

disease or parasitism should also be measured, and used by management. Dealing with such multi-indicator situations is not easy, and Caddy (1999a) suggests the use of a traffic light approach as one way of better representing multiple indicators broken down in the PSIR format, or in terms of “population characteristics” (see Annex I).

3. METAPOPOPULATIONS, NATURAL STOCK REGENERATION AND SPATIALLY EXPLICIT MANAGEMENT TOOLS

3.1 Metapopulations

Requirements for determination of a SRR include that the population under study must be more or less discrete both geographically and biologically (i.e. a stock needs to be defined; Ennis, 1986; papers in Caddy, 1989a; Caddy, 1989c). In this sense, the analysis mentioned above can be considered valid under the assumption of stationarity (Hilborn and Walters, 1992) and if the species acts as a closed population, but specific harvesting and enhancement strategies may be called for in the case of metapopulations (e.g. Tuck and Possingham, 1994).

Most sedentary benthic invertebrates are structured as metapopulations, defined as spatially segregated populations of benthic adults interconnected through pelagic larval dispersal. Each local population is replenished by larvae originated at one or more local populations (LPs), depending on the degree of connectivity and dispersal distance: minimal connectivity occurs in species with short-lived larvae and vice versa. These LPs generally present high variability in their SRR, whether they act as “sources” or “sinks” (Shepherd and Brown, 1993). In a source population, local recruitment mainly depends on the resident parental stock from this LP. This “source” also serves to replenish habitats occupied by sink populations, where local recruitment is insufficient to balance local mortality. Four models of larval replenishment apply for shellfish metapopulations (Carr and Reed, 1993; Allison, Lubchenco and Carr, 1998): (a) closed local populations with a self-replenishment pattern; (b) limited distance pattern with single or multiple sources; and long distance dispersal with (c) a single or (d) a multiple source pattern defined by a common larval pool. The precise identification of source and sink population components within the unit stock, and their habitats, is of primary interest for re-establishing a self-sustaining population, since for obvious reasons, it is desirable that the site chosen for enhancement should coincide with a natural (or former) source of recruitment for the area, especially if the objective is to re-establish a viable population.

For sedentary species, the source and sink concept evidently needs to be taken into account. Underwater observations over natural shellfish beds (e.g. Caddy, 1970; Stokebury, 2002) have revealed that shellfish aggregation occurs over a range of spatial scales. Stokebury (2002) found some 55 percent of the average harvestable biomass of sea scallops on the Bank occurred within five percent of the scallop fishing grounds, with specific areas of high density within them: a characteristic frequently noted for other shellfish populations. If these key areas are to persist in productivity, this demands that the population spatial distribution must be taken into account in designing a conservation and management scheme, and we are faced by the reality of source and sink populations (Orensanz and Jamieson, 1998). The existence of source populations which contribute to the majority of successful spawning seems to be indirectly confirmed in many cases by the persistence of productive shellfish beds in particular locations. If this is the case, when these become depleted, this reduces the recruitment to the whole population of the area. Indications suggest that for sedentary and semi-sedentary species, such source populations occur at high density within limited locations where a gyre or favourable current system has a higher probability of returning

larvae to the “source” bed (Figure 3.1). Examples of such areas for scallop populations are mentioned in Caddy (1979b) for the Bay of Fundy, and by McGarvey and Willison (1995) for Georges Bank. The role of source populations for Georges Bank scallops was commented on by McGarvey, Serchuk and McLaren (1992) who found that 82 percent of egg production from this population came from a small area on the Northern Edge and Northeast Peak of the bank. Larvae distributed elsewhere to less favourable environments may have a lower probability of reproduction due to their lower density. This is a factor of importance to fertilization by broadcast spawners such as most invertebrate resources, which their location ensures a high probability of not returning to the “mother” population. The source-sink hypothesis thus provides a useful concept and guide to management, in that it supposes a lower contribution to population replenishment is more likely to occur for mature individuals of sedentary species scattered outside of source areas, which can therefore be harvested with minor repercussions on the metapopulation. Thus the population patches labelled SO in Figure 3.1 are expected to have a higher probability of producing recruits to the parental bed than for those labelled SI, where although larval life histories may be surprisingly well adapted to a return to parental aggregations, a higher probability of larvae being carried away down current seems implied. The source and sink concept was also invoked for *Panulirus argus* by Lipcius *et al.* (1997), and seems one likely option for explaining apparent recent increases in stock range of *Homarus americanus* from core areas to some grounds (e.g. the upper Bay of Fundy) where lobster stocks were formerly less common when groundfish predators were abundant. The significance of this for the present study is that it suggests that data series be collected where possible from source populations.

