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Exploited marine invertebrates: genetics and fisheries

J. P. Thorpe[1], A. M. Solé-Cava[1,2] & P. C. Watts[1]
[1]*School of Biological Sciences, University of Liverpool, Port Erin Marine Laboratory, Port Erin, Isle of Man, IM9 6JA, U.K.*
[2]*Laboratório de Biodiversidade Molecular, Departamento de Genética, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil*
E-mail: sole@biologia.ufrj.br

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Abstract

The application of genetic techniques to invertebrate fisheries is in many ways essentially similar to that in vertebrate (i.e. finfish) fisheries, for which there is already an extensive body of published data. However, there are also relative differences which lead to particular problems in the use of genetic data to study commercially important invertebrate species. The main role for genetics of both vertebrates and invertebrates has been, and is likely to continue to be, the identification of groups of interbreeding individuals as the basis for a fishery. It is in the identification of the breeding unit that the genetic differences between vertebrates and invertebrates can be of practical significance. The genetic breeding unit, usually called a 'stock' in fisheries biology, generally shows a certain uniformity of size in most marine fish which have been studied. Smaller or less mobile fish (e.g. flatfish) may only range a few tens of kilometres to their breeding grounds, whilst in more mobile, particularly migratory pelagic species (e.g. Scombridae), the area occupied by a stock is likely to be far greater and for a few (e.g. large pelagic elasmobranchs), a single unit of stock may be almost circumglobal. However, marine fish generally, particularly those large or plentiful enough to be of commercial interest, are likely to be fairly mobile and in many cases the order of mobility is likely to be in the region we might predict from our knowledge of the biology and habits of the species. In the genetic assessment of 'stocks' for invertebrate fisheries, we face a number of additional problems, mostly related to the large evolutionary range of invertebrates exploited and their widely different biology. Although in Europe and North America marine invertebrate fisheries may be thought of as being mainly for decapod crustaceans and bivalve molluscs, globally commercially important marine invertebrate fisheries range from sponges to squid and include such diverse groups as sea cucumbers, barnacles, krill, octopuses, cuttlefish, sea anemones, ascidians, polychaetes, sea urchins, gastropods and jellyfish. An obvious feature of many of these invertebrates is that the adult (i.e. commercial) stage of the life cycle is sessile (e.g. barnacles, sponges, ascidians) or of very limited mobility (e.g. sea anemones, sea urchins, bivalves, gastropods), with the result that the dispersive phase of the life cycle is the larva. Other groups (e.g. krill, jellyfish) are planktonic or nektonic and may cover very large distances, but, unlike fish, have little control over the distance or direction of travel, whilst some of the open ocean pelagic squid are more mobile than most fish and may migrate thousands or kilometres to spawning grounds. The very low mobility of both larva and adult in some invertebrates indicates that dispersal, and hence stock size, is likely to be low and that, therefore, stocks are far more vulnerable to overfishing than in most fish species. An additional difficulty is that genetic studies to date indicate a remarkably high incidence of cryptic speciation in marine invertebrates, sometimes even in comparatively well studied commercially important species. Thus, although to date marine invertebrate fisheries have not received the same level of attention from geneticist as finfish fisheries, it is clear that for invertebrate fisheries genetic data are relatively far more important if a fishery is to be exploited without being endangered.

Introduction

Background: the application of genetics to fisheries

To date, there is an extensive literature on the various uses of genetics for the study of marine fisheries (e.g. Ryman & Utter, 1987; Carvalho & Pitcher, 1995; Ward & Grewe, 1995), but the great bulk of this published work is concerned with fisheries for fish, rather than fisheries for commercially important marine invertebrates. This concentration of applied genetics on marine fish is perhaps surprising, because in the far more extensive field of the genetics of marine organisms as a whole a much larger proportion of the effort has gone into studies of invertebrates (see Ward, 1989). Indeed, in the past, marine invertebrate species have been used extensively as models to test various hypotheses concerning environmental and other parameters claimed to affect the genetic structure of populations (e.g. Ayala et al., 1973, 1974, 1975; Nevo, 1978; Valentine & Ayala, 1978; Ayala & Valentine, 1979; Lavie & Nevo, 1981; Noy et al., 1987; Mitton et al., 1989).

A wide range of 'molecular' techniques has been applied to fisheries genetics (reviews by Park & Moran, 1995; Ward & Grewe, 1995; Carvalho & Hauser, 1998), including allozyme electrophoresis (Beaumont & Pether, 1996; Gallardo & Carrasco, 1996; Stiles et al., 1996, review by Utter et al., 1987), mitochondrial DNA restriction analysis (Epifanio et al., 1996; Ward et al., 1997; review by Ferris & Berg, 1987), microsatellite DNA (e.g. Bentzen et al., 1996; Garcia de Leon et al., 1997; Heist, 1999, review by Wright & Bentzen, 1995), minisatellite DNA (e.g. Taggart & Ferguson, 1990; Taggart et al., 1995; Volpe & Ferguson, 1996; review by O'Reilly & Wright, 1995), random amplified polymorphic DNA (RAPD) (e.g. Bielawski & Pumo, 1997; Harding et al., 1997; Heipel et al., 1998), single-stranded conformational polymorphism (SSCP) (Li & Hedgecock, 1996) and DNA sequencing (e.g. Stepien, 1995). Of these several methods, allozymes are by far the longest established and remain generally the technique of choice in the first instance on grounds of cost combined with ease of use on large samples (Utter, 1995; Ward & Grewe, 1995), but their use is limited to fresh or frozen tissue samples. More 'modern' DNA based methods can give greater resolution and can also be used on very small (e.g. biopsy) or preserved tissue samples (Ward & Grewe, 1995). Of the DNA based methods, only RFLP analysis of mitochondrial DNA has been widely used in fisheries, but still far less than allozyme electrophoresis (Wright & Bentzen, 1995).

The applications for genetic techniques in relation to invertebrate fisheries are in many ways essentially similar to those in vertebrate (i.e. finfish) fisheries (reviews by e.g. Ryman & Utter, 1987; Carvalho & Pitcher, 1995; Utter, 1995; Carvalho & Hauser, 1998). However, there are also relative differences which lead to particular problems in the use of genetic data to study commercially important invertebrate species. Some of the main putative roles for genetics in marine fisheries, for either vertebrates or invertebrates, may be summarised as:

1. understanding the structuring of populations;
2. identification of stocks (breeding units) and units for conservation;
3. mixed stock analysis;
4. genetic effects on growth rate, survival, disease resistance or other important parameters;
5. development of strains for captive breeding.

All of these possible uses are potentially relevant to both vertebrates and invertebrates, and, of course, they are not all mutually exclusive; they are not completely discrete and in any practical application there is likely to be a degree of overlap between various of them. For example, the identification of breeding units is likely to entail understanding the structuring of populations and possibly also the identification and separation of mixed stocks, and in many cases it will be the aim that will differ rather than the methods or the type of data generated.

The last two roles listed are of relevance only during captive breeding and, therefore, are applicable to fisheries genetics only if captive bred fish or invertebrates are to be released back into the natural environment. In practice, this is only likely to occur either for the restocking of species which have become severely depleted in the wild (possibly through overfishing or by being wiped out by disease or pollution) or during the practice of what has been termed 'ranching' (e.g. Isaksson, 1988). In ranching, organisms are returned to the wild, usually at an early stage in the life cycle, and are then recaptured after a suitable time interval, when they are of a suitable size to be sold. Clearly ranching is only likely to be financially viable for species which are either sessile (e.g. most bivalves) or benthic and of very limited mobility (e.g. lobsters or a few fish species) or for species which will return to the same area at some later stage in the life cycle (e.g. to breed) as with anadromous fish (e.g. many

salmonids). Thus, ranching is particularly suitable for 'low gene flow' species, including many commercially exploited invertebrates.

Genetics and stock identification

For both vertebrate or invertebrate fisheries, the main role for genetics has been, and is likely to continue to be, the identification of groups of interbreeding individuals as the basis for a fishery. It is in this area, the identification of the breeding unit, that the genetic differences between vertebrates and invertebrates can be of practical significance. The genetic breeding unit is usually called a 'stock' in fisheries biology (this is roughly equivalent to a 'population' to a geneticist); the concept of a fishery stock has been discussed in great detail by many authors (see, e.g. Altukov, 1981; Carvalho & Hauser, 1995) and there is little point in discussing it further here.

The assumption is that within a stock (however defined), there should be genetic homogeneity, but between stocks, if these are genetically isolated, genetic divergence may occur (through e.g. drift, mutation, possible selection) with time. Models of gene flow between populations vary greatly in their assumptions, but, almost irrespective of this, a clear conclusion is that, in the absence of extreme or abnormal selective forces, even very small levels of effective migration will be sufficient to preclude genetic divergence (for brief discussion of relevant models see e.g. Maynard-Smith, 1989; reviews of various aspects of gene flow between populations by Kimura & Weiss, 1964; Slatkin, 1981, 1985, 1994, 1995). Thus, even small levels of genetic divergence between putative stocks will provide an indication of reproductive isolation.

Much genetic work on fish stocks is concerned with freshwater species, many of these salmonids, and, given the generally very geographically restricted nature of most freshwater habitats, conclusions on freshwater stock sizes are mostly not particularly relevant to marine species. In general, many marine species, whether vertebrate or invertebrate, are more likely to be constrained by biological than by geographical barriers to dispersal, except perhaps over very large distances, when physical barriers (e.g. changes in temperature) may also be relevant. In most marine fish studied, the distance over which a species is likely to disperse, and thus the geographical size of a stock, generally shows a certain uniformity, admittedly within very broad limits. Smaller or less mobile fish (e.g. smaller flatfish, anchovies) may only range a few tens of kilometres to their breeding grounds (e.g. Bembo et al., 1996), and others (e.g. coral reef or rock pool species) will be even less mobile and stocks may have a very restricted range (e.g. Larcson et al., 1989; Doherty, 1995). For a few large and very mobile fish species like swordfish (Alvarez-Bremer et al., 1995; but see also Chow et al., 1997) and tuna (Chow & Ushiama, 1995), a single unit of stock may cover very great areas or even be circumglobal. Marine fish generally, particularly those large or plentiful enough to be of commercial interest, are likely to be fairly mobile and in many cases the order of mobility is likely to be in the region we might predict from our knowledge of the biology and habits of the species. Thus, whilst very small intertidal or inshore benthic marine fish may disperse very short distances, fish likely to be of fisheries potential are mostly those with stocks ranging over areas from tens to hundreds of kilometres, with a few of the more mobile larger or migratory pelagic species covering larger distances.

However, in attempting to make genetic assessments of 'stocks' for invertebrate fisheries, we face a number of additional problems. Firstly, relative dispersal capabilities and hence presumably stock sizes show much greater variation than is found in fish. In Europe and North America, marine invertebrate ('shellfish') fisheries may be thought of as being mainly for decapod crustaceans and bivalve molluscs, but globally there are commercial marine invertebrate fisheries for species ranging from sponges to squids and including such diverse groups as sea cucumbers, barnacles, krill, octopuses, cuttlefish, sea anemones, ascidians, polychaetes, sea urchins, gastropods and jellyfish (reviews by e.g. Caddy, 1989; Thorpe & Nash, 1993). An obvious feature of many of these invertebrates is that the adult (i.e. commercial) stage of the life cycle is sessile (e.g. barnacles, sponges, ascidians) or of very limited mobility (e.g. sea anemones, sea urchins, bivalves, gastropods), with the result that often the dispersive phase of the life cycle is the larva. Other commercially exploited invertebrates (e.g. krill, jellyfish) are planktonic or nektonic and may cover very large distances, but, unlike fish, will have little control over the distance or direction of travel. Conversely, however, some of the open ocean pelagic squids are more mobile than most fish and may migrate thousands of kilometres to spawning grounds.

A major problem in assessing invertebrate stocks is that for many species we have little or no knowledge

of the biology of the larval stage; indeed for many, the larva has yet to be identified, and even where the larva has been studied and the larval life span measured (usually in the laboratory), this often does not correlate with empirical levels of genetic divergence found between populations in the natural environment (see e.g. Knowlton & Keller, 1986; Todd et al., 1988, 1998). In many marine invertebrates, genetic data indicate that there is very low mobility of both larva and adult, resulting in restricted, often only localised, dispersal. If this is the case, stock sizes are likely to be low and, therefore, stocks are far more vulnerable to overfishing than in most fish species. An additional difficulty in studying invertebrate fisheries is that genetic studies to date indicate a remarkably high incidence of cryptic speciation in marine invertebrates (Knowlton, 1993; Thorpe & Solé-Cava, 1994), sometimes even in comparatively well studied commercially important species (e.g. Smith et al., 1981; Yeatman & Benzie, 1994; Chan & Chu, 1996). Thus, although to date marine invertebrate fisheries have not received the same level of attention from geneticists as finfish fisheries, it is clear that for invertebrate fisheries it is relatively far more important to have genetic data if a fishery is to be exploited without being endangered.

