Exploited marine invertebrates: genetics and fisheries

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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 geneticists 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, admit-tedly 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. Larsson 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 & Ushiam, 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 fishin 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 countries, 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.

‘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 (*Tylohrynchus 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).

**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 pharaonis* (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 rondeletii*, which occurs from northern Europe to west Africa, is extensively eaten in Japan.
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. davaucelli (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), 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 eblanee (fished Mediterranean and northwest Africa), Todarodes pacificus (northern Pacific, China to Alaska, fished by Japan), T. sagitatus (fished Norway, Italy), Nototodarus gouldi (Australia), N. sloani (New Zealand), Ommastrephes bartramii (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. dolfeini (China to southwestern U.S.A.), O. globosus (India), O. maya (Gulf of Mexico), O. membrandaceus (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.
Loligo (largely long established inshore fisheries for benthic squids) poses have been carried out on many of the (mostly) fish. Genetic studies for stock assessment or other purposes in cephalopods, particularly squid, might be expected between cephalopods, particularly squid, and some similarity of population structuring might be expected. Since they are among the most mobile of invertebrates, 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 cover 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 allosemmy 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 tranquii 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 pannixia 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 larval 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-
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 & Schnepenheim, 1983; Schnepenheim & MacDonald, 1983; Kuehl & Schnepenheim, 1986; MacDonald et al., 1986; Fevolden & Schnepenheim, 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. tenuis (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 Marenzelleria, 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).

Ascidiants

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 Echinolthrix 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 Matteaies et al., 1995; Conceição et al., 1998; barnacles, Furman et al., 1989; Ford & Mitton, 1993;
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.

Bivalve and gastropod populations 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).

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 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 10,000 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. sepioiids), 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 unstable 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; Worchester, 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