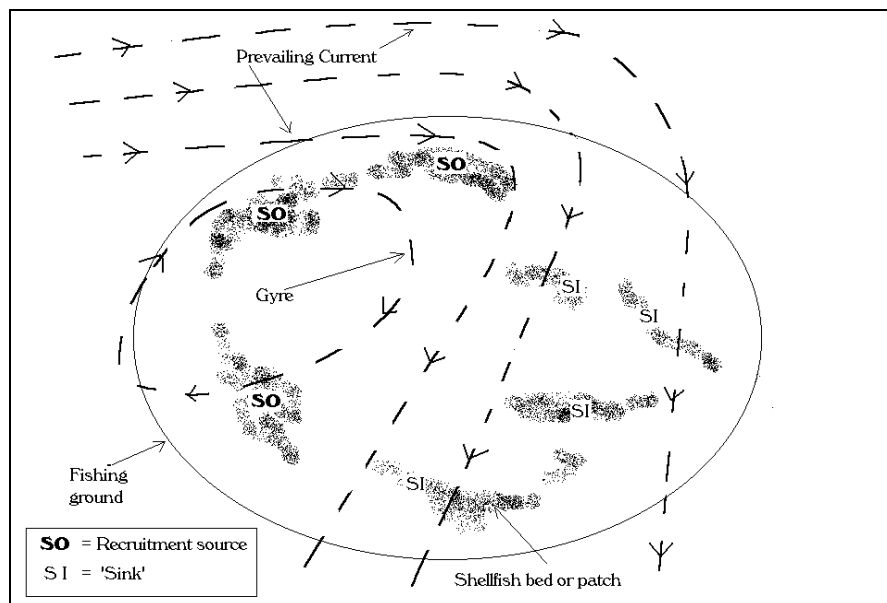


Figure 3.1 Illustrating the concept of source and sink populations in relation to the prevailing current system, which for source populations provides a measurable probability of larval return to spawning populations, which is not generally the case for sink populations.

In the case of motile bottom invertebrates such as lobsters, the hypothesis that spawning location is important was confirmed in several cases by the existence of specific aggregation areas of larger older lobsters (Campbell, 1986). The identification of an area as either a source of recruits for a wider area, or as one unlikely to produce offspring, is an issue that has been discussed for resources such as Caribbean spiny lobsters and conch (see e.g. Lipcius,

Stockhausen and Eggleston, 2001; Acosta, 2002). In this case, the very long larval life span seems to imply that this phase of the life history is adapted to the long duration of return of current systems in the wider Caribbean Sea.

We may assert with some confidence that certain locations characterized by frequent successful annual recruitments, and hence an age structure with good representation of different age classes, are source populations. Contrariwise, populations scattered thinly with one or few age classes may be considered sink populations. This situation suggests a fishing strategy that promotes high recruitment by avoiding excessive depletion of source areas, or even enhancing their recruitment potential by artificially increasing local densities in these areas, but exercising less concern with depletion of sink areas. Some evidence that this approach is successful is provided by several experimental studies. Similar suggestions as to management strategy were provided by Gutiérrez and Defeo (2003) who found dense aggregations of the scallop *Zygochlamys patagonica*, showed strong latitudinal and bathymetric gradients that suggested reproductive refugia and rotational harvest strategies be considered, and they suggested that exploitation be monitored using GIS methodologies. Aoyama (1989) noted the occasional very good year classes that characterized the fishery for the scallop *Patinopecten yessoensis* at roughly 10-20 year intervals prior to widespread use of suspended culture methods in the bay, but found recruitment became much more regular and abundant after 1970, when a significant proportion of the (spawning) biomass was in suspended culture. This leads to the reasonable conclusion that although broadcast spawners may recover from very low densities, maintaining a high spawning stock density may lead to more regular successful spawnings. This was also the conclusion of Hart (2003) for Georges Bank scallops, who showed that closure of the central part of Georges Bank and the Mid-Atlantic Bight fishing grounds to help recovery of groundfish populations, led to increases in scallop catch rates of 26x and 12x over six and three years respectively.

