by provisioning the young with yolk. The food-niche hypothesis therefore cannot explain the relative selective advantages of feeding and non-feeding larvae among different animals.

Although larvae are chiefly pelagic in low latitudes, where planktonic productivity is less seasonal, direct development is prevalent in polar regions, where planktonic production is highly seasonal and irregular, making planktotrophy too risky (see Section 3.2.4).

Environmental Constraints

In his classic work on the latitudinal distribution of larval forms, Thorson (1946) concluded that pelagic larvae rarely occur in polar regions because the seasonal pulse of primary production is too short to sustain planktotrophy. Thorson's observation was based mainly on tropicalArctic comparisons for prosobranch gastropods, and later was corroborated for Antarctic prosobranchs. In general, prosobranch species follow a cline from the almost complete absence of pelagic forms in polar seas to some 95% with pelagic larvae in the tropics. Other taxa, however, do not necessarily show this trend. Echinoderms, for example, are represented predominantly by species with pelagic larvae at all latitudes. In this case a different cline exists, with planktotrophic species predominating at lower latitudes and lecithotrophic species in polar regions (Pearse 1994). Recent year-round surveys have revealed an unexpectedly high diversity of pelagic larvae in Antarctic waters, comparable with values for temperate latitudes (Stanwell-Smith *et al.* 1997). Some taxa showed seasonal peaks in summer (molluscs and annelids presumably exploiting the microphytoplankton bloom) or winter (echinoderms and nemerteans), whereas others were present throughout the year. We must conclude, therefore, that although environmental constraints may significantly influence latitudinal variation in the relative abundance of larval types, observed trends are not entirely explicable in these terms. The lower diversity of pelagic larvae in the Arctic Ocean probably originates from the geological youth of this region rather than from environmental constraints operating on an ecological time scale.

9.3.2.3

Parental Investment

Planktotrophic, lecithotrophic and direct developing larvae represent increasing levels of energetic investment per offspring by the parent. Some of the possible selective advantages of these different levels of parental investment are discussed in the previous section, but the picture is left far from complete. Among species with direct development, parental investment varies considerably according to the amount of yolk provided per egg, the amount of encapsulating material per egg and the amount of parental care in the form of brooding or guarding the eggs and young (Fig. 9.12). Parental investment beyond the minimum required to produce a viable egg is worth while only if juvenile survivorship is significantly increased and outweighs the concomitant losses in potential fecundity or dispersal potential. For example, the winkle *Littorina saxatilis* retains its young within a brood chamber, which is a modified jelly gland, until the shell is well developed and the young are able to lead an independent existence on the shore. *Littorina compressa* has a functional jelly gland, which it uses to provide a gelatinous protective capsule round the egg mass placed beneath stones or within crevices on the midshore. Because *L.*

compressa does not brood its eggs, these can be produced more quickly, so that the fecundity of *L. compressa* is about three times that of *L. saxatilis* on the same shore. *L. compressa* therefore thrives well at midshore levels where the survivorship of egg masses is high, but at higher shore levels egg masses would become desiccated and it is here that the brooding behaviour of *L. saxatilis* places the latter species at an advantage. Greater parental investment therefore enables *L. saxatilis* to reproduce in harsher environments (high shore levels, salt-marshes) than related species which do not brood their young.

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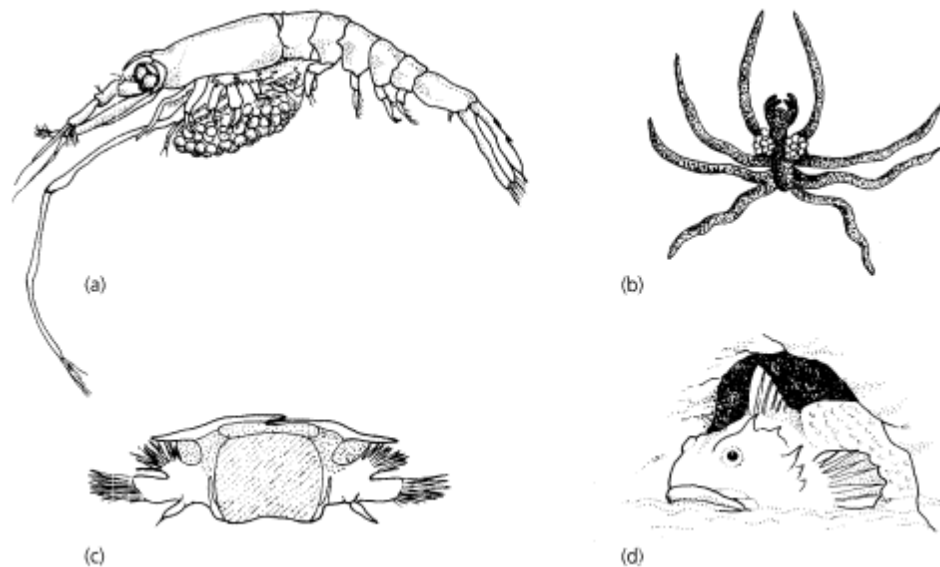


Fig. 9.12

Parental care. (a) As is typical among decapods, the euphausiid, *Nematoscelis difficilis*, carries its eggs on modified thoracic limbs. (After Briggs 1974.) (b) In pycnogonids (Arachnida), females transfer their eggs to males, which carry the eggs on modified limbs. (After Nakamura & Sekiguchi 1980.) (c) The scale worm, *Harmothoe imbricata*, broods its eggs on its back, where they are covered by plate-like processes from the parapodia (After Daly 1972.) (d) The sea scorpion (scuplin), *Cottus bubalis*, guards its egg mass. (After Hughes 1980b.)

9.3.2.4

Semelparity and Iteroparity

Organisms may reproduce sexually once and then die (semelparity) or reproduce more than once, or continually, over a protracted period (iteroparity). Care should be taken not to confuse semelparity and iteroparity, which are defined relative to the lifetime of the organism, with the terms ephemeral, annual and perennial, which are defined relative to the year. Nudibranchs, such as *Onchidoris* spp. are annuals that die after spawning and are therefore semelparous. Eels are perennials that also die after spawning and are semelparous. Winkles, *Littorina* spp. (Section 9.3.2.3), are perennials that are iteroparous, whereas some bryozoans, such as *Celleporella hyalina*, can be ephemeral and iteroparous.

Whether semelparity or iteroparity is the more advantageous depends very much on the ratio of juvenile to adult survivorship, as determined by the morphologies and habitats of the two stages. Semelparity relies on the survival of the young to maturity whereas iteroparity relies more on survival of the adult. The benthic adults of marine, sedentary invertebrates are less at risk to mortality than the dispersing larvae, and iteroparity predominates among these organisms. Apart from some very small species, most prosobranch gastropods are well protected by their shells and have a much higher life expectancy as adults than as juveniles, and are correspondingly iteroparous. Nudibranchs lack a shell and even though they use other protective devices such as acidic secretions, nematocyst-bearing dorsal cerata or crypsis, they are likely to have lower life expectancies during the benthic stages than have the armour-plated prosobranchs. All nudibranchs are semelparous. These rationalizations should be regarded with caution, however, because natural magnitudes of juvenile or adult survivorship necessary for a sound comparison have not been measured.

Semelparity in migratory fish such as salmon, eels and lampreys probably has a different evolutionary history. The life history of salmon and lampreys is partitioned between marine habitats that are highly productive, promoting growth and hence fecundity of the adults, and freshwater habitats that are

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much less productive, but safer nursery grounds for the young. The migration from feeding to nursery grounds, however, demands so much energy and entails such high risks that it pays only to do it once, committing all the remaining energy into a suicidal bout of reproduction. The reverse migration of eels, from freshwater feeding grounds to marine spawning grounds, is more difficult to understand. Eels often exploit productive, relatively safe habitats such as eutrophic muddy ponds, but the conditions on the nursery grounds in the Sargasso Sea remain unknown. Perhaps it is significant that eels have a recent marine ancestry and salmon a freshwater one.

9.3.2.5

Hermaphroditism; Why Combine Sexes?

In most actively mobile animals male and female functions are performed by separate individuals, termed gonochorists (equivalent to dioecious plants), and in a minority by single individuals, termed hermaphrodites (equivalent to monoecious plants). In simultaneous hermaphrodites male and female functions are performed together, whereas in sequential hermaphrodites the male function may precede the female function (protandry) or vice versa (protogyny). How can these sexual permutations and combinations be accounted for in terms of natural selection?

Gonochorism owes its origins to the evolution of anisogamy. Primitive sexual organisms probably had one type of gamete (isogamy) as does the unicellular alga *Chlamydomonas*. Fertilization and zygotic development require mobility, whereby unrelated gametes can encounter one another, but also energy reserves to fuel subsequent development. Mobility is facilitated by small size but hindered by bulky yolk, hence the evolutionary division of labour (anisogamy) into smaller motile sperm whose function is to seek, and larger non-motile eggs whose function is to nourish. It will often be advantageous for division of labour to be carried through to the parents, males being specialized for seeking females and perhaps defending them from other males (ensuring paternity), females being specialized for nurture of the young. Different adult morphological features are often involved, especially with regard to the reproductive organs. The combination of sexual roles within a single individual could therefore be disadvantageous because of incompatible morphology and because of the extra energetic investment in two sets of reproductive apparatus. Hermaphrodites are, however, widespread in nature, so that in certain circumstances the advantages of gonochorism must be outweighed by other factors.

A clue to one selective advantage of hermaphroditism is given by the greater preponderance of sedentary than of mobile hermaphrodites. Among gonochoristic, sedentary animals, there is a risk that neighbours may be of similar sex and unable to fertilize each other, a risk that is avoided by hermaphroditism. Similarly, mobile animals that normally occur at low densities are sometimes hermaphroditic, e.g. nudibranchs, thereby ensuring that when two mature individuals meet, they are capable of crossfertilization. An interesting alternative solution to this problem is found among several gonochoristic, oceanic angler-fish, e.g. *Ceratias holbolli*, which live at exceedingly low population densities: the dwarf male becomes organically attached to the female, deriving nourishment from her and remaining with her throughout reproductive life. The rate of encounter between sexes is so low that once contact has been made, it is advantageous to maintain it. Once having evolved in copulating animals, simultaneous hermaphroditism may be unlikely to revert to the ancestral state of separate sexes because of the stabilizing influence of gamete trading. Life-history traits usually make one or other sexual mode more advantageous in terms of potential genetic contribution to future generations. During mating, therefore, individuals should try to 'cheat', by performing only the preferred sexual role. Gamete trading probably has evolved to prevent such cheating. It involves bouts of limited performance by each individual in the non-preferred sexual role, so forcing the partner to reciprocate. Egg trading occurs, for example, in the hamlet fish, *Hypoplectrus nigricans*, and sperm trading in the sea slug, *Navanax inermis* (Leonard & Lukowiak 1991).