Marine invertebrate fisheries

Before discussing the genetics of marine invertebrate fisheries, it is important to at least outline which types of invertebrate are commercially exploited in the sea. Since many of these fisheries, although of commercial and cultural significance where they occur, are not widely known, it is intended, here, to give greater detail of some of the more diverse invertebrates which are consumed or otherwise used commercially by man. Further detail is given in various reviews (e.g. Caddy, 1989; Thorpe & Nash, 1993; see also numerous reports by FAO).

Shellfish

As mentioned above, in western society the main marine invertebrates consumed are those groups conventionally termed ‘shellfish’; that is, various crustaceans (mainly decapods; lobsters, prawns and crabs) and bivalves and, to a lesser extent, gastropod molluscs.

Throughout most of the World, the crustaceans commercially exploited are very largely decapods and fisheries for these are found in shallow continental shelf seas in most temperate or warmer areas. Of particular significance for human consumption are various species of the prawn genus *Penaeus*, which occur in shallow waters of many of the warmer countires, but which also have been extensively transported between continents (although mainly for aquaculture rather than conventional fisheries). Numerous other prawns, shrimps, crabs and lobsters are fished worldwide.

Of potentially global significance for food or for ‘fishmeal’ production, but to date only intermittently exploited on a large scale, are the krill. Although superficially prawn like these are euphausid crustaceans, not decapods. They exist in immense biomasses, particularly in the Antarctic, where *Euphausia superba* is the main species.

Another group of crustaceans eaten by man are the barnacles (Cirripedia), various of which are exploited commercially throughout the world. For example, the large stalked barnacle *Polliceps polliceps* is eaten throughout Iberia and the Atlantic Island groups (Canaries, Madeira and Azores), acorn barnacles are consumed in Chile (*Megabalanus psittacus*) and in the Azores (*M. tintabulum*) and the goose barnacle *Mytella mytella* in Japan.

From the other main ‘shellfish’ phylum, the Mollusca, bivalves are fished almost wherever they occur in shallow waters, except for close to the poles, and a very wide variety of scallops (Pectinidae), mussels (Mytilidae), Oysters (Ostreidae) and ‘clams’ are taken. Several species of bivalve, notably *Crassostrea gigas, C. virginica, Ostrea edulis* (Ostreidae) and *Pecten maximus* (Pectinidae), have been transported to many areas of the world and, following either deliberate introduction or escapes, now occur and are fished in many of these areas. Various gastropods are eaten in numerous countries, but the species of major commercial significance are mainly abalones (*Haliotis* spp.), which are found in warm temperate and warmer waters in various parts of the world.

‘Other’ invertebrate fisheries

An increasing proportion of the more usual ‘shellfish’ are derived from aquaculture rather than capture fisheries, which, as with finfish fisheries, are suffering from depleted wild populations as a result of overfishing. Against this background of worldwide overfishing and the decline of conventional shellfish stocks, other marine invertebrates are likely to continue to increase in commercial importance. Such species are widely,

if not extensively, consumed in Europe and North America, whilst elsewhere in the world, patterns of consumption vary considerably. In various areas, particularly in the tropics, artisanal fisheries for unusual invertebrates can be locally important and in the far east there is a great demand for food species not commonly eaten in the west. One group in particular, the cephalopod molluscs (octopus, squid, cuttlefish, etc.), are currently important in terms of world catches and could become greatly more important for fisheries if the technology to exploit them can be developed (see below for further discussion).

Sponges (Porifera)

Although sponges are not used as human food, in various warmer parts of the world, particular sponge species are collected commercially, usually by divers, to be sold as bath sponges. Exploited species all have a soft elastic skeletal structure, unlike most sponges which have hard calcareous or siliceous spicules. The main species collected are *Hippospongia communis*, *Spongia officinalis*, *S. zimocca* and *S. graminea*, all of which are from the order Dictyoceratida of the class Demospongiae. In some areas, increasing prices, as supplies decline, have resulted in the virtual extinction of exploited species at diving depths.

Jellyfish and sea anemones (Cnidaria)

At least three species of jellyfish, of which *Rhopilema esculenta* is the most common, are commercially important as food in Japan. Several species of sea anemones are eaten in various countries including Japan, Samoa, France, Portugal and Italy. The intertidal *Actinia equina* and *Anemonia viridis* are eaten in Italy and France.

Marine worms (Polychaeta)

Polychaetes eaten by humans are mainly what are known as palolo worms, several species of which occur in different parts of the world. These worms have a stage in the life cycle known as a sexual epitoke, which, as part of the reproductive cycle, swarms to the surface in very large numbers at predictable times of the year. They are then collected for eating. Species consumed include the Pacific palolo (*Eunice viridis*) from Polynesia, the Wawo (*Lysidice oele*) from Indonesia, the Atlantic palolo (*Eunice schemacephala*) in the Gulf of Mexico and the Japanese palolo (*Tylorrhynchus heterochaetus*) in Japan. Also of commercial significance are various polychaetes which are dug up, or even aquacultured (Olive, 1994), for use as fishing baits (e.g. *Arenicola* spp. and *Nereis* spp. in Britain).

Ascidians (Urochordata, Ascidiacea)

All species of ascidian eaten are from the single family Cynthiidae. At least two species (*Halocynthis roretzi* and *H. aurantium*) are fished commercially by the Japanese. Ascidians of the genus *Pyura* are consumed in Chile. The French eat mainly just one species, *Microcosmus claudicans.*

Sea urchins and sea cucumbers (Echinodermata)

The sea urchins are increasingly becoming subject to commercial fisheries, primarily to satisfy the Japanese market. Two species (*Paracentrotus lividus* and *Echinus esculentus*) are traditionally eaten in some Mediterranean countries and in Ireland. Similar species are eaten in the Far East, particularly Japan, in Chile and in New Zealand. Due to increasing demand, north Atlantic species are exported to Japan, and Japanese boats have created a major sea urchin fishery in Australian waters.

The market for sea cucumbers is also mainly in Japan. The very large black species *Stichopus japonicus* is taken locally, whilst several other species are exported to Japan from various parts of the Pacific.

Cephalopods

Of the cephalopod molluscs, only species of the subclass Coleoidea are important as food for man. These include the three orders Sepioidea (cuttlefish), Teuthoidea (squids) and Octopoda (octopodes) all of which are fished commercially.

Cuttlefish Cuttlefish are almost absent from the Americas, although a few species of *Semirossia* occur along the west Atlantic coast and are fished off Argentina and in the Gulf of Mexico. Elsewhere, both large (mainly *Sepia*) and small (Sepiolidae) cuttlefish are fished in the coastal waters of most temperate and tropical latitudes. The major species fished are *Sepia officinalis* (occurs down the eastern Atlantic from northern Europe to South Africa and throughout the Mediterranean and Baltic Seas), *Sepia pharoensis* (found from the Red Sea to Japan and south to Australia), *Sepiella inermis* (occurs from the Persian Gulf to eastern Asia, fished mainly in India and Sri Lanka) and *Sepiella japonica* (Japan and China), but numerous other species are caught in smaller quantities. The tiny *Sepiola rondeleti,* which occurs from northern Europe to west Africa, is extensively eaten

in many Mediterranean countries. The major markets, even for Atlantic and Mediterranean caught cuttlefish, are in Japan and Korea.

Squid There are two suborders of squids, the Myopsida which are inshore mainly demersal squids generally confined to shallower waters near shores or on continental shelves and the Oegopsida; mostly pelagic offshore squids of deep oceanic waters, which may come onto continental shelves to spawn.

All the myopsid squids currently eaten are confined to the family Loliginidae and most are from the very large genus *Loligo*, species of which are found on continental shelves worldwide. Major fishery species are *Loligo bleekeri* (Japan), *L. chinensis* and *L. edulis* (both China to Australia), *L. duvauceli* (most of Asia and north east Africa), *L. forbesi* (Sweden to Senegal, Mediterranean, Red Sea, south east Africa), *L. gahi* (southern South America, Falkland Islands), *L. japonica* (Japan, China), *L. opalescens* (Pacific coast of North America), *L. pealii* (Newfoundland to Brazil), *L. reynaudi* (South Africa), *L. vulgaris* (Europe to South Africa, Mediterranean), *Sepioteuthis lessoniana* (Red Sea to Japan and Australia) and *Alloteuthis media* (Mediterranean).

Oceanic (oegopsid) squids form well over half of the total world cephalopod catch; a few species are demersal, but most are pelagic, although this may be at great depths. For obvious reasons, the species presently exploited commercially are generally only those occurring comparatively close to the surface. Currently, only about nine (Enoploteuthidae, Octopoteuthidae, Onychoteuthidae, Gonatidae, Psychroteuthidae, Lepidoteuthidae, Histioteuthidae, Ommastrephidae, Thysanoteuthidae) of 32 recognised families have any species fished by man, although many others have potential as food. Exploited species of major commercial significance are confined to only four families:

1. Enoploteuthidae: *Watasenia scintillans* (China, Japan);
2. Onychoteuthidae: *Onychoteuthis borealijaponica* (fished off Japan and northwest U.S.A.);
3. Gonatidae: *Berryteuthis magister* (fished off Japan and northeastern Russia); and
4. Ommastrephidae: *Illex argentinus* (southeastern South America, Falkland Islands), *I. coindetii* (fished western Mediterranean and Atlantic off Spain and North Africa), *I. illecebrosus* (fished northwest Atlantic), *Todaropsis eblanae* (fished Mediterranean and northwest Africa), *Todarodes pacificus* (northern Pacific, China to Alaska, fished by Japan), *T. sagittatus* (fished Norway, Italy), *Nototodarus gouldi* (Australia), *N. sloani* (New Zealand), *Ommastrephes bartrami* (fished northern and southern Pacific) and *Dosidicus gigas* (Chile to Mexico).

Octopuses Among the octopods, only species of the suborder Incirrata are fished commercially and of these only one (Octopodidae) of the eight families is commercially important. All the main species caught are in the widely distributed genus *Octopus*: *O. briareus* (Caribbean and northern South America), *O. conispadiceus* (Japan), *O. cyaneus* (East Africa to India and Australia), *O. dofleini* (China to southwestern U.S.A.), *O. globosus* (India), *O. maya* (Gulf of Mexico), *O. membranaceus* (India to Japan and Australia, important in Japan and China), *O. variabilis* (Japan, China), *O. vulgaris* (coastal distribution from northern Europe around Africa, including Mediterranean and Red Sea, and Asia east to Japan, also western Atlantic from U.S.A. to Brazil. Fished over most of huge range, major importance Japan, northwest Africa). As with other cephalopods, much of the world market for octopus species is in Japan. For further details of species see Voss (1983) and Roper et al. (1984).

Minor food species

Many more species and other marine invertebrate groups are, or are likely to be, eaten or otherwise exploited on a limited scale somewhere in the world, but those outlined above give some indication of the diversity of marine invertebrates of use to man. An area not discussed here, but already starting to expand, is the exploitation of species of certain phyla (e.g. sponges, bryozoans, coelenterates, ascidians, nemerteans) which have allelopathic (usually anti-predator or anti-competitor) or otherwise 'useful' biologically active chemicals of value to the pharmaceutical industry (Faulkner, 1993).

Genetics of invertebrate fisheries

Outside the conventional 'shellfish' (i.e. crustaceans and shelled molluscs) fisheries, there has been remarkably little application of genetic techniques to invertebrate fisheries or fisheries related problems. Thus, the great bulk of invertebrate groups of fisheries interest have been the subject of little or no genetic study

in relation to these fisheries. However, this lack of study is not indicative of some massive oversight, but merely follows from the small scale, often artisanal, nature of many of these fisheries and the geographical location of many of them; often far from major fisheries laboratories with genetic capabilities.

Among these 'other' invertebrates, the main exception is the cephalopods, particularly squids, which have now received a limited amount of attention from geneticists interested in actual or potential commercially important species. However, the reasons for this research are again largely financial; some cephalopod fisheries are on a large scale and hence are commercially important; also they are of commercial interest to economically developed countries like Japan, United States, Canada, New Zealand, Australia and Britain.

As outlined above, from the viewpoint of their population genetics, a key feature of many commercially important marine invertebrates is the mobility of the adult (i.e. commercial) stage of the life cycle. This may be sessile (e.g. barnacles, sponges, ascidians) or of very limited mobility (e.g. sea anemones, sea urchins, bivalves, gastropods). The adults may also be planktonic or nektonic (e.g. krill, jellyfish) and may cover very large distances, but have little control over the distance or direction of travel, or, like some of the open ocean pelagic squids, they may be more mobile than most fish and may migrate thousands of kilometres to spawning grounds.