Closed local populations. The concepts provided above for self-sustaining populations apply when the degree of connectivity between LPs in a metapopulation is so weak that for management purposes, each one could be considered as a self-sustaining population. This may be true even if occasional larval exchanges between LPs are enough to maintain a certain degree of genetic flow and homogeneity. Tremblay *et al.* (1994) and Sinclair *et al.* (1985) showed that scallops subpopulations in a metapopulation could be considered self-sustaining at meso (discrete aggregations) and macro e.g. Georges Bank, (see Tremblay *et al.*, 1994) spatial scales. Defeo (1996b) provided additional evidence for Efford's (1970) hypothesis, suggesting that many local groups of broadcast spawners in open sandy coasts are self-sustaining. Association between shellfish concentrations and oceanographic features is generally believed to reflect, at least to some extent, retention mechanisms. However, the relative significance of dispersal and retention is largely one of scale (Cowen *et al.*, 2000; Palumbi, 2003; Orensanz *et al.*, 2003). In this context, Camus and Lima (2002) highlight the need to address the appropriate spatial scales to clearly define local populations, avoiding the often misleading use of common operational terms such as “grounds” or “sites” in cases when these terms are inconsistent with the actual scales at which population processes operate. Simulations of populations with particular larval dispersal regimes shows that isolation by distance is most obvious when comparing populations separated by 2-5 times the mean larval dispersal distance, and available data on fish and invertebrates suggest mean dispersal distances of 25-150 km (Palumbi, 2003).

Limited distance patterns. In short-lived pelagic larvae with a limited physical transport, enhancement options should consider placing refuges within the range of larval dispersal to

minimize risks of restocking failure of nearby subpopulations. Several small refuges would be suitable (Carr and Reed, 1993), with the size of each one depending on the relative contribution of each source population. Peterson, Summerson and Luettich Jr. (1996) showed the significance of managing metapopulations in this process-based enhancement context: limited dispersal distances of short-lived scallop larvae determine a very limited area of influence of dispersal in the replenishment of local populations, thus limiting population sizes. This has crucial connotations for enhancement and management purposes, suggesting that a precautionary approach could be taken at very low connectivity in order to avoid the serial depletion of population units (see below, and Orensanz *et al.*, 2003).

Long distance dispersal. Asymmetric connectivity between populations tends to increase according to the geographic range of a population. Extreme asymmetry is found in the case of "absolute sinks" (i.e. pseudo-populations *sensu* Orensanz *et al.*, 2003). However, some metapopulations extending along thousands of kilometres of coastline do not show genetic variation (see e.g. example by Galleguillos and Troncoso, 1991 for the Peruvian bay scallop), suggesting a high degree of connectivity among subpopulations even at larger spatial scales.

3.2 Source and sinks and their practical implications

In many sessile or sedentary invertebrates, "sources" of recruits act as "core" areas in the species range where the species occurs in all years, and where the typical age composition exhibits regular recruitment patterns with multiple age classes present. It is also typical that there are wide areas where occasional individuals or low densities usually occur, and here populations typically consist of only one or two age groups, often of old individuals. Caddy (1989b) illustrated that marked fluctuations in stock size are typical of many broadcast spawners (Figure 3.2). Peaks in abundance occur at intervals of a decade or more for some stocks, with poor recruitment in intervening years. Following onset of favourable conditions, the geographical range of the species may increase considerably, but these outer fringes of the metapopulation are typically restricted to one or two age classes: often, but not always, at low abundance. Examples of "core" areas for *Placopecten magellanicus* are the Northern Edge and Cultivator Shoal of Georges Bank (Bourne, 1964), while the southern part of the bank was only occasionally productive. In Peru, following the El Niño Southern Oscillation (ENSO) event in 1982-1983, the local scallop *Argopecten purpuratus* underwent a population explosion, occupying a wide range of habitats (Wolff, 1987). This was apparently linked to the unusual abundance of either abundant detritus from the preceding ENSO episode or the creation of oxygenated bottom water in a previously hypoxic area. This gave rise to a fishery for one, or a very few, age groups occupying areas where the species was not previously abundant. The question naturally arose as to the conservation strategy appropriate to this stock, which occupied areas where scallops were never found in abundance previously. Knowing that ENSO episodes are periodic, and that part of the current range would normally occur within hypoxic water masses, the appropriate exploitation strategy seemed to be to harvest those areas of population made up of one or two year classes, but avoid overexploiting areas where multiple year classes suggest that this "core" sub-population had survived previous ENSO episodes.