Whereas hermaphroditic animals that copulate, such as barnacles and nudibranchs, function simultaneously as males and females (Fig. 9.13e), sedentary animals that liberate sperm into the sea-water are usually sequential hermaphrodites, e.g. the protogynous tunicate *Botryllus schlosseri* (Fig. 9.13a), thus preventing self-fertilization and loss of fitness

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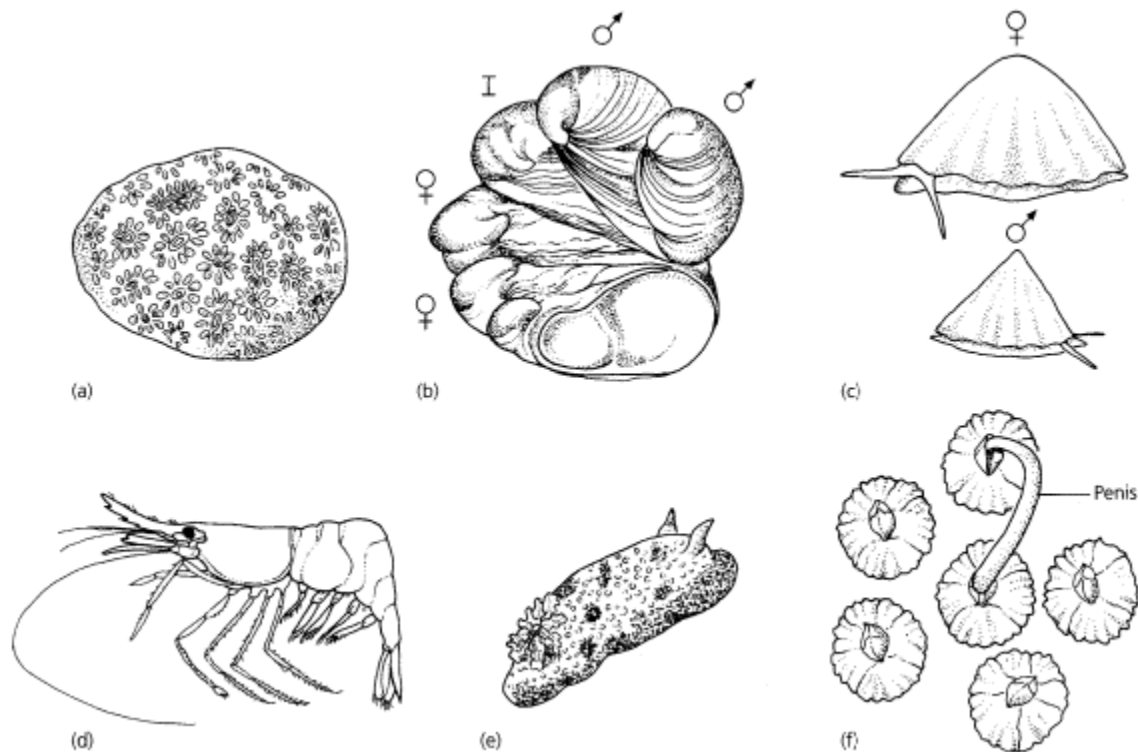


Fig. 9.13

Hermaphrodites. (a) A protogynous sequential hermaphrodite, the colonial tunicate, *Botryllus schlosseri*. (After Millar 1970.) (b) A protandrous sequential hermaphrodite, the slipper limpet, *Crepidula*. (c) A protandrous sequential hermaphrodite, the limpet, *Patella vulgata*. (d) A protandrous sequential hermaphrodite, the shrimp, *Pandalus montagui*. (After Smaldon 1979.) (e) A simultaneous hermaphrodite, the nudibranch, *Archidoris pseudoargus*. (f) A simultaneous hermaphrodite, the barnacle, *Semibalanus balanoides* (showing copulation).

cause by excessive homozygosity. The cyclical, sequential hermaphroditism of sedentary animals, however, is rather different from the permanent, sequential hermaphroditism of certain mobile animals. In populations of the limpet *Patella vulgata* most individuals become male at a relatively small size and switch to being female as they grow larger (Fig. 9.13c). A size threshold has been postulated, rather like that for planktotrophy (see Size-threshold hypothesis, Section 9.3.2.2.), below which energy reserves are inadequate to produce a sufficient number of eggs (that hatch into planktotrophic larvae). Sperm, however, are energetically cheap to produce, so that small individuals can function adequately as males. Difficulties arise with this interpretation because of intermale competition. Bigger males would be more fecund than smaller males, and as limpets are external fertilizers, the larger males should outcompete smaller ones to fertilize eggs. Indeed, a small proportion of *P. vulgata* do remain male throughout life.

Protogyny is common among coral-reef fish. In some wrasses and parrot-fish, only territory-holding males are accepted as mates by the females. Male reproductive success therefore depends on being able to defend a territory from competing males and this can only be achieved by large, strong fish. Young, small fish could not compete for territories, so they function as females until the critical size is reached.

Sometimes, sex is determined environmentally. The coral-reef fish *Anthias squammipinnis* lives in schools within territories on the reef. Each school is composed of females attended by a male. If

the male is removed, one of the females changes sex, evidently in response to visual behavioural stimuli.

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The value of this particular sex ratio, however, remains to be elucidated. Some species of shrimp, belonging to the genus *Pandalus*, are protandrous (Fig. 9.13d), but can adjust the age of sex change according to the age composition of the population, which fluctuates from year to year because of irregularities in recruitment. This flexibility is selectively advantageous because the value to an individual of being male rather than female increases when males are rarer. As first pointed out by Fisher (1930), on average the rarer sex contributes genetically to more zygotes than the commoner sex.

9.3.2.6

Reproductive Effort

Different modes of larval development and parental care represent various ways in which an animal can spend the resources (energy, nutrients, time) allotted to sexual reproduction, but what factors determine the total amount of reproductive expenditure? For simplicity and comparability energy can be regarded as the resource of overriding importance. Energy assimilated from the food is accumulated as body tissues and gametes, dissipated as heat resulting from metabolism, or lost in nitrogenous excretions, leakage of dissolved organic matter, or in the production of mucus. Usually over 50% of assimilated energy is lost as heat, but the amount varies according to the level of metabolic activity, and may exceed 80%. Muscular activity and physiological homeostatic mechanisms such as osmoregulation are metabolically costly. Because, in the long term, an animal assimilates energy at a fixed rate, increased metabolic costs must reduce somatic growth or gametogenesis, and vice versa. The proportion of assimilated energy devoted to reproduction is termed reproductive effort, and this may be expected to vary according to the life history and the degree of environmental stress. In the strict sense, reproductive effort includes not only the energy accumulated in gametes and associated structures such as egg capsules, but also the metabolic energy spent on all reproductive activities such as searching for mates, copulation, defence of young and other kinds of parental care. In practice, reproductive metabolic costs are extremely difficult to measure, so that estimates of reproductive effort are usually approximations in the form of the proportion of assimilated energy channelled into eggs or even just the ratio of egg production to somatic biomass. The pattern emerging from such measurements is complex, but there is a marked tendency for total lifetime reproductive effort to be greater in semelparous than in iteroparous animals, and for 'instantaneous' reproductive effort to increase with increased age and decreased life expectancy in iteroparous species (Fig. 9.14). Explanations for these trends are similar to those for semelparity and iteroparity (Section 9.3.2.4). If the body is unlikely to survive beyond a single reproductive season, then once sexual maturity is reached, all available energy should be committed to reproduction, depleting the body reserves to a lethal level. If the body is likely to survive beyond a single reproductive season, it becomes worth investing a greater proportion of assimilated energy in bodily maintenance. This investment provides the chance to reproduce more than once, a valuable strategy if reproductive seasons vary greatly in quality. It also takes advantage of the general tendency for fecundity to increase as the body gets bigger (Fig. 9.15). The likelihood of investment in the body paying off, however, declines as life expectancy decreases, so that less energy should be gambled on the body and more should be firmly committed to reproduction as the animal ages. More opportunistic (*r*-selected) species may be expected to have higher reproductive efforts than more stable-habitat (*K*-selected) species (see Section 9.1 and Pianka (1974)).

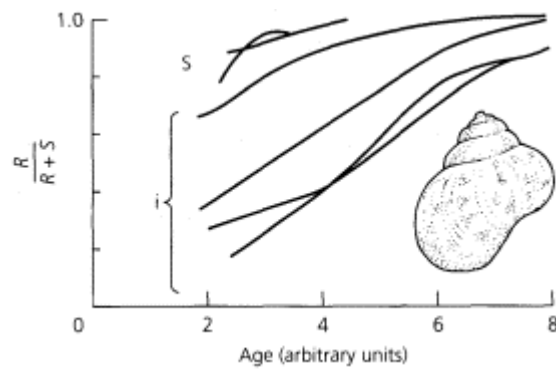


Fig. 9.14
Reproductive effort (the production of assimilated energy used in spawn production) is greater in semelparous (S) than in iteroparous (i) marine snails. (From Hughes & Roberts 1980.)

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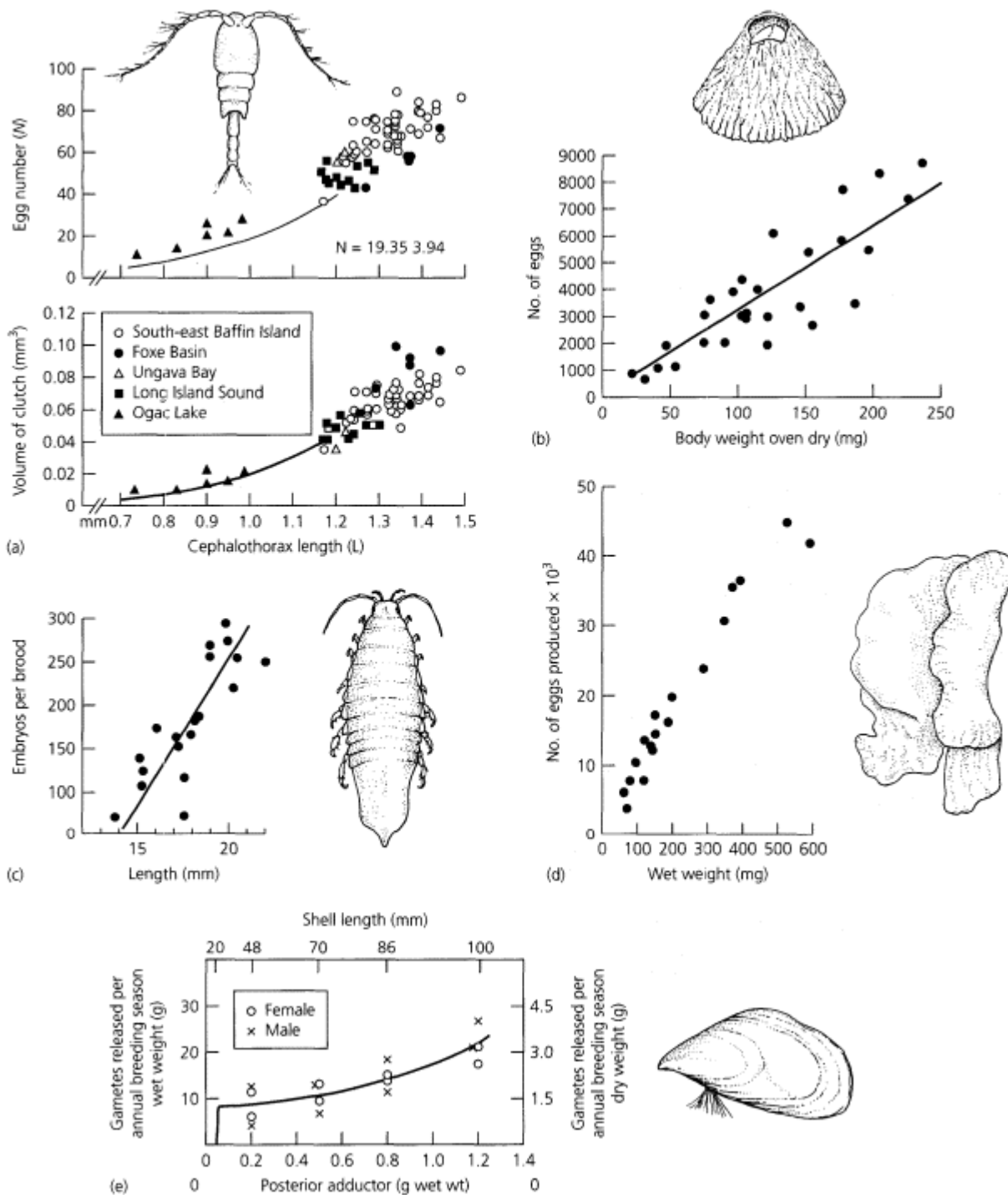


Fig. 9.15

Fecundity increases with increased body size. (a) The copepod *Pseudocalanus*. (After McLaren 1965.) (b) The barnacle *Tetraclita rufotincta*. (After Achituv & Barnes 1978.) (c) The isopod *Idotea baltica*. (After Strong & Daborn 1979.) (d) The polychaete *Harmothoe imbricata*. (After Daly 1972.) (e) The mussel *Choromytilus meridionalis*. (After Griffiths 1977.)