High mobility exploited invertebrates: the cephalopods

Since they are among the most mobile of invertebrates, some similarity of population structuring might be expected between cephalopods, particularly squid, and fish. Genetic studies for stock assessment or other purposes have been carried out on many of the (mostly) long established inshore fisheries for benthic squids (largely *Loligo* spp.) (e.g. Ally & Keck, 1978; Christofferson et al., 1978; Augustyn & Grant , 1988; Carvalho & Pitcher, 1989; Garthwaite et al., 1989; Yeatman & Benzie, 1994; Brierley et al., 1995, 1996; Katugin, 1995; Izuka et al., 1996; Kang et al., 1996) and also for a number of the more recent, but now very important, oceanic (mainly ommastrephid) squid fisheries (e.g. *Nototodarus sloani* off New Zealand, Smith et al., 1981; *Martialia hyadesi* in the Antarctic Ocean, Brierley et al., 1993a; *Illex argentinus* around the Falkland Islands, Thorpe et al., 1986; Carvalho et al., 1992).

Genetic studies of octopus species are far fewer. Allcock (1997) and Allcock et al. (1997) studied gene flow in Antarctic populations of *Pareledone turqueti*, a species with only minor commercial potential and Levy et al. (1988) found cryptic speciation in *Eledone* off Brazil.

There are also several studies using molecular genetic methods to estimate divergence for systematic or other purposes in cephalopods (see e.g. Brierley & Thorpe, 1994; Brierley et al., 1996, 1997; Allcock, 1997). Almost all these molecular population studies on cephalopods have relied on allozyme studies for their data, although microsatellite markers have been developed at least for *Loligo forbesi* (Shaw, 1997).

A major feature common to many genetic studies of cephalopod, particularly squid, populations is the generally low levels of genetic variability found in most species. Polymorphism is often low in the myopsid (inshore) squid species (e.g. Brierley et al., 1995), but is even lower in a number of the offshore and more mobile oegopsid squid (Thorpe et al., 1986; Garthwaite et al., 1989). A further notable feature of the genetic structuring of oceanic squid populations is the tendency for samples showing genetic differentiation, perhaps collected in different areas or at different times, to exhibit fixed allelic differences with no heterozygous individuals present. For example, Thorpe et al. (1986) examined a number of samples of *Illex* '*argentinus'* collected sequentially over a limited period of time in the same general area to the north of the Falkland Islands. Most samples showed no genetic variation whatsoever over 30+ individuals screened for about 40 enzyme loci, yet several of the samples were clearly genetically differentiated from all others by fixed allelic differences at a small number (2–4) of loci, with a complete absence of any heterozygotes. Similar patterns of divergence have also been found, for example, between samples of *Martialia* (Brierley et al., 1993a).

Within squid species in the open oceans, it would be reasonable to expect that single stocks of these highly mobile animals might occupy very large areas. To some extent, this is the case, but there is still often genetic differentiation with various stocks of a nominate species occurring within the same large area, in the same places, but not usually at the same time. The result is that various stocks may be found to occupy broadly the same vast area of open ocean, but the migration patterns are such that these stocks do

not generally occur sympatrically and thus they are separated temporally, being found in the same place only at different times and hence maintaining spatial separation (i.e. allopatry) at any given time (see e.g. Thorpe et al., 1986; Brierley et al., 1993a).

An additional problem, again unexpected in very mobile animals occurring mainly in areas with few obvious geographical barriers, is the apparently high level of cryptic speciation in squid (e.g. Smith et al., 1981; Thorpe et al., 1986; Brierley et al., 1993a; Yeatman & Benzie, 1994). This may, however, merely reflect inadequate taxonomy in a group with few hard parts or other obvious useful taxonomic characters.

Unexpected levels of population subdivision appear to be common in squid species (see also Augustyn & Grant, 1988; Garthwaite et al., 1989; Brierley et al., 1993b, 1995, 1996; Izuka et al., 1994; Yeatman & Benzie, 1994; Katugin, 1995; Kang et al., 1996) and clearly pose problems for the management of fisheries, since, in fisheries generally, the correct identification of management units (stocks) may be considered to be the greatest single genetic problem for stock conservation (e.g. Allendorf et al., 1987; Ferguson, 1994; Ward & Grewe, 1995) and for the maintenance of evolutionarily significant units and hence the genetic diversity of species (e.g. Ryman, 1991; Bernatchez, 1994; Currens & Busack, 1995).

In squid, the correct management of stocks is essential (Smith et al., 1981), particularly since the semelparous annual life cycle of most squid leaves species highly vulnerable to population crashes, or even extinction, through overfishing. Unlike fish, squid have only one year class with the result that there are no younger cohorts developing to help a stock recover from overfishing (Bravo de Laguna, 1989). Thus, overfishing for just 1 year can exterminate a squid stock. Indeed, this may have occurred through lack of control in the early years of the Falklands fishery for *Illex argentinus*; what may have been the main genetic stock providing the fishery in 1985 was apparently absent from the fishery in 1986 (Thorpe et al., 1986). It has been suggested that for successful continuation of a fishery at least 40% of the adult population must be allowed to spawn (Patterson, 1987).

However, despite the vulnerability of single year class stocks, it is undoubtedly true that adult squid are highly mobile, particularly the oceanic species, and so are unlikely to be unduly affected by localised overfishing in a small geographic area, since most stocks will be more widely dispersed. If a stock is exploited in only part of its range, localised overfishing will probably not be serious in the longer term.

In the other, less mobile, cephalopods the scarcity of genetic data means that there is little to go on when attempting to understand how their populations may be structured. As in squid, cryptic speciation is clearly a problem in octopodids (Levy et al., 1988; Allcock, 1997). The large allozyme based study of Antarctic octopuses by Allcock (1997) shows a major complex of similar and related species of *'Pareledone'*, many apparently sympatric. How these evolved in an area with few obvious barriers to gene flow is far from clear. However, some insight is given by her detailed study of genetic differentiation of *Pareledone turqueti* populations occurring on the continental shelf areas or shelf slopes of northern part of the Scotia Arc (Allcock et al., 1997). Here, the various shelves are separated by areas of water too deep (>4000 m) for the adult octopuses, which are benthic. The species maintains panmixia over distances of hundreds of kilometres where the water is less deep, but deep water only tens of kilometres wide leads to genetic differentiation of populations, although it had been previously supposed that the larvae should be easily able to cross this distance. Recent detailed assessments of the oceanographic regime of the area now indicate that apparently minor currents may act as insurmountable barriers to larvae within what was previously supposed to be an uninterrupted stretch of open water. Hence, there is probably no gene flow between the shelf areas and the octopuses on each constitute discrete stocks.

Among octopodids and other less mobile coastal demersal cephalopods the distribution of stocks or species is likely to be largely a function of the mobility of the larva (called a paralarva in octopodids). Most are probably planktonic for a few days or more and thus will undergo pelagic dispersal, but some larger octopus paralarvae may be demersal and hence probably disperse very little (Hochberg et al., 1992). For the planktonic larvae dispersal, over tens of kilometres might be expected, with stocks being distributed over distances of this sort of order or somewhat greater.

Against expectations of only moderate larval dispersal, it is notable that among the continental shelf cephalopods are two of the most widespread non planktonic invertebrate species. *Octopus vulgaris* occurs in coastal waters from South America north to Canada, down the other side of the Atlantic from northern Europe, including the Mediterranean, to South Africa, from there north to the Red Sea and across Asia to Japan and down to Australia. The con-

tinental shelf ommastrephid squid *Todaropsis eblanae* occurs further off shore, but otherwise has an essentially similar distribution except that it is absent from the coast of the western Atlantic. There is no reason to suppose that the larvae of either of these two species travel very far, but in *Todaropsis eblanae* the adult is highly mobile, although, being coastal, it probably does not disperse over large distances or undertake the very long spawning migrations of some other ommastrephids. The huge linear coastal distribution of the species is, therefore, of note and it is difficult to believe that panmixia can be maintained. *Octopus vulgaris* with an even longer and narrower coastal distribution is truly remarkable, because the adult is of low mobility and in practice largely sedentary. It is generally territorial and moves largely by pulling itself around the sea bed by the tentacles. Swimming is largely reserved for escape from predators. High gene flow is improbable and it is difficult to envisage how a genetic structure as a single species can be maintained over a linear distribution of the order of 50 000 km. However in both of these species the huge distributions may be artifacts of overconservative taxonomy.

Planktonic invertebrate species: krill and jellyfish

As outlined above, planktonic invertebrates eaten or otherwise exploited by man are essentially just krill (euphausids) and a few species of jellyfish, consumed mainly by the Japanese. As fisheries resource, the two groups are at opposite ends of the scale; the jellyfish, although of high value, are essentially only of modest and local significance, whilst *Euphausia superba* is present in huge biomasses over much of the vast Antarctic Ocean, where it has apparently been sporadically exploited on a fairly large commercial scale by the Russians and others. It is by a substantial margin the world's largest crustacean fishery.

In open ocean planktonic species, the a priori assumption would be of high mobility and hence genetic structuring only over long distances, if at all. Attempts at genetic studies of population structure in krill are confronted by major sampling problems, largely resulting from the difficulties of sampling animals which can be difficult to find over huge and inhospitable areas, but which form swarms which can be so large (up to several cubic kilometres of densely packed krill) that subsampling also becomes highly problematic. Further problems for sampling are that swarms are generally not random aggregations, often being predominantly of one sex or age group.

For krill, as with all open water planktonic invertebrates in the Antarctic, the major unknown in their population genetics is the extent to which they may or may not cross between water bodies. It is improbable that animals like krill, salps or ctenophores can move under their own power for significant horizontal distances, and, consequently, they are more or less obliged to drift with the bodies of water in which they find themselves. However, krill probably have some control over their own buoyancy and are able to regulate the depths at which they float. By doing this, they have the potential to select currents at different depths to transport them in some 'preferred' direction. Whether they actually do this is not known.

The main water mass of the Antarctic Ocean is thought to rotate in an easterly direction about the Antarctic continent, but at a speed which would take several years for a complete circumnavigation. Thus, over an extended time scale krill and other planktonic species may be unable to avoid a high degree of genetic mixing and gene flow, with the result that all Antarctic krill may constitute a single panmictic stock. Alternatively, oceanographic data indicate the separation of water masses in different areas of the Antarctic Ocean. For example, the Weddell-Scotia confluence, which closely follows the Scotia Arc, seems to separate the body of water to the east from that immediately to the west, whilst other water bodies show rotational gyres of long duration (e.g. 1 year plus in the Weddell Sea), which presumably retain, and thus genetically isolate, planktonic species occurring within them.

Against this background, currently available genetic data are difficult to interpret in terms of population structuring in *Euphausia superba*. There are several genetic studies of krill (e.g. Ayala et al., 1975; Ayala & Valentine, 1979; Fevolden, 1984) and some have led to the conclusion that there is little or no genetic structuring and possibly just a single interbreeding population in the Antarctic (e.g. Grant, 1983; MacDonald & Schneppenheim, 1983; Schneppenheim & MacDonald, 1983; Kuehl & Schneppenheim, 1986; MacDonald et al., 1986; Fevolden & Schneppenheim, 1989). Other studies have given more equivocal results, with variation between samples, but no clear pattern of stock structuring (e.g. Fevolden, 1985) or have indicated geographical differences (e.g. Patarnello et al., 1996).

Jellyfish are the other group of planktonic organisms eaten by man. Commercially exploited jellyfish

are likely to be of at least moderate size and, since they live for considerable periods of time, widespread dispersal is likely. This hypothesis is supported by, for example, the occasional stranding of tropical jellyfish or siphonophores on temperate coasts. There appear to be no published studies of population genetic structuring for any jellyfish species, but intraspecific genetic differentiation in open ocean pelagic species is likely only over distances of hundreds, or more probably thousands, of kilometres. The dispersal of jellyfish can be further enhanced by the possible transport in the ballast water of ships (Greenberg et al., 1996). However, if stocks are to be assessed it should be borne in mind that genetic and other data indicate that cryptic speciation occurs (Brewer, 1991).

Low mobility exploited marine invertebrates: the importance of larval dispersal

The great bulk of species of marine invertebrates fished by man have adults of limited or zero mobility. However, most of these have planktonic larval stages, many of which are presumed to travel large distances away from the adult, thus allegedly effecting widespread gene dispersal. The identification of fishery stocks in such species is just one facet of what has become a major research area in marine biology – the extent of dispersal and the evolutionary role of marine invertebrate larvae.