Arntz *et al.* (1987) showed dramatic fluctuations in the recreationally and commercially harvested sandy beach bivalves *Donax peruvianus* and *Mesodesma donacium* and the mole crab *Emerita analoga* in Peru, as a response to the strong ENSO mentioned above. After the dominant *M. donacium* disappeared following the ENSO, due to the increase in sea surface temperature, *D. peruvianus* increased in density from five percent to percentages between 60

and 100 percent, and *E. analoga* increased from < 1 to 29 percent. This increase in abundance was accompanied by an expansion of the distribution range to beaches previously unoccupied by these species. This suggests differential responses to climatic events and also potential interspecific interactions because of competitive release of resources by dominant members of the faunal community.

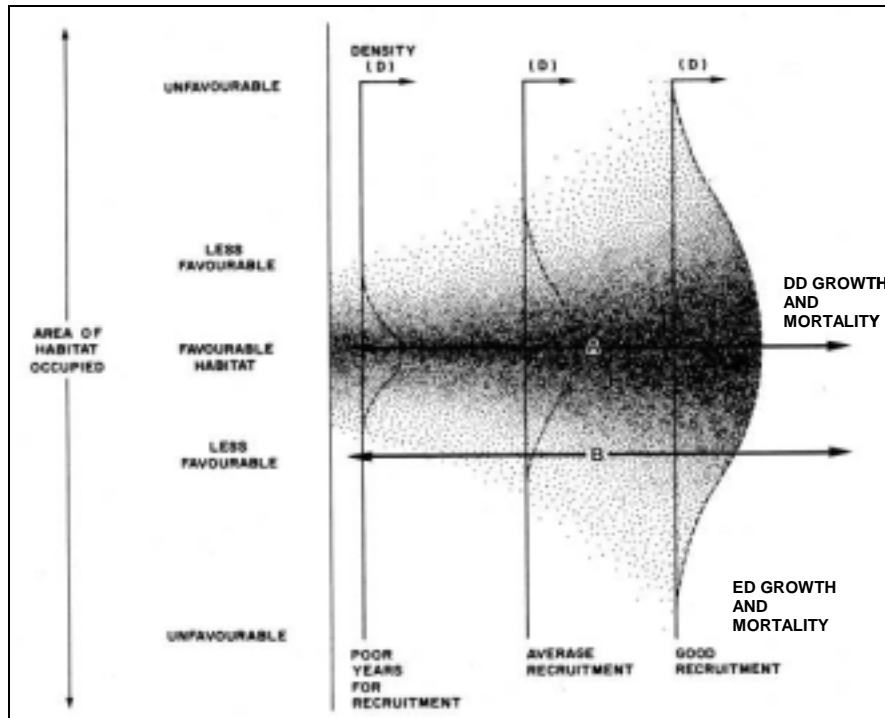


Figure 3.2 Variations in the spatio-temporal extent of recruitment and consequent stock contraction or expansion (from Caddy, 1989b). In "core" favourable habitats, density-dependent (DD) mechanisms prevail, lowering growth and mortality, whereas environmentally dependent (ED) mechanisms primarily regulate growth and mortality rates in unfavourable habitats during periods of good recruitment. The arrow marked A shows the time axis and the roughly constant density within source populations. The arrow marked B shows that sink populations may be absent from these peripheral areas in poor recruitment years.