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9.3.2.7

History and Phylogeny

Because nature is so complex and dependent on contingency, most ecological theories will have only limited applicability. For example, the diversity of life histories shown by rough periwinkles in the North Atlantic probably can be understood more through history and phylogeny than in terms of r - and K -selection. Rough periwinkles form a group of closely related species and ecotypes derived from an oviparous ancestral form that invaded the North Atlantic from the Bering Strait some 30 million years ago (Section 10.2.1). Two species, *Littorina arcana* and *L. compressa*, retain the ancestral trait of oviparity, laying jelly-coated egg masses beneath stones and within crevices. The jelly gland of a third species, *L. saxatilis*, is modified into a series of brood chambers, where the eggs develop until hatched. This difference in reproductive mode is uncorrelated with any aspect of demography that has been studied and so is uninterpretable in terms of life-history theory. The relatively recent (within 34 million years) evolutionary transformation of the jelly gland into a brood chamber, however, has enabled *L. saxatilis* to colonize habitats such as salt-marshes, estuaries, mobile pebble beaches and silty shores that would be lethal to egg masses. The presence of oviparous and ovoviviparous forms on European shores therefore represents a phase in adaptive radiation, probably having little, if anything, to do with demographical regimes envisioned by life-history theory.

Rough periwinkles also differ in size at birth and at sexual maturation. Despite the claims of certain researchers, there is no conclusive evidence linking any such differences with factors that could be interpreted in terms of r - and K -selection. The sizes of hatchlings and adults are more likely to reflect the diverse nature of mortality factors, such as desiccation, dislodgement, mechanical impact and predation operating in different microhabitats and on different shores (Hughes 1995).

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10

Speciation and Biogeography

10.1

Introduction

Within an ecosystem, such as a coral reef, rocky shore, or tract of sediment, the numbers and kinds of organisms present are determined by the availability of resources, competition, predation, environmental disturbances, local colonizations and extinctions, all acting on an ecological time scale and therefore having an immediate influence on the biota (Chapters 1, 3 and 57). The possible combinations of species present, however, will depend on the pool of potentially available species in the geographical area. Guilds of herbivorous grazers on rocky shores are dominated by periwinkles, top shells and limpets in temperate regions, but by a wider range of gastropods together with grapsid crabs on tropical shores (Section 5.1.2.2). Shallow, sublittoral, rocky substrata are colonized by kelps in temperate latitudes and by corals in the tropics (Figs 5.14 and 6.3). Geographical faunistic and floristic variations are determined not only by immediate ecological and environmental factors, but also by processes of speciation, colonization and extinction acting on an evolutionary time scale. Of course, ecological and evolutionary time scales merge, and at a detailed level are meaningful only with reference to the generation times of particular organisms. Fruitful generalizations can be made, however, and the following examination of speciation and biogeographical patterns forms a natural extension of the ecological discussions in previous chapters.

10.2

Speciation

10.2.1

Allopatric Speciation

The number of species living on Earth represents a balance between rates of speciation and extinction. Causes of extinction are little understood, but somehow must be related to changes in the physical environment, to changes in the biological environment as competitors, predators and pathogens evolve, or, in small isolated populations, to accidents of chance. From the fossil record, it appears that major episodes of extinction tend to occur in waves rather than gradually, suggesting the influence of climatic changes.

The influence of ecological factors is illustrated by the recent extinction of the limpet, *Lottia alveus*. This limpet lived and grazed entirely upon the blades of sea-grass, *Zostera marina*, in the western North Atlantic. When populations of the host plant were eradicated by a pathogen in the 1930s, the limpet became extinct.

The influence of climatic factors is illustrated by increasing rates of extinction and speciation accompanying the acceleration of glacial cycles in late Pliocene and Pleistocene time. Beginning some 2.7 million years ago, these cycles brought about changes in sea-level of up to 100 m, changes of up to 26°C in sea surface temperature, together with fluctuations in upwelling, current strength and wind patterns. In the Caribbean, there was a wave of extinction of planktonic foraminiferans, molluscs and corals, and this was followed by rapid speciation, producing the present fauna of very young species (Jackson 1994).

Speciation occurs when an ancestral gene pool diverges either as a result of genetic drift or in response to natural selection. Divergence is facilitated by the spatial isolation of gene pools. If by

subsequent migration the populations meet, interbreeding may combine incompatible genes, resulting in low fitness. In this case, reproductive isolating mechanisms will evolve, creating separate species.

Incipient reproductive isolation is occurring among populations of the small harpacticoid copepod *Tisbe clodiensis* from different parts of the Mediterranean

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and Atlantic coasts of Europe. Individuals from most populations interbreed in the laboratory, but this results in progeny of reduced viability. Evidently the geographically isolated gene pools have become modified by local conditions so that when alien gametes combine, the finely tuned genetic architectures break down, resulting in hybrids of low fitness. Reproductive isolating mechanisms have not evolved between these disjunct populations, and indeed would be expected to occur only if the populations had become sympatric.

Such an event has evidently happened among German populations of small littoral isopods belonging to the *Jaera albifrons* species complex. By allowing individuals access only to mates from other species of the *albifrons* complex, hybridization can be induced in the laboratory and although the F1 progeny are viable, the F2 progeny show reduced viability. In nature, the frequency of hybrids is less than 1%, because of the operation of behavioural, reproductive isolating mechanisms between sympatric populations. Mating is preceded by courtship, and females refuse males presenting alien stimuli.

The formation of species from a geographically discontinuous, ancestral gene pool is called allopatric speciation. Geographical discontinuity can result from environmental forces that fragment the ancestral population, a process known as vicariance. For example, fossils show that when the Bering Strait opened during Late Pliocene time, some 3.54.0 million years ago, *Littorina squalida* extended its range from the northern Pacific, across the Arctic Ocean and into the Atlantic, probably following an eastward route (Reid 1996). Climatic cooling towards the end of Pliocene time then eliminated the periwinkle from the Arctic Ocean. Isolated from the ancestral population in the Pacific, the Atlantic population diverged to become *L. littorea*.

Geographical discontinuity also can result from the colonization of isolated habitats peripheral to the central population (peripheral isolates mechanism). Typically, colonizing populations are small, perhaps even just a single fertilized female, with the result that rapid genetic differentiation occurs through founder effects, inbreeding, drift or selection. A possible example of this concerns *L. horikawai*, confined to a relatively small area off Kyushu. The sister species, *L. sitkana*, is widespread in the northern Pacific, but the nearest population to Kyushu is some 1200 km distant, suggesting a rare colonizing event (Reid 1996).

When peripheral populations become larger relative to the central population, the situation increasingly resembles vicariance, the difference between vicariance and peripheral isolates mechanisms of allopatric speciation being only one of degree. As an arbitrary criterion for the peripheral isolates mechanism, it has been proposed that the ratio of distributional areas between sister species should exceed 20 : 1.

If, as is thought to be the case, allopatric divergence of gene pools is the principal mechanism of speciation, then the rate of speciation ought to be highest in the most heterogeneous environments, where opportunities for spatial isolation and divergent selection are greatest. These opportunities are less likely to arise in the water column than on the sea bed, and accordingly only about 2% of marine species are entirely pelagic. Environmental conditions within the interstices of sediments are more monotonous throughout the world than are those on exposed surfaces. Consequently, geographical variations are far more pronounced among epifaunas than among infaunas. Gastropods, for example, tend to have restricted geographical distributions and entirely different species live in the tropics than in temperate regions. Infaunal polychaetes on the other hand, tend to have wide geographical limits and many are cosmopolitan.

Not only the physical nature of the environment, but also the dispersability of organisms will influence the opportunity for speciation. Gene flow is more restricted among animals with direct development than among those with pelagic larvae, and more restricted among those with short-lived than among those with long-lived, pelagic larvae. For example, periwinkles in the *Littorina*

saxatilis species complex brood their young or lay benthic egg masses from which crawling young emerge. Dispersal is therefore almost entirely by crawling and perhaps occasionally by rafting on floating objects, so that gene flow between distant populations must be very slight indeed. On European shores, at least three species and several other morphs of undetermined taxonomic status exist within the *saxatilis* complex. Two geographically outlying populations

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occur in South Africa, probably having been transported as juveniles accidentally lodged on the bodies of palearctic waders during the winter migration. Because of evolutionary processes such as founder effect, drift and possibly selection influencing small, isolated breeding groups, these populations have become phenotypically (Plates 29 and 30, facing p. 208) and genetically distinct from northern populations (Reid 1996). As expected, electrophoresis of allozymes shows that there is considerable genetic variation even among local populations of the *saxatilis* complex, but that populations of *L. littorea*, which has planktotrophic larvae, are genetically more homogeneous even from both sides of the Atlantic Ocean.

Larval dispersal, however, does not necessarily result in genetic homogeneity. The oyster, *Crassostrea virginica*, has a larval phase lasting several weeks and, as expected, populations in estuaries along the coast of Florida are homogeneous for allozyme markers. On the other hand, genetic markers on mitochondrial and nuclear DNA reveal differences north and south of a point in mid-Florida. Reeb & Avise (1990) suggested that the allozymes are subject to balancing selection, making them similar among populations, whereas the DNA markers are selectively neutral, showing a genetic pattern that has not yet reached equilibrium, but reflects the effects of historical events. Northern and southern populations may have been isolated when large coastal estuaries drained during the Pleistocene lowering of sea-level. Genetic divergence resulting from this vicariant event still persists, even though subsequent rise in sea-level has restored panmixia.