For a number of years, a major use for genetic techniques in marine biology has been to attempt to understand how populations of marine species are structured. Clearly, if two or more populations of a species become geographically separated, they are likely to start to diverge genetically, mostly by genetic drift and sometimes by natural selection. There are numerous proposed models of gene flow between allopatric populations, but, as outlined above, a major conclusion from nearly all of these is that even very small levels of gene flow between populations are likely to greatly reduce or effectively eliminate divergence of gene frequencies under most natural conditions. Among marine invertebrates, a large proportion of the studies of genetic structuring have been carried out on temperate species, many of these intertidal or benthic shallow subtidal. In most of these the adults are either sessile (e.g. bivalves, barnacles, sponges, bryozoans) or of very limited mobility (e.g. snails, limpets, crabs, worms), with the result that, for most of them, the pelagic larva is the main dispersive phase of the life cycle. However, the potential for dispersal of the larvae is not always realised, and there have been many reported cases of high population structuring in species supposed to have long-lived planktotonic larvae (e.g. Knowlton & Keller, 1986; Todd et al., 1998).

Sponges

The Porifera (sponges) have received a moderate amount of attention from population geneticists, although not generally with any aim at stock identification (reviewed by Solé-Cava & Thorpe, 1994). From the available studies it appears that in general, as in sea anemones, levels of genetic polymorphism in sponges are very high (see Solé-Cava & Thorpe, 1991) and genetic structuring is frequently on a small scale, with species often showing clear differentiation over distances of only tens of kilometres (e.g. Benzie et al., 1994; Davis, 1996; Klautau et al., 1999).

The main implication of sponge population genetic data to date is that larval dispersal is limited and that gene pools and hence ‘stocks’ are likely to be very much localised. This is not surprising, since sponge larvae that have been studied are mostly short lived. It is, however, worrying for the future of sponge fisheries because most commercial species are thought to take a considerable time (10 years +) to reach a marketable size and, if recruitment is localised and growth is slow, fishing will need to be very carefully controlled to avoid major damage to stocks.

Sea anemones

Sea anemones are nowhere commercially very important, but they are eaten in several parts of the world. From the numerous studies of sea anemone population genetics (reviewed by, e.g. Shick, 1991; Perrin et al., 1999), it is difficult to draw many generalised conclusions about the level or geographical scale of structuring. Most species are thought to have planktonic larvae, albeit of short duration, and are therefore presumed to undergo gene dispersal. Species with little differentiation over long distances (e.g. *Oulactis mucosa* in Australia; Hunt & Ayre, 1989) are apparently rare, but the causes of the genetic variation found in most species are not always clear. Data for several species appear to show increased genetic divergence with distance and hence provide support for gene dispersal by pelagic larvae, but the rate of divergence with distance can vary markedly between closely related species or even between populations of the same

species in different areas. For example, within Britain (Solé-Cava & Thorpe, 1992) or over a European scale (Monteiro et al., 1997) the edible *Actinia equina* (*sensu* Stephenson, 1935) appears to show generally much greater genetic change with distance than the Australian *A. tenebrosa* (Ayre, 1984; Ayre et al., 1991) or the South American *A. bermudensis* (Russo et al., 1994).

To define a stock in a commercially exploited sea anemone is probably straightforward in species, like *Oulactis,* which show apparent genetic homogeneity over considerable distances, but in many species, like *Actinia equina*, this must be difficult; indeed in any organism which is clonal, or which makes extensive use of self fertilisation, the whole concept of a stock is arguably inapplicable. Other complications are that, at least at allozyme loci, levels of genetic variation are often, but not invariably, very high, (Solé-Cava & Thorpe, 1991) and cryptic species are common (see, e.g. Perrin et al., 1999).

Polychaetes

Genetic homogeneity over large distances does not seem to be characteristic of polychaete populations, although several studies indicate a lack of differentiation over 10 km or more (e.g. Abbiati & Maltagliati, 1996). However, genetic differentiation over moderate to short distances is also noted (e.g. Bristow & Vadas, 1991; Abbiati & Maltagliati, 1992). Atypical patterns of differentiation are found in *Marenzellaria*, which shows little differentiation within populations in the Baltic or in the North Sea, but clear differences between these areas (Bastrop et al., 1995; Roehner et al., 1996). These results are explained because the species is not native to Europe; the Baltic and North Sea populations have apparently been introduced from different areas of the Atlantic coast of North America (Bastrop et al., 1998).

Ascidians

There are few genetic studies of population structuring in ascidians. Available data suggest that in some species the very small tadpole larvae may be amongst the least dispersive of all free swimming marine larvae. Results for the colonial ascidian *Botryllus schlosseri* indicate genetic differentiation over short distances in European populations (Sabbadin, 1978 and that larval dispersal is typically of the order of only a metre in a population from the north eastern United States (Grosberg, 1987, 1991). In British populations of the solitary species *Dendrodoa grossularia*, distances may be even smaller (Evans, 1994), although dispersal can be as high as 1.5 km in *Ascidia mentula* (Havenhand, 1991). The implication from these very few studies is that larval dispersal and gene flow in ascidians are minimal and hence that there will be little chance of overfished stocks recruiting from elsewhere. However, wide geographical distributions of some species (e.g. *Botryllus schlosseri, Ciona intestinalis*) are surprising if dispersal is so low and may indicate an ability to raft or to undergo anthropogenic dispersal (e.g. Boyd et al., 1990). Alternatively the distributions may merely reflect inadequate resolution of conventional taxonomy (Knowlton, 1993; Thorpe & Solé-Cava, 1994).

Echinoderms

Of the several major groups of echinoderms, only the echinoids (sea urchins) and holothurians (sea cucumbers) are routinely eaten by man. Population genetic studies on echinoderms are largely confined to sea urchins and many have been carried out by the Japanese (e.g. Marcus, 1977; Matsuoka & Nakamura, 1990, 1991; Watts et al., 1990; Mladenov et al., 1997).

Very long distance dispersal probably occurs in several species; most notably in *Echinothrix diadema*, which maintains gene flow across 5400 km of very deep water, between the Eastern and Central Pacific (Lessios et al., 1998) and in the edible *Evechinus chloroticus* which is considered to maintain high levels of gene flow over distances from 250 to 2200 km (Mladenov et al., 1997). However, other species show divergence over very short distances (Minokawa et al., 1992), or apparently similar species can differ greatly in levels of dispersal. Within the widely eaten genus *Strongylocentrotus, S. lividus* is considered to show panmixia from Alaska to California (Debenham, 1997), whilst *S. purpuratus* is markedly subdivided genetically between local populations in California (Edmands et al., 1996). Both of these species have apparently similar long lived larvae.

Crustaceans

As might be expected there is a considerable literature on the population genetics of marine crustaceans. The uses of genetics in assessing crustacean stocks have been reviewed by Lavery & Keenan (1995). Numerous studies indicate that in many species genetic differentiation occurs mainly over large distances (e.g. talitrids, De Matthaeis et al., 1995; Conceição et al., 1998; barnacles, Furman et al., 1989; Ford & Mitton, 1993;

Pannacciulli et al., 1997; crabs, McMillen-Jackson et al., 1994; Lavery et al., 1995; shrimps or prawns, Mattoccia et al., 1987; Benzie et al., 1992; Staton & Felder, 1995 and lobsters, Ovenden & Brasher, 1994; Thompson et al., 1996; Harding et al., 1997), although local differentiation occurs in some species (e.g. Siberman et al., 1994; Jorstad, 1999) and predictably in those without larval dispersal (e.g. Piertney & Carvalho, 1995). Most species apparently show low diversity on a local scale (Benzie et al., 1992; De Matthaeis et al., 1995; Lavery et al., 1995), but oceanographic or other barriers to larval dispersal can disrupt gene flow (Staton & Felder, 1995). Several species are considered to show particularly long distance gene flow, for example, between various Pacific islands (Lavery et al., 1996), between Australia and New Zealand (Booth et al., 1990) and between Greece and Spain (Mattoccia et al., 1987).

Bivalves and gastropods

Marine bivalves have been widely studied over several decades by population geneticists, with the result that a large body of data is now available, much of it on commercial species (e.g. Koehn et al., 1973, 1984; Ahmad et al., 1977; Buroker, 1984; Karl & Avise, 1992; Lewis & Thorpe, 1994a,b; Patwary et al., 1994; Heipel et al., 1998). In bivalves, the adults are almost invariably sessile (a few burrowing species can move over short distances) and, therefore, only the larvae are able to disperse. In broad terms, genetic differentiation occurs only over distances of tens to hundreds of kilometres (e.g. Skibinski et al., 1978; Saavedra et al., 1987; Jarne et al., 1988; Backeljau et al., 1994; King et al., 1994) and in some cases only over very large distances. For example, Moraga et al. (1994) concluded that there was gene flow between apparently isolated *Bathymodiolus* populations at deep hydrothermal vents in different ocean basins in the west Pacific and differentiation only between west and east Pacific populations. Similarly, Meehan (1985) only found substantial differentiation between *Macoma* populations in transatlantic comparisons.

There is also the possibility that apparently homogeneous population structure may show microgeographic or year class related genetic differences when very large sample sizes are used to enhance statistical resolution (see e.g. David, 1997). Another example of this effect of sample size is from studies of populations of the commercially important scallop *Aequipecten (Chlamys) opercularis* in the northern Irish sea. This species was thought to show no genetic heterogeneity over this geographic area (Beaumont & Beveridge, 1984; Macleod et al., 1985), but the use of much larger samples revealed stable and significant, if small, allele frequency differences between stocks on a much smaller geographic scale (Lewis & Thorpe, 1994a,b).

In gastropods, few studies of population genetics are specifically directed at commercial species, although there are some data for abalone populations (e.g. Prince et al., 1987; Shepherd & Brown, 1993; Mgaya et al., 1995), whelks (Berger, 1983) and on the (locally) commercially important limpet fisheries of the Macaronesian Islands (Corte-Real et al., 1996a,b; another study of limpets by Hurst & Skibinski, 1995). Within the gastropods, the scale of genetic differentiation between populations or stocks appears generally to be related to larval type and length of larval life. Many species are thought to be very widely dispersed (e.g. Scheltema, 1986, 1989), but there are also several in which the expected larval dispersal is difficult to reconcile with the scale of genetic subdivision (e.g. Todd et al., 1988, 1998). Conversely, the littoral whelk *Bullia digitalis* shows little differentiation over large distances around the coasts of southern Africa, despite having a (lecithotrophic) larva which is apparently non planktonic (Grant & Da Silva-Tatley, 1997).

Possibilities for future exploitation of marine invertebrate stocks

Many of the world's conventional shellfish fisheries, like those for finfish, are overexploited and in decline. It is unlikely, therefore, that there is great scope for future expansion of fisheries for crabs, lobsters, prawns, bivalves or gastropods, but as fish stocks, which provide the great bulk of wild caught marine animals, appear certain to continue to decline other resources are needed.

Also, as mentioned above, there is already a certain pressure on various lower marine invertebrates, like sponges, bryozoans and ascidians, to provide biologically active natural products for the pharmaceutical industry (e.g. Higa, 1991; Higa et al., 1992; Faulkner, 1995). One such product is bryostatin, which appears to act against various cancer cells (e.g. Lilly et al., 1991; Schuchter, 1991; Berkow et al., 1993). Bryostatin is obtained from the bryozoan *Bugula neritina*, but huge quantities of the bryozoan are needed; for example Schaufelberger et al. (1991) based their work on bryostatin on a sample of l0 000 gallons

(about 45 000 kg) of *Bugula*. With collection on a large scale any small invertebrate in pharmaceutical demand may become overexploited unless aquaculture can take over (see also Olson, 1996).

Future demand for invertebrate food species will presumably depend partly on the success of the aquaculture of fish and shellfish and whether untapped sources (e.g. deep sea species) can be exploited. However, whilst most of the numerous other marine invertebrate groups are eaten little or not at all in most areas, thus apparently leaving scope for the expansion of the fisheries, most of the species within these groups are either inedible or present in only relatively small biomasses. Abundant marine invertebrates for future exploitation could be Antarctic krill (*Euphausia superba*) and oceanic squid, particularly some of the deeper living species.

Krill stocks are thought to be unnaturally high, because of the near elimination of their major predators, the larger baleen whales, and offer a potentially very great fishery resource, although of low value and palatability. However, krill are also considered the 'cornerstone' species for the whole vast Antarctic marine ecosystem and, hence, major exploitation could be a serious problem and overfishing a disaster.