The concept illustrated in Figure 3.2, is that contractions/expansions in the geographic range of the stock have implications at the meso- or macro-scales (i.e. for the individual fishing ground and for the total area of the metapopulation). Defeo (1993a) and Defeo and de Alava (1995) showed that recruitment in the clams *Mesodesma mactroides* and *Donax hanleyanus* along a 22-km open sandy coast was an aggregated process. A clear sequential pattern of alongshore replenishment occurs from the central zones of regular recruitment to the marginal portions of the beach, which are periodically affected freshwater discharge. These species appear to show contagious distributions, and only when good sites are fully occupied, are marginal sites occupied by later settlers. Long-term analysis confirmed in practice the hypothesis in Figure 3.2 as due to changes in habitat suitability and the capacity for recolonization, in a habitat showing a continuous gradient in environmental conditions. Figure 3.3 illustrates diagrammatically the

longshore distribution of *M. mactroides* following the distributional concept illustrated in the previous Figure.

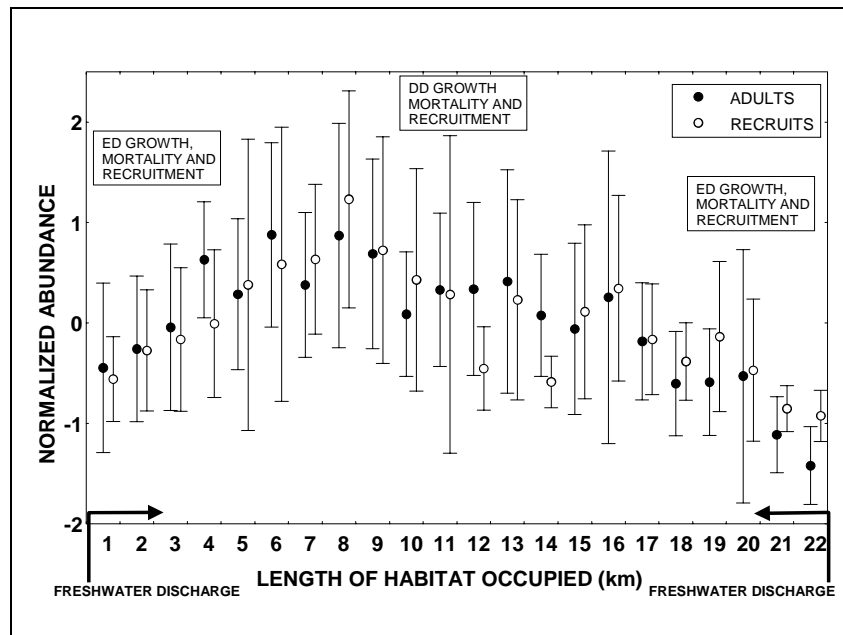


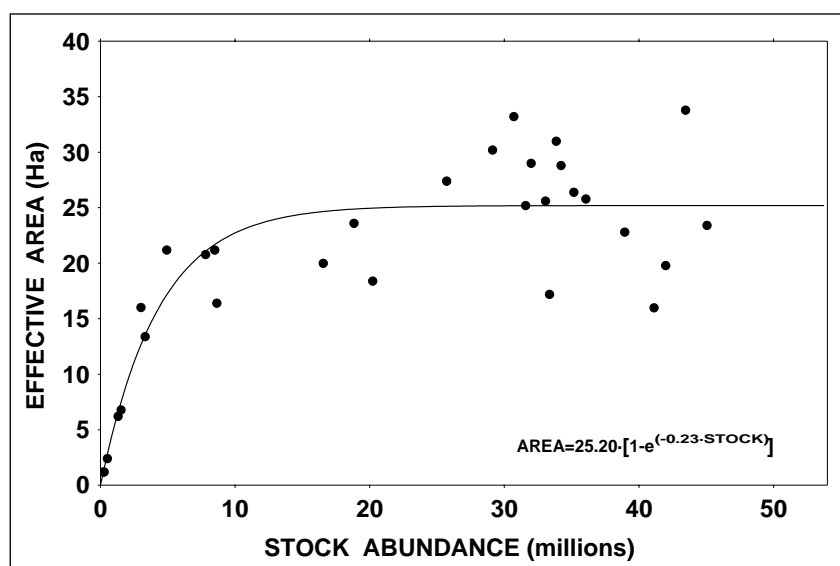
Figure 3.3 Diagrammatic representation of variations in the alongshore variability of the yellow clam *Mesodesma mactroides* over favourable and unfavourable loci, following Caddy's hypothesis of habitat suitability. Recruits occupied unfavourable habitats only during periods of good recruitment.