The production of pelagic larvae, however, does not necessarily lead to thorough genetic mixing. Inside Long Island Sound is a population of *Mytilus edulis* genetically distinct from populations outside, as revealed by the electrophoresis of allozymes (Lassen & Turano 1978). The Sound has a typical estuarine hydrography, whereby less saline water flows out on top of a more saline, compensating bottom current. Larvae of resident mussels are carried out of the Sound in the surface current, but oceanic larvae fail to penetrate the Sound because when freshwater discharge is low during the summer breeding season, the weakened bottom current fails to flow over a sill near the mouth of the Sound. Genetic isolation of the Sound population is therefore imposed by hydrographical conditions.

A consequence of reduced dispersability and hence reduced interpopulation gene flow is that gene pools can become closely adjusted through natural selection to local conditions, but this is also likely to make them more vulnerable to environmental changes and prone to extinction. Enhanced dispersability and extensive interpopulation gene flow prevent localized differentiation of gene pools, so that species with long-lived, widely dispersing larvae must be broadly adapted to a range of environmental conditions and therefore less liable to extinction. It is sometimes possible to deduce the larval mode of life from the larval shell of fossilized gastropods. Scheltema (1978) thus deduced that the mean evolutionary longevity of species with teleplanic larvae (i.e. living several months to a year in the plankton) is about 19 million years, whereas that of species with direct development is only about 3 million years.

10.2.2

Sympatric Speciation.

At least in theory, geographical isolation is not always a prerequisite for speciation. When different selective forces act on different parts of a continuous population, they may, if strong enough to override the effect of gene flow, cause divergence within the gene pool, eventually leading to reproductive isolation. Perhaps the easiest kind of situation to envisage is where an ancestral gene pool diverges in response to the extreme conditions at opposite ends of a strong environmental gradient.

A difficulty with the concept of sympatric speciation is that very high selection pressures would be needed to counteract the homogenizing effect of gene flow. Attempts to cause sympatric,

genetic divergence in laboratory cultures of *Drosophila* have met with varied success, and only rarely has convincing evidence of sympatric, genetic divergence and reproductive isolation been found in the field (e.g. copper-tolerant plants on copper-mine tailings). Genetic responses to strong selection pressures associated with environmental gradients are frequently found in nature, but gene flow usually persists, preventing speciation and resulting in gradual changes in gene frequency (clines) along the gradients. For example, Schopf & Gooch (1971)

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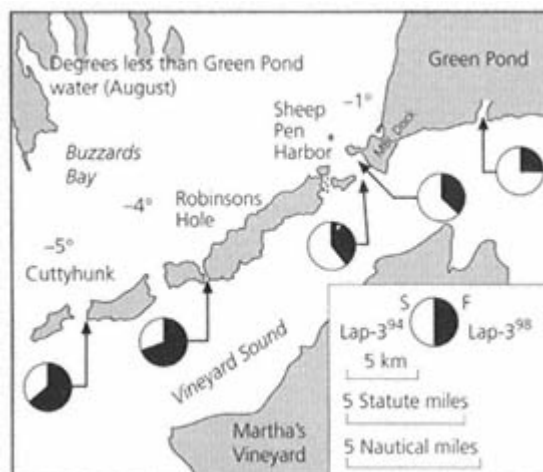


Fig. 10.1

Cline in frequencies of 'slow' (S) and 'fast' (F) alleles at a leucine-amino-peptidase locus of *Mytilus edulis* associated with a temperature gradient. 'Slow' and 'fast' refer to the relative speeds at which the proteins marking the different alleles move during electrophoresis. (After Schopf & Gooch 1971.)

found that the frequencies of two alleles at a leucine-amino-peptidase (Lap) locus in the bryozoan *Schizoporella unicornis* changed along the coastline of Cape Cod, paralleling a gradient in summer water temperature (Fig. 10.1).

Williams (1977) interpreted the data differently, proposing that there was probably sufficient mixing of larvae by currents to prevent any local genetic responses within the coastal population of *S. unicornis*. Larvae with a similar range of genetic qualities would be produced all along the coast each year. The clinal changes in gene frequencies could then only be caused by recurrent environmental elimination of locally inappropriate genotypes.

Without knowing the details of evolutionary history it is difficult to judge whether closely related, coexisting species have evolved sympatrically or have evolved allopatrically and subsequently become sympatric by range extension. However, the rapidly increasing number of sympatric 'sibling' or 'cryptic' species that are being discovered with the aid of electrophoresis of allozymes and other detailed taxonomic methods suggest that allopatric speciation cannot account for all cases. Sibling or cryptic species are groups of species that are morphologically difficult or impossible to distinguish within each group, yet do not interbreed. Examples are bryozoans of the *Alcyonidium gelatinosum* species complex, discovered from differences in allozyme markers among samples taken from the Bristol Channel (Thorpe *et al.* 1978), two forms of the subtidal nudibranch *Doto coronata*, which, in the Irish Sea, feed on two different hydroids and also differ in allozyme profiles (Morrow *et al.* 1992), and the flat periwinkles *Littorina obtusata* and *L. fabalis* (formerly *mariae*) (Plate 31, facing p. 208), the former living mid-tidally on *Ascophyllum nodosum* or *Fucus vesiculosus* and the latter living on *F. serratus* or kelp at lower levels on British shores. Sibling speciation in marine invertebrates has been reviewed by Knowlton (1993). (For a general discussion of speciation in marine habitats, see Palumbi (1994).)

10.2.3

Environmental Harshness and Instability

Whether allopatric or sympatric processes are involved in speciation, genetic diversity will be enhanced by environmental heterogeneity. But other factors can also be important. Harsh environments (e.g. extremes of temperature or salinity) and fluctuating environments will cause strong selection for physiological robustness or phenotypic plasticity rather than genetic variability. Genetic variability within several species of crustacean on European shores decreases from marine, brackish-water to rock-pool habitats as the environment becomes harsher and more variable (Table 10.1).

Environmental variability hinders the fine tuning of genotypes to local conditions and is of particular significance with regard to fluctuations in food supply. Stable food resources allow competition to generate selection for trophic specialization. Fluctuating food resources render trophic specialization less feasible because animals will need to become more opportunistic in times of food shortage. Among species of krill, levels of genetic variation are correlated with the trophic stability of the environment. Heterozygosity increases in the order *Euphausia superba* from highly seasonal Antarctic waters, *E. mucronata* from Chilean waters with moderately irregular upwellings, and *E. distinguenda* from the trophically stable waters of the equatorial eastern Pacific. *E. superba* is apparently represented by relatively homogeneous generalist genotypes and *E. distinguenda* by more heterogeneous specialist genotypes.

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Table 10.1 Mean genetic variation in species in three different environments. (After Battaglia *et al.* 1978.)

Variable	Environment and species		
	Marine	Brackish water	Rock pools
	<i>Tisbe clodiensis</i>	<i>Tisbe holothuriaet**</i>	<i>Tigiriopus</i>
	<i>Tisbe holothuriae*</i>	<i>Gammarus insensibilis</i>	<i>brevicornis</i>
	<i>Tisbe biminiensis</i>		<i>Tigiriopus fulvus</i>
Mean number of alleles per locus	1.982	1.788	1.297
Mean percentage of loci polymorphic (0.99)	56.84	42.03	18.27
Mean percentage of loci polymorphic (0.95)	46.78	38.89	16.13
* Banyuls-sur-Mer.			
** Sigean.			

10.3

Biogeography

10.3.1

Geographical Range

In addition to historical events (examples in Section 10.2.1), factors determining geographical range include dispersal ability, physiological tolerances and habitat requirements.

In some animal groups such as cone shells, geographical range is correlated with developmental mode, those species with planktotrophic larvae having the greatest ranges (Kohn & Perron 1993). In other groups such as species of *Littorina*, there is no such correlation (Reid 1996). Factors contributing to such lack of correlation include colonizing ability, discussed in Section 9.3.2.2, and the possibility of long-distance dispersal by post-larval or even adult stages. Small gastropods and bivalves with direct development can produce mucous threads that are caught by currents, so effecting dispersal (Martel & Chia 1991). A wide range of animals are dispersed by rafting on flotsam such as dislodged algal fronds, pieces of wood, pumice and, in recent times, on plastic and glass containers. Pumice probably has been an important rafting medium throughout evolutionary time, as it is continually produced in all oceans and is abundantly recorded in marine rock formations back to Precambrian time (Jokiel 1990). Pumice stranded on tropical beaches commonly bears coral colonies that have established themselves on the 'raft' as planula larvae (Section 6.3.1). Animals also may 'board' a raft by clinging to it, e.g. amphipods, or swimming within its shelter, e.g. reef fish (Myers 1994).

The dispersal potential of rafting is very great. Tree trunks and pumice washed ashore at Cocos Atoll in the early 1900s had been drifting in the Pacific for some 20 years after the eruption of Krakatoa, 1000 km to the northeast. Over geological time, drifting coral skeletons probably have been an important means of rafting. A skeleton of *Symphyllia agaricia*, afloat on the Great Barrier Reef, was found to be covered in coralline and filamentous algae and also to support goose barnacles, decapod crustaceans, oysters, gastropods, foraminiferans and bryozoans. The sizes of these organisms indicated that the skeleton had been drifting for several months, deriving buoyancy from gas trapped in the septal chambers (De Vantlier 1992).

Physiological limitation of range by temperature is particularly pertinent to latitudinal distribution (also discussed in Section 10.3.6) and its effect sometimes is detectable in the fossil record. When the climate was cooler during glacial periods in Pleistocene time, *Littorina littorea* occurred on the coast of Morocco, 850 km south of its present limit. During warmer interglacial periods the range of *L. littorea* extended to Siberia, over 2000 km north of its present limit (Reid 1996). The general limitation of kelp forests to cooler waters and of coral reefs to warmer seas is discussed in Sections 5.2.1 and 6.1.

Habitat requirements may limit geographical range; for example, on the western Atlantic coast,

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shores south of Connecticut are almost entirely sedimentary and the southward distribution of rocky shore organisms is limited to isolated rocky outcrops, harbour walls and jetties. Similarly, reef corals are largely absent from the sandy coastline of West Africa (Section 6.2).

10.3.2

Latitudinal Gradients of Species Diversity

The latitudinal decrease in species diversity from equatorial to polar regions was considered briefly in Chapter 3, but can now be considered in further detail in the context of the determinants of speciation.

10.3.2.1

Area Effect and Environmental Heterogeneity

The diversity of habitats and opportunities for the genetic isolation of populations on continental shelves increases as the total area of shelf increases. Therefore, the amount of speciation among shelf faunas ought to be higher in parts of the world with greater areas of shelf, assuming, as seems likely, that there is no compensating increase in extinction rate. The species diversity of bivalves and bryozoans is indeed correlated with continental shelf area, which decreases away from the equator, but there is much residual variation (Fig. 10.2). Schopf *et al.* (1978) suggested that the correlation between species diversity and shelf area would improve if total shelf area could be replaced by a measure of habitable shelf area. The proportion of shelf suitable for bivalves and bryozoans may vary independently of latitude. For example, the southeastern coast of North America is sandy and more suitable for infaunal bivalves than the southwestern coast, which has coarser sediments and more rocky areas favouring epibenthic animals such as bryozoans.