The squid probably offer greater potential. They currently make a useful contribution (about 2–3% by weight) to fisheries on a global scale, but with a price much higher than most fish. Squids collectively rank (by weight of catch) as the sixth most commercially important species in world fishery statistics. Since about 1970, world catches have increased annually by an average of about 6%, but there is considered to be potential to greatly increase current landings. Estimates of stocks sizes are necessarily very approximate because there has been little or no relevant scientific study of the stocks of most squid species (see Clarke, 1977; Roper et al., 1984). Indeed, it is likely that there are still many species as yet unknown (M. R. Clarke, pers. comm.).

Evidence pointing to large untapped squid populations comes from several sources (e.g. Clarke, 1977, 1987). For a few species, there are adequate scientific data for stocks to be estimated. For example, the large (up to 150 kg) cranchid squid *Mesonychoteuthis hamiltoni* is abundant in Antarctic waters and the flesh is considered to be of excellent quality and flavour (see Voss, 1983; Roper et al., 1984). This species is not caught commercially at all, but the stock is estimated at about 90 Mmt (i.e. larger than the total annual catch of fish by man). A second example is the very large squid *Architeuthis* (Architeuthidae) which is thought to be distributed throughout all the oceans apart from close to the poles. Very few have been caught by man, but its frequent consumption by whales (identified mainly from the beaks which remain undigested in whale stomachs) and occasional stranding in shallow water suggest it is not rare. As individuals weigh up to about 1000 kg, the total biomass is likely to be huge. Current direct estimates by fishery biologists of total world squid stocks vary considerably up to about 500 Mmt, but indirect estimates from other sources indicate that even this figure may be conservative (see e.g. Voss, 1973, 1983; Clarke, 1987; Thorpe & Nash, 1993).

Studies of the squid consumed by various predators suggest very large populations. In the Antarctic penguins and elephant seals, for example, are thought to take annually about 13 Mmt and 4.5 Mmt, respectively (neither of these, incidentally, eats any of the estimated 90 Mmt of *Mesonychoteuthis hamiltoni*). Sperm whales eat mainly squid found on or near the bottom in depths restricted by their diving capabilities. Sperm whale populations have been seriously depleted by over exploitation, but even so they probably eat annually a weight of squid equivalent to about twice the entire world catch of fish by man (Clarke, 1977, 1980, 1987).

Thus various sources of evidence indicate that oceanic squids are present in very large numbers and may be present in biomasses which exceed known stocks of exploited fish species. Since most squid are thought to be annual and semelparous (they grow for a year, spawn and die), they 'turn over' faster than most fish species and thus, if well managed, should be able to sustain high rates of exploitation. As long as enough adults survive to spawn, the entire stock can be exploited, because there are no juveniles which need to be preserved for future breeding (see Patterson, 1987). However, for many of the oceanic squids the depths at which they live and our lack of knowledge of their biology and behaviour present major problems for the development of commercial fisheries. Technological advances will be necessary before most species can be caught in commercial quantities.

Conclusions

It is clear that for most invertebrate fisheries, as with finfish fisheries, the key to understanding the stock structure for fisheries purposes will lie in understand-

ing the mobility of the species. However, whereas in fish the mobility concerned is generally that of the fish that constitute the stock, in invertebrates the mobility which is critical is in most species likely to be that of the larva. This difference occurs simply because in fish the adult spawning stocks are generally likely to be the most mobile phase of the life cycle, whilst in most invertebrates the larva is far more mobile. In only a few invertebrates, like squid, is the mobile phase likely to be the adult, and even here, in some of the neritic species or the smaller benthic cuttlefish (e.g. sepiolids), it is possible that the dispersal of the pelagic larva is the main determinant of the geographical area occupied by a stock. The mobility of the adult is probably also the main factor influencing dispersal in planktonic species (e.g. krill, jellyfish), which may have little control over the magnitude or direction of their drifting.

However, in the great bulk of exploited marine invertebrate phyla the pelagic larva provides the main apparent means of gene dispersal. In various species which disperse via larvae (e.g. some molluscs, crustaceans and sea urchins; for references see above) genetic data indicate long distance dispersal (i.e. thousands of kilometres), but in many species from the same and other groups dispersal is apparently much less, and in some invertebrates with free swimming larvae (e.g. ascidians, sponges), these apparently travel short distances only. There are also, of course, numerous species without a dispersive larva. In these, the larva may be benthic, or may simply not occur, with, for example, the eggs hatching to produce a miniature adult.

When estimating the geographical area occupied by marine invertebrate 'stocks' it must be borne in mind that ideas that larvae evolved with the 'aim' of dispersal for the 'good of the species' (e.g. Hansen, 1980; Jablonski & Lutz, 1983) lead us to expect more dispersal than may occur in some (many?) species. There is still debate as to why different species have larvae and numerous putative functions have been hypothesised (reviews by many authors, e.g. Strathmann, 1980, 1985, 1990; Todd, 1985; Todd et al., 1988, 1998; Grosberg, 1992). It is not our aim to discuss in detail the 'roles' of larvae, but some of the suggestions apart from maximising dispersal are:

1. Maximising fecundity;
2. Finding more favourable habitats;
3. Reducing overcrowding and localised inbreeding;
4. Finding 'patchy' resources (e.g. space or food);
5. Tracking temporally unstable food supplies;
6. Exploiting temporally unstable substrata;
7. Exploiting the plentiful food supply in the plankton; and
8. Avoiding patchily distributed predators.

Most of these possible functions are not mutually exclusive and indeed many larvae probably achieve more than one of them, and to attempt to firmly ascribe the existence of larvae in any given species to any particular evolutionary function is possibly naive.

To further complicate the understanding of dispersal, it has become increasingly clear in recent years that in various sessile marine species long distance dispersal is achieved by means other than the regular planktonic transport of larvae. The main methods proposed are rafting on naturally occurring (e.g. wood, pumice, algae, turtles) or anthropogenic (e.g. plastics, buoys) floating substrates (e.g. Winston, 1982; Frazier et al., 1985, 1991, 1992; Highsmith, 1985; Jokiel, 1989; Smith et al., 1989; Harms, 1990; Cornelius, 1992; Helmuth et al., 1994; Worcester, 1994; Ingolfsson, 1995), or transport on the hulls or in the ballast water of ships (e.g. Carlton, 1985, 1987, 1992; Carlton & Geller, 1993; Carlton & Hodder, 1995; Pierce et al., 1997; Ruiz et al., 1997; Watts et al., 1998). In their detailed analysis of the correlates of species ranges in cheilostome Bryozoa, Watts et al. (1998) conclude that an ability to be transported by ships conveys a wider range than any likely to be achieved through the dispersive capability of the larva.

Thus, within marine invertebrates the range of dispersal strategies is vast and these can differ between closely related (e.g. congeneric) species or even between geographically separated populations of the same species. In fish estimates of genetic structuring for stock, assessment can often be made by extrapolation from earlier similar studies, but in most invertebrates stock assessments can only be made safely by treating each species and fishery as a separate entity.

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References

Abbiati, M. & F. Maltagliati, 1992. Genetic population structure of *Neanthes succinea* (Polychaeta: Nereididae). J. mar. biol. Ass. U.K. 72: 511–517.

Abbiati, M. & F. Maltagliati, 1996. Allozyme evidence of genetic differentiation between populations of *Hediste diversicolor* (Polychaeta: Nereididae) from the western Mediterranean. J. mar. biol. Ass. U.K. 76: 637–647.

Ahinad, M., D. 0. F. Skibinski & J. A. Beardinore, 1977. An estimate of the amount of genetic variability in the common mussel *Mytilus edulis*. Biochem. Genet. 15: 833–846.

Allcock, A. L., 1997. The genetics and taxonomy of Southern Ocean Octopodidae, with special reference to the genus *Pareledone*. Unpublished thesis, University of Liverpool, Port Erin, Isle of Man.

Allcock, A. L., A. S. Brierly, J. P. Thorpe & P. G. Rodhouse, 1997. Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turgueti*. Mar. Biol. 129: 97–102.

Allendorf, F., N. Ryman & F. Utter, 1987. Genetics and fishery management: past present and future. In Ryman, N. & F. Utter (eds), Population Genetics and Fishery Management. University of Washington Press, Seattle: 1–20.

Ally, J. R. R. & S. C. Keck, 1978. A biochemical genetic population structure study of market squid, *Loligo opalescens*, along the Californian coast. Calif. Fish Game 169: 113–121.

Altukov, Y. P., 1981. The stock concept from the viewpoint of population genetics. Can. J. Fish. aquat. Sci. 38: 1523–1528.

Alvarez-Bremer, J. R., J. Mejuto & B. Ely, 1995. Global population structure of the swordfish (*Xiphias gladius*) as revealed by the analysis of the mitochondrial control region. Collect. Vol. Sci. Pap. Iccat 44: 206–216.

Augustyn, C. J. & W. S. Grant, 1988. Biochemical and morphological systematics of *Loligo vulgris vulgaris* Lamark and *Loligo vulgaris reynaudi* D'Orbigny nov. comb. (Cephalopoda: Myopsida). Malacologia 29: 215–233.

Ayala, F. J. & J. W. Valentine, 1979. Genetic variability in the pelagic environment: a paradox? Ecology 60: 24–29.

Ayala, F. J., J. W. Valentine, D. Hedgecock & L. G. Barr, 1974. Deep-sea asteroids: high genetic variability in a stable environment. Evolution 29: 203–212.

Ayala, F. J., J. W. Valentine & G. S. Zuinwalt, 1975. An electrophoretic study of the Antarctic zooplankton *Euphausia superba*. Limnol. Oceanog 20: 635–640.

Ayala, F. J., G. S. Zuinwalt, D. Hedgecock & J. W. Valentine, 1973. Genetic variation in *Tridacna maxima*, an ecological analogue of some unsuccessful evolutionary lineages. Evolution 27: 177–191.

Ayre, D. J., 1984. The effects of sexual and asexual reproduction on geographic variation in the sea anemone *Actinia tenebrosa*. Gecologia 62: 222–229.

Ayre, D. J., J. Read & J. Wishart, 1991. Genetic subdivision within the eastern Australian population of the sea anemone *Actinia tenebrosa*. Mar. Biol. 109: 379–390.

Backeljau, T., P. Boucher & F. Gofas, 1994. Genetic variation, systematics and distribution of the venerid clam *Chamelea gallina*. J. mar. biol. Ass. U.K. 74: 211–223.

Bastrop, R., K. Juerss & C. Sturmbauer, 1998. Cryptic species in a marine polychaete and their independent introduction from North America to Europe. Mol. Biol. Evol. 15: 97–103.

Bastrop, R., M. Roehner & K. Juerss, 1995. Are there two species of the polychaete genus *Marenzellaria* in Europe? Mar. Biol. 121: 509–516.

Beaumont, A. R. & C. M. Beveridge, 1984. Electrophoretic survey of genetic variation in *Pecten maximus, Chlamys opercularis, C. varia* and *C. distorta* from the Irish Sea. Mar. Biol. 81: 299–306.

Beaumont, A. R. & S. M. J. Pether, 1996. Allozyme variation and gene flow between cockle *Cerastoderma edule* populations in southern United Kingdom. Fish. Res. 28: 263–275.

Bembo, D. G., G. R. Carvalho, N. Cingolani, E. Amen, G. Giannetti & T. J. Pitcher, 1996. Allozymic and morphometric evidence for two stocks of the European anchovy *Engraulis encrasicolus* in adriatic waters. Mar. Biol. 126: 529–538

Bentzen, P., C. T. Taggart, D. E. Ruzzante & D. Cook, 1996. Microsatellite polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. Can. J. Fish. aquat. Sci. 53: 2706–2721.

Benzie, J. A. H., S. Frusher & E. Bailment, 1992. Geographical variation in allozyme frequency in populations of *Penaeus monodon* (Crustacea: Decapoda). Aust. J. mar. Freshwat. Res. 43: 715–725.

Benzie, J. A. H., C. Sandusky & C. R. Wilkinson, 1994. Genetic structure of dictyoceratid sponge populations on the western Coral Sea reefs. Mar. Biol. 119: 335–345.

Berger, E. M., 1983. Population genetics of marine gastropods and bivalves. In Russell-Hunter, W. D. (ed.), The Mollusca. Academic Press, London: 563–596.

Berkow, R. L., L. Schlabach, R. Dodson et al., 1993. *In vivo* administration of the anti cancer agent bryostatin 1 activates platelets and neutrophils and modulates protein kinase activity. Cancer Res. 53: 2810–2815.

Bernatchez, L., 1994. Molecular biology techniques in fishery management: applications and perspectives. Bull. fr. Peche Piscic. 332: 1–9.

Bielawski, J. P. & D. E. Pumo, 1997. Randomly amplified polymorphic DNA (RAPD) analysis of Atlantic coast striped bass. Heredity 78: 32–40.