10.3.2.2

Trophic Stability

Prosobranch gastropods are one of the most diverse groups of marine macroinvertebrates and they show a strong latitudinal decrease in diversity from equatorial to polar regions. This trend may partly

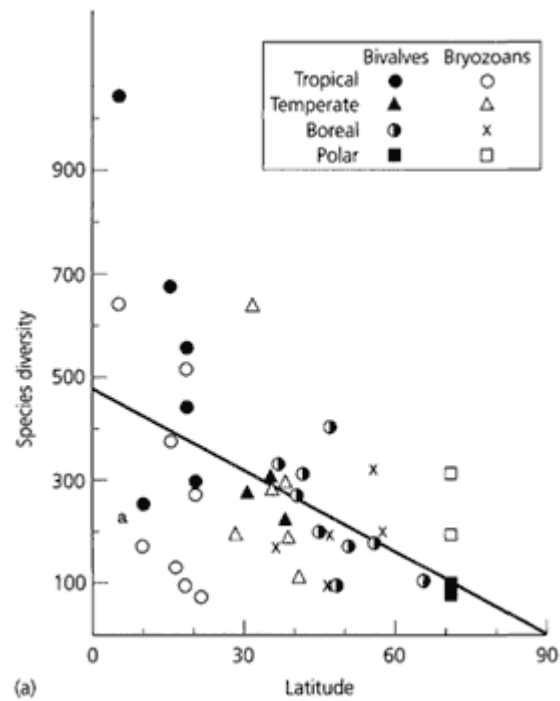


Fig. 10.2
(a) Latitudinal changes in species diversity of bryozoans and bivalves.

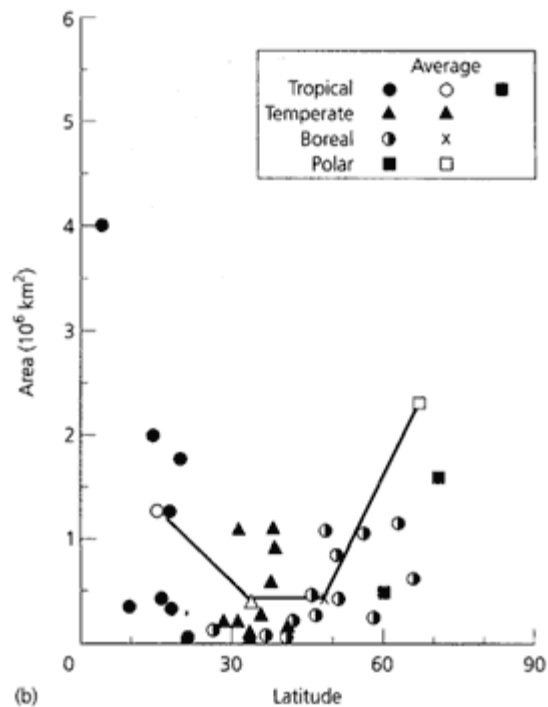


Fig. 10.2
(b) Latitudinal changes in a continental shelf area. (After Schopf *et al.* 1978.)

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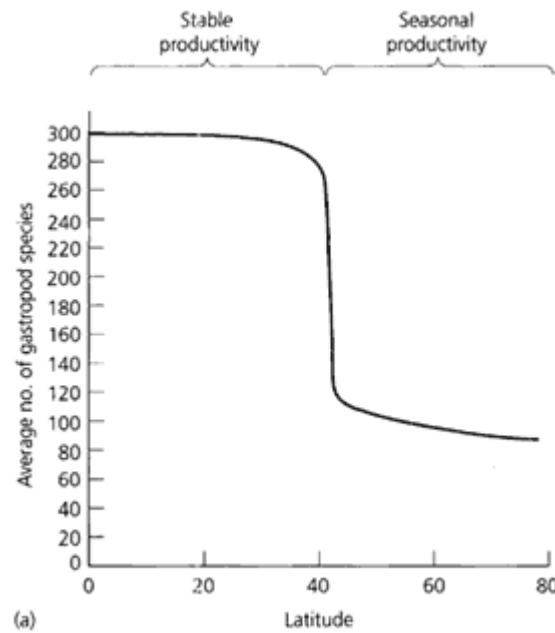


Fig. 10.3
(a) Latitudinal changes in the species diversity of gastropods in the eastern North Atlantic.

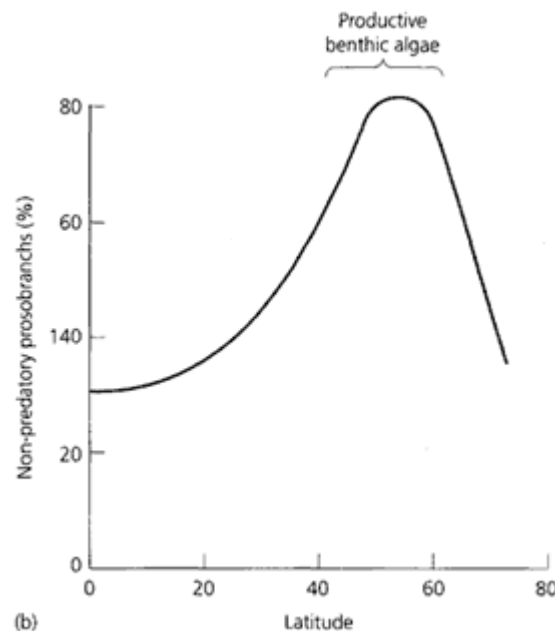


Fig. 10.3
(b) Latitudinal changes in the percentage of gastropods represented by algal grazers. (After Taylor & Taylor 1977.)

be due to latitudinal changes in the area of habitat, as with bivalves and bryozoans, but is also due to the trophic stability of the environment (Taylor & Taylor 1977). A sharp drop in the diversity of

eastern Atlantic gastropods occurs round about latitude 40°N, coinciding with a change from a tropical oceanic regime in which primary production is continuous throughout the year, to a temperate oceanic regime in which primary production is seasonally pulsed. The trophic stability of tropical habitats allows specialized feeding behaviours to evolve, whereas at higher latitudes trophic instability has the opposite effect. Tropical families of predatory gastropods have narrower diets than families from higher latitudes. For example, the Cassidae feed on echinoids, the Tonnidae on holothurians, the Mitridae on sipunculan worms, most Conidae, Vasidae and Bursidae on polychaetes, and the Harpidae on decapod crustaceans. By contrast, the Buccinidae, which are abundant at high latitudes, are opportunistic feeders, whose diets include polychaetes, sipunculans, crustaceans, molluscs, echinoids and carrion. A given supply of food resource can either be partitioned among many species with narrower diets and smaller populations or among fewer species with wider diets and large populations, so that more species exist in low latitudes where diets are relatively narrower than at higher latitudes where diets are wider.

The Turridae are an exception which proves the rule of trophic stability. These predators are abundant at high latitudes yet appear to be specialist feeders on polychaetes. Their prey are, however, deposit-feeding worms whose population dynamics are little affected by the seasonally pulsed primary production.

Quality of the food resource changes throughout the world and this influences faunal species composition rather than species diversity. The proportion of non-predatory gastropods rises between latitudes 40 and 60°N (Fig. 10.3). This is due to a surge in the number of algal-grazing species in response to the high benthic algal productivity of temperate regions (Chapter 5).

10.3.2.3

Diversity Associated with Coral Reefs.

Because of the physiology of the cnidariandinoflagellate symbiosis, reef-building corals are

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confined to shallow, clear waters within the 20°C winter isotherms (Chapter 6). The intricate three-dimensional architecture of corals and associated reef structures creates multitudinous microhabitats that support very rich faunas, an effect that is reinforced by the extremely high, stable productivities of coral-reef ecosystems. Coral reefs, therefore, account for a significant proportion of the high overall species diversity of tropical shelf faunas.

10.3.3

Oceanic Differences in Species Diversity

The highest diversity of shallow benthic species in the world is in the tropical Indo-Pacific, followed by the tropical Pacific coast of America. The lowest tropical benthic species diversities occur on both sides of the Atlantic. Within the Indo-Pacific the highest diversity is centred on the Indo-Malayan region (Fig. 10.4), where most of the diversity-promoting factors previously described occur together. First, the equatorial location is associated with stable, non-seasonal, primary production (Section 10.3.2.2). This stability is enhanced by the numerous small islands and continental land masses surrounded by a large ocean, a geographical configuration that produces a very even maritime climate and stable water column. Secondly, the continental shelf is dissected by numerous deep basins between the islands and continents, providing good opportunities for the genetic isolation of populations (Section 10.3.2.1). Thirdly, the coral reefs provide a spatially heterogeneous environment and stable high primary productivity (Section 10.3.2.3).

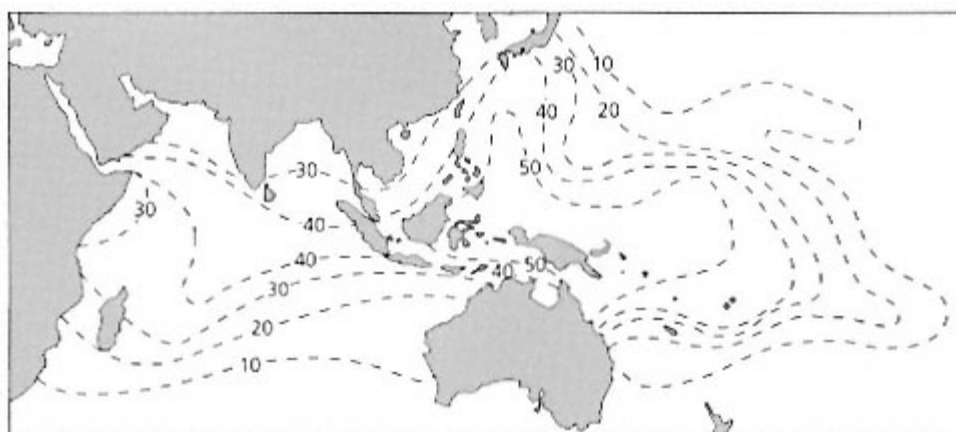


Fig. 10.4

Generic diversity of hermatypic corals in the Indo-Pacific. The centre of diversity is in the Indo-Malayan region. (After Stehli & Wells 1971.)

The reduced species diversity of shallow, benthic assemblages outside the Indo-Pacific region is partly correlated with the increased continentality of the climate. As a result of land having a lower specific heat than water, temperature fluctuations increase as the ratio of continuous land surface to sea surface increases. This ratio is least among the archipelagos and peninsulas of the Indo-Pacific, greater along the west American shelf where large continents border a large ocean, and greatest in the Atlantic where large continents face a small ocean.

Other theories attempting to explain the negative gradient in species richness radiating from the Indo-Malayan region are based on the geographical origin and dispersal of newly evolved species. The centre-of-origin theory proposes that speciation occurred principally within the Indo-Malayan region, perhaps on account of factors such as those described above, and that newly evolved species diffused outwards from this centre over geological time. The centre-of-accumulation

theory proposes that speciation occurred principally in peripherally isolated archipelagos, from where species were transported to the central region by prevailing oceanic currents. Over geological time, this process would cause species to accumulate in the central, Indo-Malayan region. The provincial overlap theory proposes that the Indo-west Pacific is composed of several biogeographical provinces (including Pacific Ocean, Indian Ocean and Indonesian), each with different geological and evolutionary histories. These

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provinces overlap in the Indo-Malayan region, creating an area of exceptionally high species diversity.

The first two of these three theories can be tested, with the use of neutral genetic markers such as those on mtDNA, by examining patterns of allelic distribution in the central and peripheral regions. The centre-of-origin model predicts that movement to the periphery of the Indo-West Pacific is uncommon, each event involving relatively few colonists. These initially will carry with them a small, probably random, sample of alleles from the large, central population. If the peripheral region is reached relatively quickly, the randomly sampled alleles will be preserved. If, on the other hand, the periphery is reached slowly via a series of stepping-stone islands, alleles in the peripheral populations are likely to be highly modified compared with those in the ancestral gene pool. The centre-of-accumulation hypothesis predicts that, because new species originate at the periphery, the most ancient alleles should exist in peripheral populations, compared with those in the centre. Preliminary data for the sea-urchin, *Echinometra* sp. nov. A, show that an outlying population at Tahiti has a cluster of highly derived mtDNA alleles. At Fiji, one step closer to the Indo-Malayan region, some of the alleles are evolutionarily basal to the Tahitian alleles, supporting the stepping-stone version of the centre-of-origin hypothesis (Palumbi 1996).

10.3.4

Geographical Barriers

Physical features of the oceans and continents, such as unfavourable currents, large stretches of cold, deep water or shallow, warm water, and land barriers, may impede dispersal and colonization, with important consequences to the species diversity of shelf faunas. However, such barriers to range extension seldom are absolute over a geological time scale because very occasionally they may be crossed via some fortuitous event, such as rafting. The crossing of geographical barriers by species is termed jump dispersal.

The East Pacific Barrier (Fig. 10.5) is a wide stretch of deep water between Polynesia and America that has greatly restricted the spread of tropical, Indo-West Pacific, shallow-water species to the coasts of tropical America. Only about 6% of tropical, Indo-West Pacific, shore fish have managed to cross the East Pacific Barrier, as has a similarly small proportion of shallow-water invertebrates. Consequently,

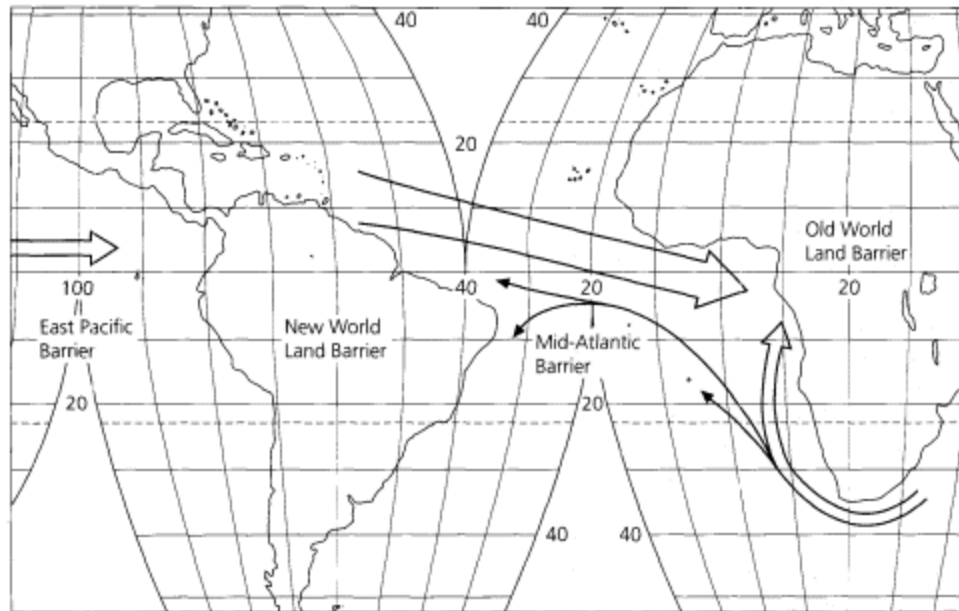


Fig. 10.5
Zoogeographical barriers separating the tropical shelf regions. The arrows indicate the direction and approximate relative amount of colonization that has occurred. (After Briggs 1974.)

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the tropical East Pacific shelf fauna is depauperated by the existence of the East Pacific Barrier. Because of the prevailing currents, no species originating in the eastern Pacific have managed to extend westwards across the East Pacific Barrier.

Other barriers with similar zoogeographical effects (Fig. 10.5) include the New World Land Barrier, which prevents movement of tropical marine species between the eastern Pacific and western Atlantic, the Mid-Atlantic Barrier, a broad stretch of deep water that separates tropical western and eastern shelf faunas, and the Old World Land Barrier, which separates the tropical eastern Atlantic and Mediterranean from the Red Sea and tropical Indian Ocean.

Warm, shallow, tropical shelf waters isolate the shallow, benthic faunas of northern and southern temperate regions. A number of species, however, such as the barnacle *Semibalanus balanoides* and the colonial tunicate *Botryllus schlosseri* (see Fig. 9.13a), are able to extend across the equator by living in deeper, cooler water, a phenomenon known as equatorial submergence.

Because the relative positions of land masses and associated shelf areas have changed drastically over geological time as a result of plate tectonics (Section 10.3.7), distances separating modern biogeographical areas may not resemble situations in the past. The occurrence of closely related taxa on either side of an apparent geographical barrier may have originated not by jump dispersal but by tectonic events, including the separation of land masses, or deep submergence of intermediate habitat such as islands, reefs and guyots, by subsidence of the ocean floor. Direct evidence of population splitting by tectonic processes is limited by the destruction of material at the subduction zones. Close to the Pacific subduction zones, for example, the ocean floor is only some 150 million years old, so the geological record does not extend beyond Jurassic times. Tectonic plates, on the other hand, have a much longer geological history, and so biogeographical inferences can be made by comparing taxonomic distributions among plates.

Many species, for example of fish, molluscs and crustaceans, show plate endemism, being confined to a particular plate even though geographical barriers to dispersal may appear weak. The circumtropical amphipod genus *Globosolembos* has nine species distributed among several tectonic plates. By comparing this geographical distribution with phylogenetic relationships among the species, it is possible to make inferences about how plate tectonics has influenced their biogeography. On a phylogenetic cladogram (Fig. 10.6) the first dichotomy separates four species on the AfricanIndian Ocean and IndiaAustralian plates from five species on the Pacific, North American and AfricanAtlantic plates. This dichotomy corresponds to the 'Andesite' line, along which the rocks of the Pacific Basin are compositionally distinct from those of land masses to the west. The geological significance of this apparent barrier remains conjectural, but it is possible that species absent from the Pacific plate never have been present on it. The second dichotomy separates an Atlantic species from a group of Pacific plate and western Atlantic species, corresponding to the opening of the Atlantic in early Jurassic time some 165180 million years ago. The third dichotomy separates two South Pacific species from a Hawaiian and a western Atlantic species, reflecting changing geography resulting from plate movements and volcanism (Myers 1994).

On the one hand, major differences in regional biotas may be interpretable in terms of plate tectonics. For example, the suturing of Africa with Europe in late Cretaceous time formed a physical barrier to dispersal of stenothermic, tropical shallow-water taxa across the Tethys Sea (see Fig. 10.8), resulting in great taxonomic differences between the floras and faunas of the Caribbean Sea and Indian Ocean. On the other hand, similar associations between corals, sea-grasses and mangroves, occurring in widespread but disjunct areas of tropical ocean (Section 10.3.7), may be derived from an association that once extended throughout the Tethys Sea. Continental movements during EoceneMiocene time led to extensive extinctions, notably in the Caribbean and eastern Pacific, so fragmenting the original distribution.

In summary, many large-scale biogeographical patterns can be understood in terms of Tectonic, Eustatic, Climatic and Oceanographic processes (TECO, Rosen 1984). TECO processes fall into several major categories: (1) splitting marine biotas by tectonic rifting, orogenic changes in direction of large rivers discharging into shelf areas, sea-level rise, and changes in ocean currents; (2) combining species pools through tectonic convergence and sea-level lowstands; (3) shifting, contracting and

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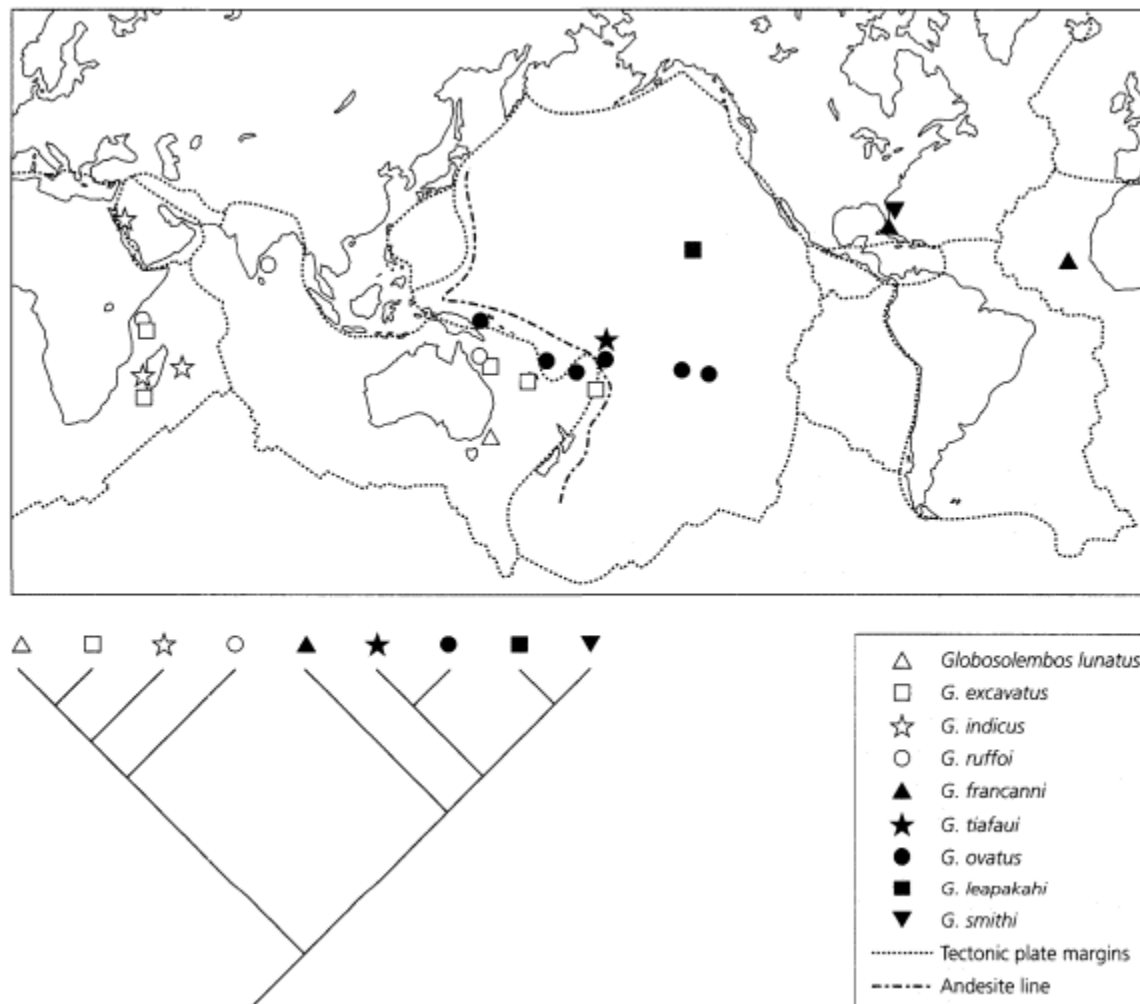


Fig. 10.6
Geographic distribution of amphipod crustaceans of the genus *Globosolembos*,
with cladogram of phylogenetic relationships. (After Myers 1994.)

expanding species ranges through climate change and variation in continental shelf area; (4) controlling immigration rates through changes in distances between islands and in current regimes; (5) indirectly controlling extinction through climate change.