Booth, J. D., R. J. Street & P. J. Smith, 1990. Systematic status of the rock lobsters *Jasus edwardsii* from New Zealand and *J. novaehollandiae* from Australia. New Zealand J. mar. Freshwat. Res. 24: 239–249.

Boyd, H. C., I. L. Weissman & Y. Saito, 1990. Morphologic and genetic verification that Monterey *Botryllus* and Woods Hole *Botryllus* are the same species. Biol. Bull. 178: 239–250.

Bravo de Laguna, J., 1989. Managing an international multispecies fishery. The Saharan trawl fishery for cephalopods. In Caddy, J. F. (ed.), Marine Invertebrate Fisheries: Their Assessment and Management. Wiley, New York: 591–612.

Brewer, R. H., 1991. Morphological differences between and reproductive isolation of two populations of the jellyfish *Cyanea* in Long Island Sound, U.S.A. Hydrobiologia 216: 471–477.

Brierley, A. S., A. L. Allcock, J. P. Thorpe & R. D. Clarke, 1996. Biochemical genetic evidence supporting the taxonomic separation of *Loligo edulis* and *Loligo chinensis* (Cephalopoda: Teuthoidea) from the genus *Loligo*. Mar. Biol. 127: 97–104.

Brierley, A. S., M. R. Clarke & J. P. Thorpe, 1997. *Ctenopteryx sicula*, a bathypelagic loliginid squid? Am. malacol. Bull 12: 137–144.

Brierley, A. S., P. G. Rodhouse, J. P. Thorpe & M. R. Clarke, 1993a. Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martialia hyadesi* from the Patagonian shelf and Antarctic Polar frontal zone. Mar. Biol. 116: 593–602.

Brierley, A. S. & J. P. Thorpe, 1994. Biochemical genetic evidence supporting the taxonomic separation of *Loligo gahi* from the genus *Loligo*. Antarctic Sci. 6: 143–148.

Brierley, A. S., J. P. Thorpe, M. R. Clarke & H. Martins, 1993b. A preliminary biochemical genetic investigation of the population structure of *Loligo forbesi* Steenstrup, 1856 from the British Isles and the Azores. In Okutani, T., K. O'Dor & T. Kubodera (eds), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Shimizu City, Japan: 59–67.

Brierley, A. S., J. P. Thorpe, G. J. Pierce, M. R. Clarke & P. R. Boyle, 1995. Gene variation in the neritic squid *Loligo forbesi* (Myopsida, Loliginidae) in the Northeast Atlantic ocean. Mar. Biol. 122: 79–86.

Bristow, G. A. & R. L. Vadas, 1991. Genetic variability in bloodworm (*Glyera dibranchiata*) populations in the gulf of Maine. Mar. Biol. 109: 311–319.

Buroker, N. E., 1984. Gene flow in mainland and insular populations of *Crassostrea* (Ostreidae). Biol. Bull. 166: 550–557.

Caddy, J. F., 1989. Marine invertebrate fisheries: their assessment and management. Wiley, London.

Carlton, J. T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanog. mar. Biol. ann. Rev. 23: 313–371.

Canton, J. T., 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bull. mar. Sci. 41: 425–465.

Carlton, J. T., 1992. Introduced marine and estuarine mollusks of North America: an end of the 20th-century perspective. J. Shellfish Res. 11: 489–505.

Carlton, J. T. & J. B. Geller, 1993. Ecological roulette: the global transport of indigenous organisms. Science 261: 78–82.

Carlton, J. T. & J. Hodder, 1995. Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. Mar. Biol. 121: 721–730.

Carvalho, G. R. & L. Hauser, 1995. Molecular genetics and the stock concept in fisheries. In Carvalho, G. R. & T. J. Pitcher (eds), Molecular Genetics in Fisheries. Chapman and Hall, London: 55–79.

Carvalho, G. R. & L. Hauser, 1998. Advances in the molecular analysis of fish population structure. Ital. J. Zool. 65: 21–33.

Carvalho, G. R. & T. J. Pitcher, 1989. Biochemical genetic studies on the Patagonian squid *Loligo gahi* d'Orbigny. II. Population structure in Falkland waters using isozymes, morphometrics and life history data. J. exp. mar. Biol. Ecol. 126: 243–258.

Carvalho, G. R. & T. J. Pitcher. 1995. Molecular Genetics in Fisheries. Chapman and Hall, London.

Carvalho, G. R., A. Thompson & A. L. Stoner, 1992. Genetic diversity and population differentiation of the shortfin squid *Illex argentinus* in the south-west Atlantic. J. exp. mar. Biol. Ecol. 158: 105–121.

Chan, T. Y. & K. H. Chu, 1996. On the different forms of *Panulirus longipes femoristriga* (Von Martens, 1872) (Crustacea: Decapoda: Palinuridae), with a description of a new species. J. nat. Hist. 30: 367–387.

Chow, S., H. Okamoto, Y. Uozumi, Y. Takeuchi & H. Takeyama, 1997. Genetic stock structure of the swordfish (*Xiphias gladius*) inferred by PCR-RFLP analysis of the mitochondrial DNA control region. Mar. Biol. 127: 359–367.

Chow, S. & H. Ushiama, 1995. Global population structure of albacore (*Thunnus alalunga*) inferred by RFLP analysis of the mitochondrial ATPase gene. Mar. Biol. 123: 39–45.

Christofferson, J. P., A. Foss, W. E. Lambert & B. Welge, 1978. An electrophoretic study of select proteins from the market squid *Loligo opalescens* along the California coast. Calif. Fish. Game 169: 123–133.

Clarke, M. R., 1977. Beaks, nets and numbers. Symp. zool. Soc. Lond. 38: 89–126.

Clarke, M. R., 1980. Cephalopods in the diet of sperm whales in the southern hemisphere and their bearing on sperm whale biology. Discovery Rep. 37: 1–324.

Clarke, M. R., 1987. Biomass of cephalopods–estimation from predation. In Boyle, P. R. (ed.), Cephalopod Life Cycles. Academic Press, London: 22 1–237.

Conceição, M. B., J. D. D. Bishop & J. P. Thorpe, 1998. Genetic relationships between ecologically divergent species of talitrid amphipod (Crustacea). Mar. Ecol. Prog. Ser. 165: 225–234.

Cornelius, P. F. S., 1992. The Azores hydroid fauna and its origin, with discussion of rafting and medusa suppression. Arquipelago 10: 75–99.

Corte-Real, H. B. S. M., S. J. Hawkins & J. P. Thorpe, 1996a. An interpretation of the taxonomic relationship between the limpets *Patella rustica* and *P. piperata*. J. mar. Biol. Ass. U.K. 76: 717–732.

Corte-Real, H. B. S. M., S. J. Hawkins & J. P. Thorpe, 1996b. Population differentiation and genetic confirmation of the taxonomic status of the exploited limpet *Patella candei* in the Macaronesian islands (Azores, Madeira, Canaries). Mar. Biol. 125: 141–152.

Currens, K. P. & C. A. Busack, 1995. A framework for assessing genetic vulnerability. Fisheries 20: 24–31.

David, P., P. Mireille-Ange, P. Anne-Françoise & J. Philippe, 1997. Fine-grained spatial and temporal population genetic structure in the marine bivalve *Spisula ovalis*. Evolution 51: 1318–1322.

Davis, A. R., D. J. Ayre, M. R. Billingham, C. A. Styan & G. A. White, 1996. The encrusting sponge *Halisarca laxus*: population genetics and association with the ascidian *Pyura spinifera*. Mar. Biol. 126: 27–33.

De Matthaeis, E., M. Cobolli, M. Mattocia & F. Scapini, 1995. Geographic variation in *Talitrus saltator* (Crustacea: Amphipoda). Boll. Zool. 62: 77–84.

Debenham, P., 1997. Molecular approaches to assessing red sea urchin (*Strongylocentrotus franciscianus*) populations: Implications of sequence variation for evolution and population genetics of the species. Unpublished thesis, University of California, Santa Barbara.

Doherty, P. J., S. Planes & P. Mather, 1995. Gene flow and larval duration in seven species of fish from the great barrier reef. Ecology 76: 2373–2391.

Edmands, S., P. E. Moberg & R. S. Burton, 1996. Allozyme and mitochondrial DNA evidence of population subdivision in the purple sea urchin *Stronglylocentrotus purpuratus*. Mar. Biol. 126: 443–450.

Epifanio, J. M., J. B. Koppelman, M. A. Nedbal & D. P. Philipp, 1996. Geographic variation of paddlefish allozymes and mitochondrial DNA. Trans. am. Fish. Soc. 125: 546–561.

Evans, R., 1994. Reproduction of the unitary larvaceous ascidian *Dendrodoa grossularia*. Unpublished thesis. University of Liverpool, Port Erin, Isle of Man.

Faulkner, D. J., 1993. Academic chemistry and the discovery of bioactive marine natural products. In Attaway, D. H. & O. R. Zaborsky (eds), Marine Biotechnology – Pharmaceutical and Bioactive Natural Products. Plenum Press, New York: 459–474.

Faulkner, D. J., 1995. Marine natural products. Natur. Product Rep. 12: 223–269.

Ferguson, A., 1994. Molecular genetics and fisheries: Current and future perspectives. Rev. Fish Biol. Fish. 4: 389–392.

Ferris, S. D. & W. J. Berg, 1987. The utility of mitochondrial DNA in fish genetics and fishery management. In Ryman, N. & F. Utter (eds), Population Genetics and Fishery Management. University of Washington Press, Seattle: 277–300.

Fevolden, S. E., 1984. Biotic and physical environmental impact on genetic variation of krill. J. Crust. Biol. 4: 206–223.

Fevolden, S. E., 1985. Genetic variation of *Euphausia superba* Dana in the Antarctic Peninsula waters. Sarsia 71: 169–175.

Fevolden, S. E. & R. Schneppenheim, 1989. Genetic homogeneity of krill (*Euphausia superba* Dana) in the Southern Ocean. Polar Biol. 9: 533–539.

Ford, M. J. & J. B. Mitton, 1993. Population structure of the pink barnacle, *Tetraclita squamosa rubescens*, along the California coast. Mol. mar. Biol. Biotechnol. 2: 147–153.

Frazier,J. G. et al., 1985. Epizoan communities on marine turtles. 1. Bivalve and gastropod mollusks. Mar. Ecol. 2: 127–140.

Frazier, J. G., I. Goodbody & C. Ruckdeschel, 1991. Epizoan communities on marine turtles. 2. Tunicates. Bull. mar. Sci. 48: 763–765.

Frazier, J. G., J. E. Winston & C. Ruckdeschel, 1992. Epizoan communities on marine turtles. 3. Bryozoa. Bull. mar. Sci. 52: 1–8.

Furman, E. R., A. B. Yule & D. J. Crisp, 1989. Gene flow between populations of *Balanus improvisus* Darwin (Cirripedia) in British estuaries. Sci. mar. 53: 465–472.

Gallardo, M. H. & J. I. Carrasco, 1996. Genetic cohesiveness among populations of *Concholepas concholepas* (Gastropoda, Muricidae) in southern Chile. J. exp. mar. Biol. Ecol. 197: 237–249.

Garcia de Leon, F. J., L. Chikhi & F. Bonhomme, 1997. Microsatellite polymorphism and population subdivision in natural populations of European sea bass *Dicentrarchus labrax* (Linnaeus, 1758). Mol. Ecol. 6: 51–62.

Garthwaite, R. L., C. J. Berg & J. Harrigan, 1989. Population genetics of the common squid *Loligo pealei* Le Seur, 1821, from Cape Cod to Cape Hatteras. Biol. Bull. 177: 287–294.

Grant, W. S., 1983. Population genetics of krill and comparison with other marine organisms. Polar Res. 4: 246–266.

Grant, W. S. & F. M. Da Silva-Tatley, 1997. Lack of genetically subdivided population structure in *Bullia digitalis* a South African gastropod with lecithotrophic development. Mar. Biol. 129: 123–137.

Greenberg, N., R. L. Garthwaite & D. C. Potts, 1996. Allozyme and morphological evidence for a newly introduced species of *Aurelia* in San Francisco Bay, California. Mar. Biol. 125: 401–410.

Grosberg, R. K., 1987. Limited dispersal and proximity dependent mating success in the colonial ascidian *Botryllus schlosseri*. Evolution 41: 130–142.

Grosberg, R. K., 1991. Sperm-mediated gene flow and the genetic structure of a population of the colonial ascidian *Botryllus schlosseri*. Evolution 45: 130–142.

Grosberg, R. K., 1992. For adults only? Supply side ecology and the history of larval biology. Trends Ecol. Evol. 7: 130–133.

Hansen, T. A., 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. Paleobiology 6: 193–207.

Harding, G. C., E. L. Kenchington, C. J. Bird, D. S. Pezzack & D. C. Landry, 1997. Genetic relationships among subpopulations of the American lobster (*Homarus americanus*) as revealed by random amplified polymorphic DNA. Can. J. Fish. aquat. Sci. 54: 1762–1771.

Harms, J., 1990. Marine plastic litter as an artificial hard bottom fouling ground. Helg. Meer. 44: 503–506.

Havenhand, J. N., 1991. Fertilisation and the potential for dispersal of gametes and larvae in the solitary ascidian *Ascidia mentula*. Ophelia 33: 1–15.

Heipel, D. A., J. D. D. Bishop, A. R. Brand & J. P. Thorpe, 1998. Population genetic differentiation of the great scallop *Pecten maximus* in western Britain investigated by randomly amplified polymorphic DNA. Mar. Ecol. Prog. Ser. 162: 163–171.

Heist, E. J. & J. R. Gold, 1999. Microsatellite DNA variation in sandbar sharks (*Carcharhinus plumbeus*) from the Gulf of Mexico and mid-Atlantic Bight. Copeia 1999: 182–186

Helmuth, B., R. R. Veit & R. Holberton, 1994. Long-distance dispersal of a subantartic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. Mar. Biol. 120: 421–426.

Higa, T., 1991. Bioactive phenolics and related compounds. Bioorg. mar. Chem. 4: 33–90.

Higa, T. et al., 1992. Miyakolide: a bryostain like macrolide from a sponge, *Polyfibrospongia* sp. J. am. chem. Soc. 114: 7587–7588.

Highsmith, R. C., 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Mar. Ecol. Prog. Ser. 25: 169–175.

Hochberg, E. G., M. Nixon & R. B. Toll, 1992. Octopoda. Smiths. Contr. Zool. 513: 213–280.

Hunt, A. & D. J. Ayre, 1989. Population structure in the sexually reproducing sea anemone *Oulactis muscosa*. Mar. Biol. 102: 537–544.

Hurst, C. D. & D. O. F. Skibinski, 1995. Comparison of allozyme and mitochondrial DNA spatial differentiation in the limpet *Patella vulgata*. Mar. Biol. 122: 257–263.

Ingolfsson, A., 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Mar. Biol 122: 13–21.

Isaksson, A., 1988. Salmon ranching: a world review. Aquaculture 75: 1–33.

Izuka, T., S. Segawa & T. Okutani, 1996. Biochemical study of the population heterogeneity and distribution of the oval squid *Sepioteuthis lessoniana* complex in southwestern Japan. Am. malacol. Bull. 12: 129–135.

Izuka, T., S. Segawa, T. Okutani & K. Namuchi, 1994. Evidence on the existence of three species of the oval squid *Sepioteuthis lessoniana* complex in Ishigaki Islands, Okinawa, south west Japan. Jap. J. Malacol. 53: 217–228.

Jablonski, D. & R. A. Lutz, 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58: 21–89.

Jane, P., P. Berrebi & 0. Guelorget, 1988. Genetic and morphological variability of five populations of the clam *Ruditapes decussatus* (Mollusca: Bivalvia). Oceanol. Acta 11: 401–407.

Jokiel, P. L., 1989. Rafting of reef corals and other organisms at Kwajalein Atoll. Mar. Biol 101: 483–493.

Jorstad, K. E. F. E., 1999. Population genetic structure of lobster (*Homarus gammarus*) in Norway, and implications for enhancement and sea-ranching operation. Aquaculture 173: 447.

Kang, Y. J., Y. H. Kim, Y. K. Hong, J. Y. Park & K. Y. Park, 1996. A population genetic analysis of the common squid, *Todarodes pacificus* Steenstrup in the Korean waters. J. korean Fish. Soc. 29: 320–331.

Karl, S. A. & J. C. Avise, 1992. Balancing selection at allozyme loci in oysters: implications from nuclear RFLPs. Science 256: 100–102.

Katugin, 0. N., 1995. Genetic differentiation in *Berryteuthis magister* from the North Pacific. In Aiken, D. E., S. L. Waddy & G. Y. Conan (eds), Shellfish Life Histories and Shell-Fishery Models. ICES, Copenhagen: 459–467.

Kimura, M. & G. H. Weiss, 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49: 561–576.

King, T. L., R. Ward & E. G. Zimmerman, 1994. Population structure of eastern oysters (*Crassostrea virginica*) inhabiting the Laguna Madre, Texas and adjacent bay systems. Can. J. Fish. aquat. Sci. 51: 215–222.

Klautau, M., C. A. M. Russo, C. Lazoski, N. Boury-Esnault, J. P. Thorpe & A. M. Solé-Cava, 1999. Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula*. Evolution (in press).

Knowlton, N., 1993. Sibling species in the sea. Ann. Rev. Ecol. Syst. 24: 189–216.

Knowlton, N. & B. D. Keller, 1986. Larvae which fall far short of their potential: highly localized recruitment in an alphaeid shrimp with extended larval development. Bull. mar. Sci. 39: 213–223.

Koehn, R. K., J. G. Hall, D. J. Innes & A. J. Zera, 1984. Genetic differentiation of *Mytilus edulis* in eastern North America. Mar. Biol 79: 117-126.

Koehn, R. K., F. J. Turano & J. B. Mitton, 1973. Population genetics of marine pelecypods. II. Genetic differences in microhabitats. Evolution 27: 100–105.

Kuehl, S. & R. Schneppenheim, 1986. Electrophoretic investigation of genetic variation in two krill species *Euphausia superba* and *E. crvstallorophias* (Euphausiidae). Polar Biol. 6: 17–23.

Larcson, J. M., V. M. Riccardi, S. W. Calhoun & D. C. Morizot, 1989. Genetic differentiation of bicolor damselfish (*Eupomacentrus partitus*) populations in the Florida Keys. Mar. Biol. 103: 445–451.

Lavery, S. & C. Keenan, 1995. Genetic analyses of crustacean stock structure and stock size. In Courtney, A.J. & M. G. Cosgrove (eds), Proceedings of the Workshop on Spawning Stock Recruitment Relationships. Department of Primary Industries, Brisbane, Australia: 116–121.

Lavery, S., C. Moritz & D. R. Fielder, 1995. Changing patterns of population structure and gene flow at different spatial scales in *Birgus latro* (the coconut crab). Heredity 74: 531–541.

Lavery, S., C. Moritz & D. R. Fielder, 1996. Indo-Pacific population structure and evolutionary history of the coconut crab *Birgus latro*. Mol. Ecol. 5: 557–570.

Lavie, B. & E. Nevo, 1981. Genetic diversity in marine molluscs: A test of the niche-width variation hypothesis. Mar. Ecol. 2: 335–342.

Lessios, H. A., B. D. Kessing & D. R. Robertson, 1998. Massive gene flow across the world's most potent marine biogeographical barrier. Proc. r. Soc. Lond. B 265: 583–588.

Levy, J. A., M. Haimovici & M. Conceição, 1988. Genetic evidences for two species to the genus *Eledone* (Cephalopoda: Octopodidae) in south Brazil. Comp. Biochem. Physiol. 90B: 275–277.

Lewis, R. I. & J. P. Thorpe, 1994a. Are queen scallops, *Aequipecten (Chlamys) opercularis* (L.), self recruiting? Can. tech. Rep. Fish. aquat. Sci. 1994: 214–221.

Lewis, R. I. & J. P. Thorpe, 1994b. Temporal stability of gene frequencies within genetically heterogeneous populations of the queen scallop *Aeguipecten (Chlamys) opercularis*. Mar. Biol. 121: 117–126.

Li, G. & D. Hedgecock, 1996. Mitochondrial DNA variation within and among larval cohorts of Pacific oyster, *Crassostrea gigas*, detected by PCR-SSCP analysis. J. Shellfish Res. 15: 511–512.

Lilly, M., C. Brown, G. Pettit & A. Kraft, 1991. Bryostatin 1: a potential anti leukemic agent for chronic myelomonocytic leukemia. Leukemia 5: 283–287.

MacDonald, C. M. & R. Schneppenheim, 1983. Breeding structure and stock identity in the Antarctic krill *Euphausia superba* Dana. Polar Res. 4: 240–245.

MacDonald, C. M., R. Williams & M. Adams, 1986. Genetic variation and population structure of krill (*Euphausia superba* Dana) from the Prydz Bay region of Antarctic waters. Polar Biol. 6: 233–236.

Macleod, J. A. A., J. P. Thorpe & N. A. Duggan, 1995. A biochemical genetic study of queen scallop *Chlamys opercularis*) stocks in the northern Irish Sea. Mar. Biol. 87: 77–82.

Marcus, N. H., 1977. Genetic variation within and between geographically separated populations of the sea urchin *Arabacea punctulata*. Biol. Bull. 153: 560–570.

Matsuoka, N. & Y. Nakamura, 1990. Enzyme variation within the population of the sea urchin *Glyptocidaris crenularis* from Japanese waters. Comp. Biochem. Physiol 96B: 335–338.

Matsuoka, N. & Y. Nakamura, 1991. Genetic distance and protein polymorphism in two sea urchin species of the order Arabacioidea and implications for their evolution. Comp. Biochem. Physiol. 98B: 21–27.

Mattoccia, M., G. La Rosa, E. De Mathaeis, M. Cobolli-Sbordoni & V. Sbordoni, 1987. Patterns of genetic variation and differentiation in Mediterranean populations of *Penaeus kerathurus* (Crustacea: Decapoda). In, Tiews, K. (ed.), Selection, Hybridisation and Genetic Engineering in Aquaculture. ICES, Copenhagen: 131–142.

Maynard-Smith, J., l989. Evolutionary Genetics. Oxford University Press, New York.

McMillen-Jackson, A. L., T. M. Bert & P. Steele, 1994. Population genetics of the blue crab *Callinectes sapidus*: modest population structuring in a background of high gene flow. Mar. Biol. 118: 53–65.

Meehan, B. W., 1985. A genetic comparison of *Macoma balthica* from San Francisco Bay (California) and Coos Bay (Oregon), U.S.A. J. Shellfish Res. 7: 170.

Mgaya, Y. D., E. M. Gosling, J. P. Mercer & J. Donlon, 1995. Genetic variation at three polymorphic loci in wild and hatchery stocks of the Abalone, *Haliotis tuberculata* Linnaeus. Aquaculture 136: 71–80.

Minokawa, T., S. Amemiya & N. Matsuoka, 1992. Genetic variation and differentiation in two local Japanese populations of the sea urchin *Asthenosoma ijimai*: electrophoretic analysis of isozymes. Zool. Sci. 9: 1299.

Mitton, J. B., C. J. Berg, Jr. & K. S. Orr, 1989. Population structure, larval dispersal and gene flow in the queen conch, *Strombus gigas*, of the Caribbean. Biol. Bull. 177: 356–362.

Mladenov, P. V., R. M. Allibone & G. P. Wallis, 1997. Genetic differentiation in the New Zealand sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea). New Zealand J. mar. Freshwat. Res. 31: 261–269.

Monteiro, F. A., A. M. Solé-Cava & J. P. Thorpe, 1997. Extensive genetic divergence between populations of the common intertidal sea anemone *Actinia equina* from Britain, the Mediterranean and the Cape Verde Islands. Mar. Biol. 129: 425–433.

Moraga, D., D. Jollivet & F. Denis, 1994. Genetic differentiation across the west Pacific populations of the hydrothermal vent bivalve *Bathymodiolus* sp. and the east pacific population of *Bathymodiolus thermophilus*. Deep Sea Res. 41: 1551–1557.

Nevo, E., 1978. Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. 13: 121–177.

Noy, R., B. Lavie & E. Nevo, 1987. The niche-width variation hypothesis revisited: genetic diversity in the marine gastropods *Littorina punctata* (Ginelin) and *L. neritoides* (L.). J. exp. mar. Biol. Ecol. 109: 109–116.

Olive, P. J. W., 1994. Polychaeta as a world resource: a review of patterns of exploitation as a sea angling bait and the potential for aquaculture based production. Mem. Mus. natn. Hist. nat., Paris 162: 603–610.

Olson, S. G., 1996. Curing cancer through aquaculture. Sea Technol. 37: 89–94.

O'Reilly, P. & J. M. Wright, 1995. The evolving technology of DNA fingerprinting and its application to fisheries and aquaculture. J. Fish Biol. 47: 29–55.

Ovenden, J. R. & D. J. Brasher, 1994. Stock identity of the red (*Jasus edwardsii*) and green (*J. verreauxi*) rock lobsters inferred from mitochondrial DNA analysis. In Philips, B. F., J. S. Cobb & J. Kittaka (eds), Spiny Lobster Management. Blackwell, London: 230–249.