10.3.5 *Deep-Sea Benthos*

Deep-sea, benthic, faunal diversity is extraordinarily high (Chapter 7). Although the physical conditions are extreme compared with those of more familiar shallow habitats, they are stable. Relatively large particles, such as dead vertebrates, are quickly consumed by scavengers, as demonstrated by the rapid exploitation of bait lowered to the sea bed. Scavengers, mainly fish, disperse the organic matter as faeces, thereby evening out the spatial distribution of food for deposit feeders.

The predictability of the deep-sea environment would therefore seem conducive to specialization. However, the problem remains of explaining how competitive exclusions are prevented in such an

apparently homogeneous habitat and how gene pools diverge in the apparent absence of barriers to gene flow. Dayton & Hessler (1972) proposed that generalist 'croppers' keep prey population densities

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sufficiently low to prevent competitive exclusions (Chapter 7). But would not the evolutionary arms race between predators and prey tend to offset this in such a stable environment? Hessler & Sanders (1967) suggested that the long geological history of stability in the deep sea has allowed the evolution of numerous species with narrow niches, but they did not indicate how the resources are partitioned or how genetic divergence and reproductive isolation take place. It has been suggested that many deep-sea species have not evolved from common ancestors *in situ* but are derived from ancestral immigrants from shallow waters. Comparative morphological studies of deep-sea isopods, however, indicate a long history of *in situ* evolution. The explanation of speciation and faunal diversity in the deep sea therefore remains an important problem, for the deep-sea environment accounts for a very large proportion of the biosphere.

10.3.6

Latitudinal Zonation

Just as species are vertically zoned on shores in response to the terrestrial-marine environmental gradient (Section 5.1.1), so they also tend to be horizontally zoned on a geographical scale in response to a complex gradient associated with latitudinal changes in climate. The latitudinal climatic gradient is particularly pronounced on the east coast of North America. The south-flowing, cold Labrador Current and the north-flowing, warm Florida Current cause a very rapid change from arctic to tropical temperature regimes within 20° of latitude (Fig. 10.7). Not surprisingly, the latitudinal zonation of many eastern North American intertidal species is correlated with critical boundaries where temperatures become too extreme for reproduction or adult survival.

Along the western coast of North America the climatic gradient is much more gradual and factors other than temperature become important in determining latitudinal, zonal boundaries. Behrens-Yamada (1977) identified factors limiting the latitudinal distribution of two species of periwinkle by transplanting the snails beyond their normal ranges. The southern limit of *Littorina sitkana* and the northern limit of *L. planaxis* occur at about latitude 43°N. *L. planaxis* transplanted further north survived and reproduced for 4 years, but the potential northerly range of this species is curtailed by south-flowing currents that prevent the northward spread of the pelagic larvae. *L. sitkana* transplanted south of its natural range succumbed both to desiccation, because of a lack of damp microhabitats, and to predation by crabs, which are more abundant in the high intertidal zone to the south.

10.3.7

Plate Tectonics and Provincialization

Waves of extinction and taxonomic diversification are prominent features in the fossil record. Sometimes extinction coincided with a reduction in taxonomic diversity (diversity-dependent extinction), suggesting that the carrying capacity of the biosphere had somehow declined, but at other times waves of extinction did not affect taxonomic diversity (diversity-independent extinction), evidently because lost lineages were replaced quickly by new ones. The most likely cause of diversity-independent extinction is a change in climate that causes unadaptable species to die out but does not affect the carrying capacity of the biosphere, so that taxa soon evolve to utilize vacated niches.

A density-dependent wave of extinction occurred in Mid- to Late Permian time (just over 200 million years ago), reducing the diversity of most taxa to their lowest levels since Cambrian time, when fossils first became numerous. The cause of the Permian crash in taxonomic diversity remain in debate, but the surge of rediversification during the Mesozoic-Cenozoic period (180-120 million years ago) is much better understood.

Before the Mesozoic period the continents were grouped together, surrounded by the huge Pacific Ocean and partly divided by the Tethys Sea (Fig. 10.8). During the Mesozoic period the continents began to separate owing to sea-floor spreading and this must have altered the climate considerably (for an account of plate tectonics and its biogeographical implications, see Valentine (1973) and Gray & Boucot (1979)). The huge continuous area of the pre-Mesozoic supercontinent would have intensified temperature fluctuations, producing a more continental world climate (Section 10.3.3). Separation of the continents had several important effects. First, the increased coastline per unit area of land ameliorated the world climate, making continental shelf areas more stable and therefore more conducive to the evolution of species with specialized niches (Section 10.3.2.2). Secondly, separation of the continents promoted faunistic and floristic isolation,

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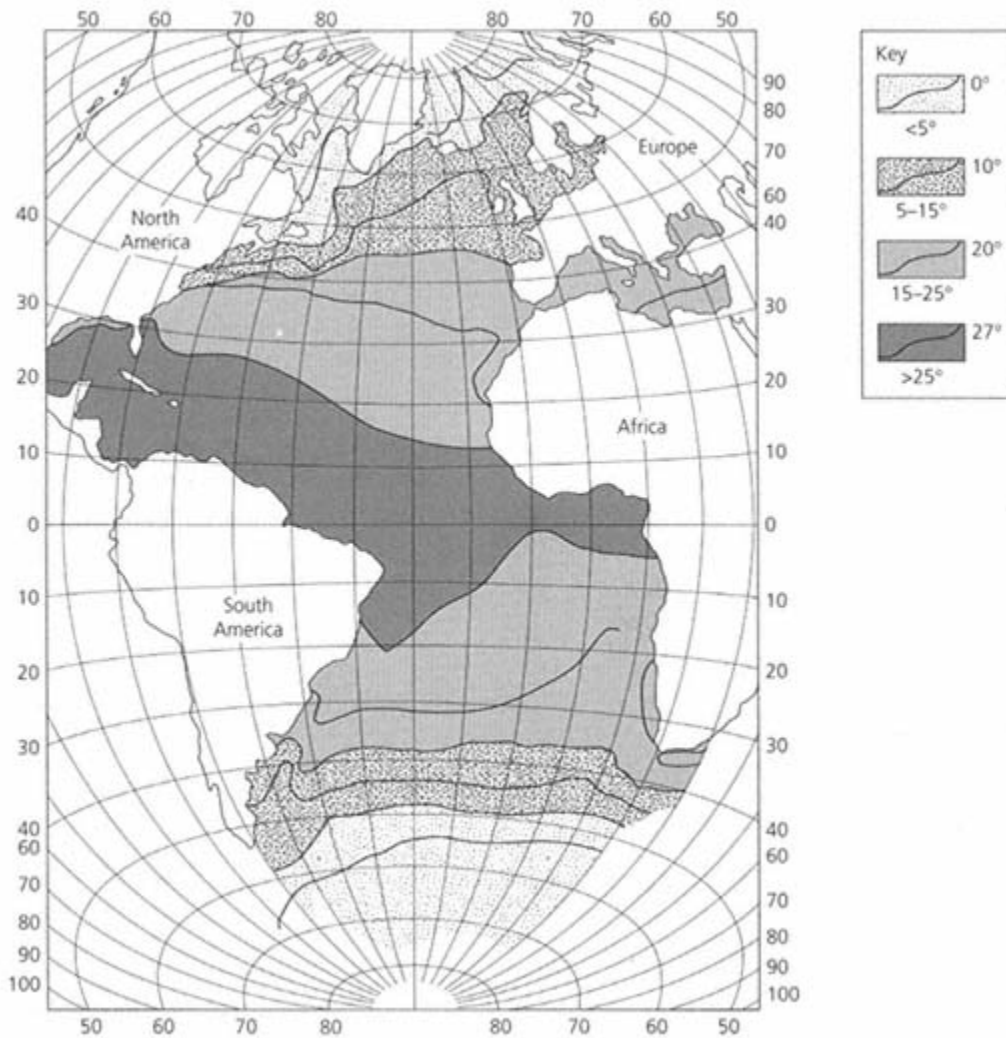


Fig. 10.7
Mean annual temperature isotherms of the surface water of the Atlantic, showing the compressed temperature gradient on the east coast of North America. (After Ekman 1967.)

increasing the opportunities for allopatric evolution. Consequently, biotas of geographically separate shelves developed different taxonomic compositions, or in biogeographical terminology, developed provincial differences. During early Jurassic time there seems to have been no provinciality at all, as ammonite and bivalve taxa were cosmopolitan. By Middle and Late Jurassic time there were two, welldefined faunal realms, and today over 30 marine provinces are recognized. Thirdly, the changing positions of the continents altered the pattern of oceanic circulation so as to intensify the equatorialpolar temperature gradient. Owing to the isolation of the Arctic Ocean by continental topography and of the Antarctic seas by the Circumpolar Current, polar seas at present are as cold as they can ever be. The pronounced, latitudinal, temperature gradient led to latitudinal zonation (Section 10.3.6) and increased provinciality. The glacial cycle, which may have started in association with changing continental configuration and oceanic circulation, has not caused massive extinctions. This is because the predominantly northsouth continental orientation allows species to move gradually with the latitudinal advance and retreat of cooler conditions.

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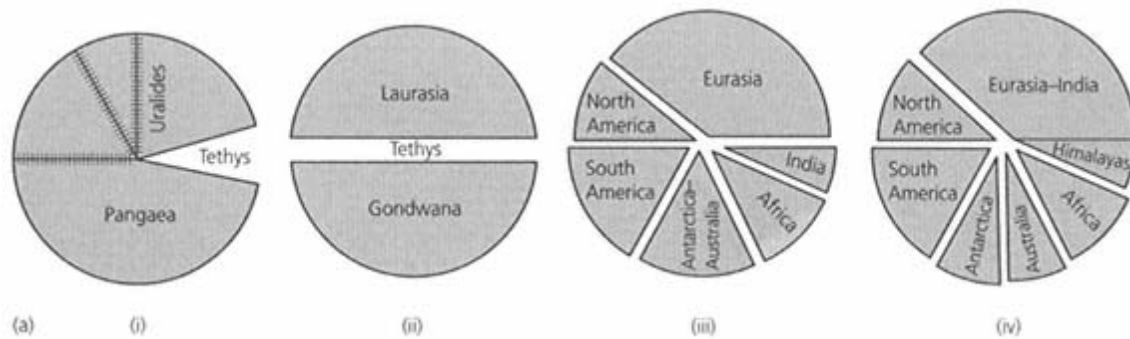


Fig. 10.8

(a) Inferred continental and oceanic configurations during the last 200300 million years. (i) In Permian time, Pangaea is partly intersected by the Tethys Sea. (ii) In Early Mesozoic time, Laurasia and Gondwana are separated by the Tethys Sea. (iii) At the end of the Cretaceous period, Gondwana is highly fragmented. (iv) At the present, India is joined to Eurasia. (After Valentine 1973.)

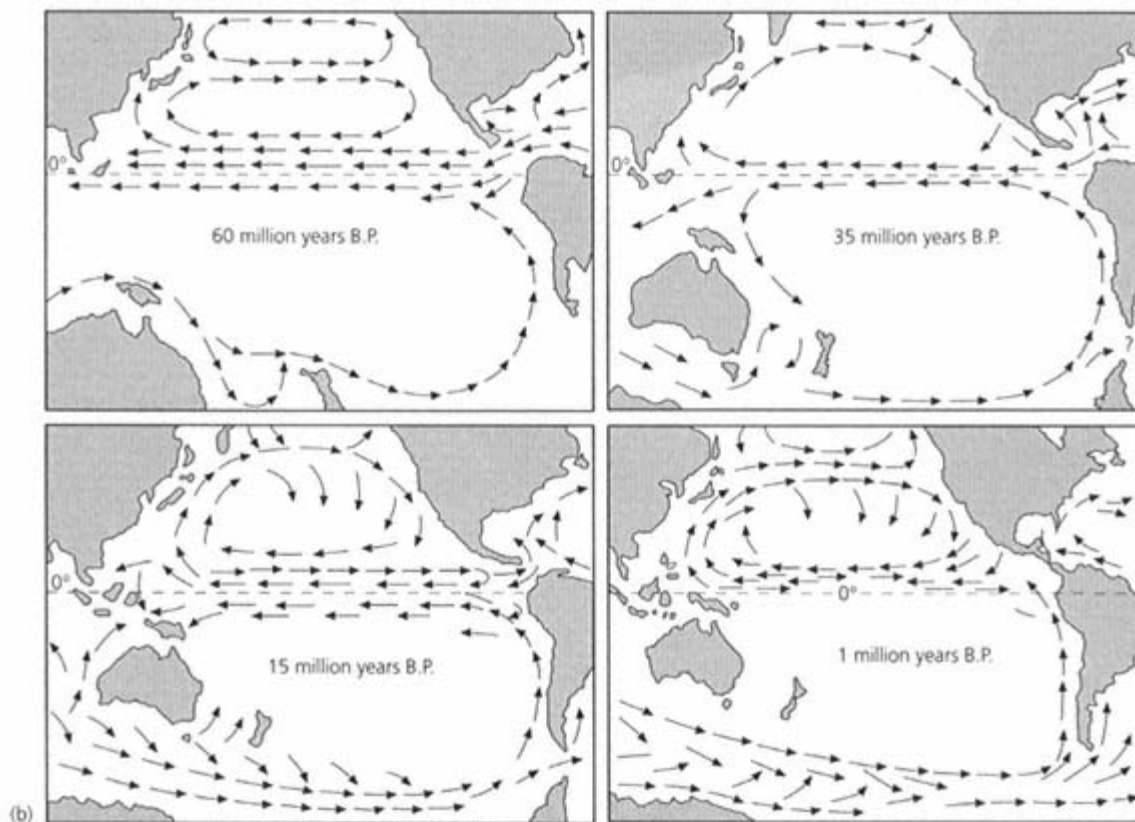


Fig. 10.8

(b) Changing configuration of continents in the Pacific region during the last 60 million years and the associated changes in surface currents. (After Van Andel 1979.)

10.3.8

The Effects of Man

Current theories of plate tectonics and evolutionary ecology could not be expected to predict the small but significant effects that man himself has had on contemporary biogeography. Man's technology has resulted in the passive transportation of organisms throughout the world and even the opening up of new dispersal routes between previously isolated seas.

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Organisms are dispersed attached to the hulls of ships or to commodities such as oysters. Most hitch-hikers will be killed in transit or will fail to establish themselves in foreign localities because conditions are unsuitable for their growth or reproduction, or because there are too few simultaneous arrivals to form a viable breeding group (propagule). Opportunistic (*r*-selected) species (Section 9.1), with their high potential population growth rates and ability to flourish from small initial densities, are the most likely organisms to spread by hitch-hiking. Examples include the Australasian barnacle *Elminius modestus*, which was first noticed in Chichester harbour, England, in 1945 and now thrives in moderately sheltered localities throughout Britain. Presumably *Elminius* was given the opportunity to breed and recruit young while ships were laid up during the Second World War. In 1890 a shipment of American oysters brought the slipper limpet *Crepidula fornicata* to Essex, since when the stow-away has become firmly established in the oyster beds of southwest Britain.

Successful immigrants can make an impressive ecological impact. In the early nineteenth century the cord grass *Spartina alterniflora* was introduced from America to Southampton Water, where it hybridized with the European species *S. maritima*, forming a sterile hybrid *S. townsendii*. This hybrid subsequently became polyploid, forming the sexual species *Spartina anglica*, which is so vigorous that it has spread throughout much of the British Isles, forming dense stands where once there were open mud flats. Animals such as *Scrobicularia plana* and *Macoma balthica* disappear as *Spartina anglica* monopolizes the substratum, but other species such as *Littorina rudis* and *Anurida maritima* move in.

Ecological impact of the shore (or green) crab, *Carcinus maenas*, is being studied in California. Although *C. maenas* has been transported about the world by human activities for over two centuries, it has only recently reached the North Pacific, first having been recorded in San Francisco Bay in 1989. By 1995, *C. maenas* had extended its range northward to Bodega Harbor, apparently the result of larval recruitment by a single cohort carried by the prevailing northward surface currents. Enclosure experiments have shown that *C. maenas* significantly reduces densities of bivalves and infaunal crustaceans in sheltered bays, and it is predicted that the alien will have great impact on the benthic ecology of the region (Grosholz & Ruiz 1995).

As well as carrying organisms about with him, man has assisted their dispersal by connecting the Red Sea to the Mediterranean. Organisms began to disperse along the Suez Canal immediately after its opening in 1869. Currents flow from the Red Sea to the Mediterranean for 10 months of the year so that most invertebrate migration has been in this direction. At least 140 animal species, including fish, decapod crustaceans, molluscs, polychaetes, ascidians and sponges have reached the Mediterranean via the Suez Canal.

The Panama Canal, connecting the Pacific to the Atlantic, has a salinity of less than 1‰ and therefore can only be negotiated by a few euryhaline species such as the blue crab *Callinectes sapidus*. The proposal for a sea-level canal, if implemented, would probably have important biogeographical consequences. The eastern and western Central American shelf faunas contain approximately 8000 and 6000 species, respectively. Bringing these species into contact could cause the extinction of many of them.

Finally, man has severely depleted many of the populations he exploits. Stellar's sea-cow (Section 5.2.4.2) and the great auk were exterminated, and the large whales seem dangerously close to a similar fate. Ecological consequences of such over-indulgences are not yet predictable, but could be far-reaching. Nevertheless, accelerating alteration of habitat and transportation of species around the world are beginning to have far-reaching effects. Regionally distinct biotas are threatened by the extinction of endemics and their replacement by opportunistic species that are good colonizers.

Human impact on the marine biota is, at present, miniscule compared with biogeographical events that have occurred in the geological past.

Useful texts on speciation, biogeography, and plate tectonics in the marine context include those by Ekman (1967), Valentine (1973), Briggs (1974), Gray & Boucot (1979), Myers (1994) and Palumbi (1994).

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whose diet then probably consists of heterotrophic microflagellates, small phytoplankton and suspended detritus particles in that size range. Mesozooplankton ($> 200 \mu\text{m}$ in size), such as copepods, feed to a large degree on microzooplankton, and on phytoplankton and suspended detritus, thus completing the shunt of energy via the so-called 'microbial loop' in aquatic ecosystems. This 'loop' is a parallel food chain to the conventional 'grazing' chain of phytoplankton-zooplankton-fish. The excretory products, mainly faecal pellets, of the water column organisms contain much material of potential food value. These faeces, together with detrital substances derived from the fringing seaweeds (and in some areas from unconsumed phytoplankton), collectively known as particulate organic matter (POM), form the substrate for bacterial growth and, ultimately, for bacterial-dependent populations of heterotrophic protists and small metazoans. As these aggregations sink through the water, they are consumed by members of the zooplankton, which digest the living microbiota and microfauna, until eventually the recycled aggregations reach the sea bed. There they support a deposit- and suspension-feeding benthos which, in regions below the photic zone, is ultimately similarly dependent on bacterial production. In some areas of sea bed, genuinely primarily producing bacteria can fix carbon dioxide by chemosynthesis and these, too, will pass organic matter into the benthic food web, as will those bacteria that chemosynthetically can regenerate organic matter using the end products of previous photosynthetic activity. Some of these various chemosynthetic bacteria are symbiotic in gutless animals and supply all of their host's nutritional requirements (as indeed can symbiotic photosynthetic algae in their shallow-water flatworm, cnidarian, mollusc or sea-squirt partners).

Herbivorous and detritivorous planktonic organisms are consumed by the carnivorous zooplankton, and equivalent benthic carnivores take the deposit and suspension feeders. All these planktonic and benthic consumers then form the food of the nekton, which occupy the uppermost portions of the marine food web over all but the deepest regions of the abyssal trenches. The large majority of the nekton are carnivores, although a limited number of species can consume the primary producers and even fewer appear able to take the detrital-bacterial aggregates.

As a consequence of primary production being a surface-water phenomenon and because shallow-water zones are the most productive regions of the sea per unit area, secondary production declines with both distance away from the coast and depth in the sea. Where deep waters lie immediately adjacent to the coast, however, detrital bonanzas may occur at great depths, and debris from coastal tracheophytes is found over large areas of the abyssal plain; nevertheless, the abyssal benthos is the slowest growing, longest lived and least productive of all marine systems. Relative food shortage places a selective premium on efficiency of utilization, and hence passage of materials through the food web is most efficient in the open ocean, on coral reefs and probably in the deep sea, and least efficient in areas of upwelling, in estuaries and in shallow waters generally.

Total animal biomass in the sea has been estimated at $1000 \times 10^6 \text{ t}$ (dry weight), a comparable value to that occurring on the continents. However, this biomass probably produces more than three times more organic matter per year than does the terrestrial/fresh-water fauna; the marine biomass produces $3025 \times 10^6 \text{ t}$ (dry weight) as compared with the continental production of $900 \times 10^6 \text{ t}$ (dry weight). Thus, although marine primary production is much lower than that on land, marine secondary production is much greater (primary to secondary production ratios of 1 : 0.008 on land and 1 : 0.06 in the sea). This is a result of the greater digestibility of marine primary production, the greater efficiency of trophic relationships in the sea and, in part, the ectothermic nature of marine consumers (less of the food energy has to be devoted to fuelling a temperature differential between body and environment). Man currently exploits about $100 \times 10^6 \text{ t}$ (wet weight) of marine production, with the world catch consisting of a wide diversity of animals including crustaceans, molluscs, echinoderms, fish and marine mammals.

So far in this synopsis, we have been following the passage of food materials from their fixation to the top consumers, but essential elements such as nitrogen and phosphorus are present in finite amount and unless these are cycled through the ecosystem back to the primary producers, productivity will cease. Supply of nutrients is probably the most frequent rate-limiting process in the sea, both

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