Pannacciulli, F. G., J. D. D. Bishop & S. J. Hawkins, 1997. Genetic structure of populations of two species of *Chthamalus* in the north east Atlantic and Mediterranean. Mar. Biol. 128: 73–82.

Park, L. K. & P. Moran, 1995. Developments in molecular genetic techniques in fisheries. In Carvalho, G. R. & T. J. Pitcher (eds), Molecular Genetics in Fisheries. Chapman and Hall, London: 1–28.

Patarnello, T., L. Bargelloni, V. Varotto & B. Battaglia, 1996. Krill evolution and the Antarctic ocean currents: evidence of vicariant specification as inferred by molecular data. Mar. Biol. 126: 603–608.

Patterson, K. R., 1987. Fishy events in the Falklands. New Scientist 1562: 44–48.

Patwary, M. U., E. L. Kenchington, C. J. Bird & E. Zouros, 1994. The use of random amplified polymorphic DNA markers in genetic studies of the sea scallop *Placopecten magellanicus* (Gmellin, 1791). J. Shellfish Res. 13: 547–553.

Perrin, M. C., J. P. Thorpe & A. M. Solé-Cava, 1999. *Actinia equina*: a genetic role model and reproductive enigma. Oceanogr. mar. Biol. ann. Rev. (in press).

Pierce, R. W., J. T. Carlton, D. A. Carlton & J. B. Geller, 1997. Ballast water as a vector for tintinnid transport. Mar. Ecol. Prog. Ser. 149: 295–297.

Piertney, S. B. & G. R. Carvalho, 1995. Microgeographical genetic differentiation in the intertidal isopod *Jaera albifrons*. 2. Temporal variation in allele frequencies. J. exp. mar. Biol. Ecol. 188: 277–288.

Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot, 1987. Experimental evidence or limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). J. exp. mar. Biol. Ecol. 106: 243–263.

Roehner, M., R. Bastrop & K. Juerss, 1996. Colonization of Europe by two American genetic types or species of the genus *Marenzelleria* (Polychaeta: Spionidae). An electrophoretic analysis of allozymes. Mar. Biol. 127: 277–287.

Roper, C. F. E., M. J. Sweeney & C. E. Naun, 1984. FAO species catalogues. Vol 3. Cephalopods of the world. An annotated and illustrated guide to species of interest to fisheries. FAO, Rome.

Ruiz, G. M., J. T. Carlton, E. D. Grosholz & A. H. Hines, 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. Am. Zool. 6: 621–632.

Russo, C. A. M., A. M. Solé-Cava & J. P. Thorpe, 1994. Population structure and genetic variation in two tropical sea anemones (Cnidaria, Actinidae) with different reproductive strategies. Mar. Biol. 119: 267–276.

Ryman, N., 1991. Conservation genetics considerations in fishery management. J. Fish Biol. 39: 211.

Ryman, N. & F. Utter, 1987. Population genetics and fishery management. Washington University Press, Seattle, Washington.

Saavedra, C., C. Zapata, A. Guerra & G. Alvarez, 1987. Genetic structure of populations of the flat oyster *Ostrea edulis*) from the north west of the Iberian Peninsula. Inv. Pesq. 51: 225–241.

Sabbadin, A., 1978. Genetics of the colonial ascidian *Botryllus schlosseri*. In Battaglia, B. & J. A. Beardinore (eds), Marine Organisms, Genetics Ecology and Evolution. Plenum Press, New York: 195–207.

Schaufelberger, D. E. et al., 1991. The large scale isolation of bryostatin 1 from *Bugula neritina* following current good manufacturing processes. J. nat. Prod. 54: 1265–1270.

Scheltema, R. S., 1986. Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among central Pacific islands. Bull. mar. Sci. 39: 241–256.

Scheltema, R. S., 1989. Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. In Ryland, J. S. & P. A. Tyler (eds), Reproduction, Genetics and Distribution of Marine Organisms. Olsen & Olsen, Fredensborg, Denmark: 183–188.

Schneppenheim, R. & M. MacDonald, 1983. Population genetics of krill (*Euphausia superba*. Polar Res.4: 439.

Schuchter, R. L. et al., 1991. Successful treatment of murine melanoma with bryostatin 1. Cancer Res. 51: 682–687.

Shaw, P. W., 1997. Polymorphic microsatellite markers in a cephalopod: the veined squid *Loligo forbesi*. Mol. Ecol. 6: 297–298.

Shepherd, S. A. & L. D. Brown, 1993. What is an abalone stock–Implications for the role of refugia in conservation. Can. J. Fish. aquat. Sci. 50: 2001–2009.

Shick, J. M. 1991. A Functional Biology of Sea Anemones. Chapman & Hall, London.

Siberman, J. D., S. K. Shaver & P. J. Walsh, 1994. Mitochondrial DNA variation in seasonal cohorts of spiny lobster (*Panulirus argus*) post larvae. Mol. mar. Biol. Biotechnol. 3: 165–170.

Skibinski, D. O. F., M. Ahmad & J. A. Beardmore, 1978. Genetic evidence for naturally occurring hybrids between *Mytilus edulis* and *Mytilus galloprovincialis*. Evolution 32: 354–364.

Slatkin, M., 1981. Estimating levels of gene flow in natural populations. Genetics 99: 323–335.

Slatkin, M., 1985. Gene flow in natural populations. Ann. Rev. Ecol. Syst. 16: 393–430.

Slatkin, M., 1994. Gene flow and population structure. In Real, L. A. (ed.), Ecological Genetics. Princeton University Press, Princeton, New Jersey: 3–17.

Slatkin, M., 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics 139: 457–462.

Smith, J. M. B., P. Rudall & P. E. Keage, 1989. Driftwood on Heard Island. Polar Rec. 25: 223–228.

Smith, P. J., P. E. Roberts & R. J. Hurst, 1981. Evidence for two species of arrow squid in the New Zealand fishery. New Zealand J. mar. Freshwat. Res. 15: 247–253.

Solé-Cava, A. M. & J. P. Thorpe, 1991. High levels of genetic variation in natural populations of marine lower invertebrates. Biol. J. linn. Soc. 44: 65–80.

Solé-Cava, A. M. & J. P. Thorpe, 1992. Genetic divergence between colour morphs in populations of the common intertidal sea anemones *Actinia equina* and *A. prasina* (Anthozoa: Actiniaria) in the Isle of Man. Mar. Biol. 112: 243–252.

Solé-Cava, A. M. & J. P. Thorpe, 1994. Evolutionary genetics of marine sponges. In Van Soest, R. W. M., T. M. G. Van Kempen & J. C. Braekman (eds), Sponges in Time and Space. A. A. Balkema, Rotterdam: 55–63.

Staton, J. L. & D. L. Felder, 1995. Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea, Decepoda, Thalassinoidea) in the Western Atlantic and Gulf of Mexico. Bull. mar. Sci. 56: 523–536.

Stepien, C. A., 1995. Population genetic divergence and geographic patterns from DNA sequences: examples from marine and freshwater fishes. Am. Fish. Soc. Symp. 17: 263–287.

Stiles, S., J. Choromanski, D. Schweitzer & Q. Z. Xue, 1996. Preliminary investigations of genetics and breeding of the bay scallop, *Argopecten irradians*. J. Shellfish Res. 15: 461.

Strathmann, R. R., 1980. Why does a larva swim so long? Paleobiology 6: 373–376.

Strathmann, R. R., 1985. Feeding and nonfeeding larval development and life history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16: 339–361.

Strathmann, R. R., 1990. Why life histories evolve differently in the sea. Am. Zool. 30: 197–207.

Taggart, J. B. & A. Ferguson, 1990. Minisatellite DNA fingerprints of salmonid fishes. Anim. Genet. 21: 377–389.

Taggart, J. B., E. Verspoor, P. T. Galvin, P. Moran & A. Ferguson, 1995. A minisatellite DNA marker for discriminating between European and North-American Atlantic salmon (*Salmo salar*). Can. J. Fish. aquat. Sci. 52: 2305–2311.

Thompson, A. P., J. R. Hanley & M. S. Johnson, 1996. Genetic-structure of the western rock lobster *Panulirus cygnus*, with the benefit of hindsight. Aust. J. mar. freshwat. Res. 47: 889–896.

Thorpe, J. P., J. N. Havenhand & K. R. Patterson, 1986. Report of the University of Liverpool (Department of Marine Biology) to the Falkland Islands Development Corporation on stock and species identities of Patagonian Shelf *Illex*. Falkland Islands Development Corporation, Port Stanley, Falkland Islands.

Thorpe, J. P. & R. D. M. Nash, 1993. Other invertebrates used as food. In Macrae, R. R. Robinson & M. Sadler (eds), Encyclopaedia of Food Science, Food Technology and Nutrition. Academic Press, London: 2898–2902.

Thorpe, J. P. & A. M. Solé-Cava, 1994. The use of allozyme electrophoresis in invertebrate systematics. Zool. Scr. 23: 3–18.

Todd, C. D., 1985. Settlement timing hypothesis: a reply to Grant and Williamson. Mar. Ecol. Prog. Ser. 23: 197–202.

Todd, C. D., J. N. Havenhand & J. P. Thorpe, 1988. Genetic differentiation, pelagic larval transport and gene flow between local populations of the intertidal marine mollusc *Adalaria proxima* (Alder & Hancock). Funct. Ecol. 2: 441–451.

Todd, C. D., W. J. Lambert & J. P. Thorpe, 1998. The genetic structure of intertidal populations of two species of nudibranch molluscs with planktotrophic and pelagic lecithotrophic larval stages: are pelagic larvae 'for' dispersal? J. exp. mar. Biol. Ecol. 228: 1–28.

Utter, F. M., 1995. Perspective of molecular genetics and fisheries into the 21st century. In Carvalho, G. R. & T. J. I. Pitcher (eds), Molecular Genetics in Fisheries. Chapman and Hall, London: 105–109.

Utter, F. M., P. Aebersold & G. Winans, 1987. Interpreting genetic variation detected by electrophoresis. In Ryman, N. & F. Utter (eds), Population Genetics and Fishery Management. University of Washington Press, Seattle: 21–46.

Valentine, J. W. & F. J. Ayala, 1978. Adaptive strategies in the sea. In Battaglia, B. & J. A. Beardmore (eds), Marine Organisms: Genetics, Ecology and Evolution. Plenum Press, New York: 323–345.

Volpe, J. P. & M. M. Ferguson, 1996. Molecular genetic examination of the polymorphic Arctic charr *Salvelinus alpinus* of Thingvallavatn, Iceland. Mol. Ecol. 5: 763–772.

Voss, G. L. 1973. Cephalopod resources of the world. FAO, Rome.

Voss, G. L., 1983. Review of cephalopod fishery biology. Mem. natl. Mus. Vic. 44: 229–241.

Ward, R. D., 1989. Molecular population genetics of marine organisms. In Ryland, J. S. & P. A. Tyler (eds), Reproduction, Genetics and Distribution of Marine Organisms. Olsen and Olsen, Fredensborg, Denmark: 235–249.

Ward, R. D., N. G. Elliott, B. H. Innes, A. J. Smolenski & P. M. Grewe, 1997. Global population structure of yellowfin tuna, *Thunnus albacares*, inferred from allozyme and mitochondrial DNA variation. Fish. Bull. 95: 566–575.

Ward, R. D. & P. M. Grewe, 1995. Appraisal of molecular genetic techniques in fisheries. In Carvalho, R. & T. J. Pitcher (eds), Molecular Genetics in Fisheries. Chapman and Hall, London: 29–54.

Watts, P. C., J. P. Thorpe & P. D. Taylor, 1998. Natural and anthropogeneic dispersal mechanisms in cheilostomatid Bryozoa. Phil. Trans. r. Soc., Lond. B 353: 453–464.

Watts, R. J., M. S. Johnson & R. Black, 1990. Effects of recruitment on genetic patchiness in the urchin *Echinometra mathaei* in Western Australia. Mar. Biol. 105: 145–151.

Winston, J. E., 1982. Drift plastics–an expanding niche for a marine invertebrate? Mar. Pollut. Bull. 13: 348–351.

Worcester, S. E., 1994. Adult rafting versus larval swimming: dispersal and recruitment of a botryllid ascidian on eelgrass. Mar. Biol. 121: 309–317.

Wright, J. M. & P. Bentzen, 1995. Microsatellites: genetic markers for the future. In Carvalho, G. R. (ed.), Molecular Genetics in Fisheries. Chapman & Hall, London: 117–121.

Yeatman, J. & J. A. H. Benzie, 1994. Genetic structure and distribution of *Photololigo* spp. in Australia. Mar. Biol. 118: 79–87.