The above mentioned effects of the environmental gradient in salinity, and of major densities of recruits in marginal habitats in years of good recruitment, as well as those related to differential mortality and growth, seem to explain the observed pattern of longshore distribution of yellow clams over time. The species occupies a habitat with widely varying environment characteristics: in benign environmental conditions, adult-larval interactions are more intense in favourable than in marginal habitats, where harsh and fluctuating habitat conditions lead to lower densities and limited biological interactions: here the population is physically controlled (see also Schoeman and Richardson, 2002). The above phenomenon has immediate repercussions when planning stock enhancement initiatives. Enhanced recruitment within area closures may lead to larval replenishment of adjacent areas in which space and or food are perhaps more abundant. This should apply to under-saturated sites (Peterson and Summerson, 1992; Orensanz *et al.*, 2003) due to the low abundance of the exploited fraction of the population in these areas.

Evidence for the expansion or contraction of the spatial range of a population in response to changes in abundance and environmental suitability is more easily seen for sedentary than seasonally migrating species. However, a very different situation arises when we consider "saturated" sites, where compensatory processes are strong. Figure 3.4 shows that the effective area occupied by *Mesodesma mactroides* follows an asymptotic relationship with respect to stock size along the 22 km of beach analysed, indicating a clear "bottleneck" in habitat availability and suitability when resident population abundance exceeds some limiting carrying capacity. The recognition that there is a maximum area available to the stock suggests that when the stock reaches abundance higher than 15 million individuals, a limitation of available space

may preclude further expansion of the stock. At this point, compensatory mechanisms are likely to intensify (Defeo, 1996b). In fact this level of adult abundance is consistent with that suggested by other analyses, such as a population SRR (see Chapter 2).

Figure 3.4 Relationship between the effective area occupied by the yellow clam *Mesodesma mactroides* stock in Uruguayan beaches and the corresponding stock abundance.



Perhaps more importantly, a common observation is that “source populations” are often in areas where there is a high probability of returning water masses or gyres, assisting in retaining larvae, or returning them to the local area, as mentioned for scallops (see Caddy, 1979b; McGarvey, Serchuk and McLaren, 1993; Manuel *et al.*, 1996) and the gastropod *Concholepas concholepas* in Chile (Poulin *et al.*, 2002a, b). Following Sinclair’s hypothesis (Sinclair, 1987), the combination of geographic diversity and local and stable oceanographic structures, provides the basis for larval retention areas. Thus, we would expect “source” areas of larvae to be associated with standing gyres, and in the case of the Bay of Fundy and Georges Bank scallop populations, this seems the case. In many cases, a geographical feature (a bay or headland) helps create conditions for larval retention in some localities. These areas are of great value to the metapopulation as a whole, and should be the focus of intense conservation efforts. If the above situation applies, one would expect age analysis of the “source” populations to show fairly regular age structure, while “sink” populations would be made up of few age groups, occurring irregularly in time. Thus, the age structure of the population is probably a good index of the local degree of retention of the larvae for the local population, and hence the probability that their offspring will return to the parental grounds. Figure 3.5 shows the size structure of a recreationally harvested mole crab *Emerita brasiliensis* in a sandy beach of Uruguay, as a function of the distance to the discharge point of a freshwater canal. The length frequency distributions showed marked spatial differences. The virtual disappearance of females >22 mm CL and <12 mm CL close to the canal suggests respectively, higher mortality rates and recruitment failure.

High mortality rates of older crabs close to unfavourable conditions are due to habitat unsuitability and insufficient food. Crabs in unsuitable habitat also show reduced growth rates and fecundity (Figure 3.6). Thus, eggs here are produced only by younger females which significantly decreased their fitness to reproduce and total reproductive output. The absence of recruits here was attributed to hydrodynamic effects resulting in high pre-settlement and early post-settlement mortality rates (Lercari and Defeo, 1999). Recruits were found near the freshwater discharge only during years of good recruitment. However, low

growth and high mortality rates precluded many from achieving a size at maturity. By describing this case in some detail, we show that the effects of habitat suitability and stock contraction/expansion may occur at a variety of spatial scales, ranging from meso (e.g. a fishing ground) to megascale (*i.e.*, the entire distribution pattern of a species: see Defeo and Cardoso, 2002), a situation which while it may also apply to fish species, is rarely evident from available data.

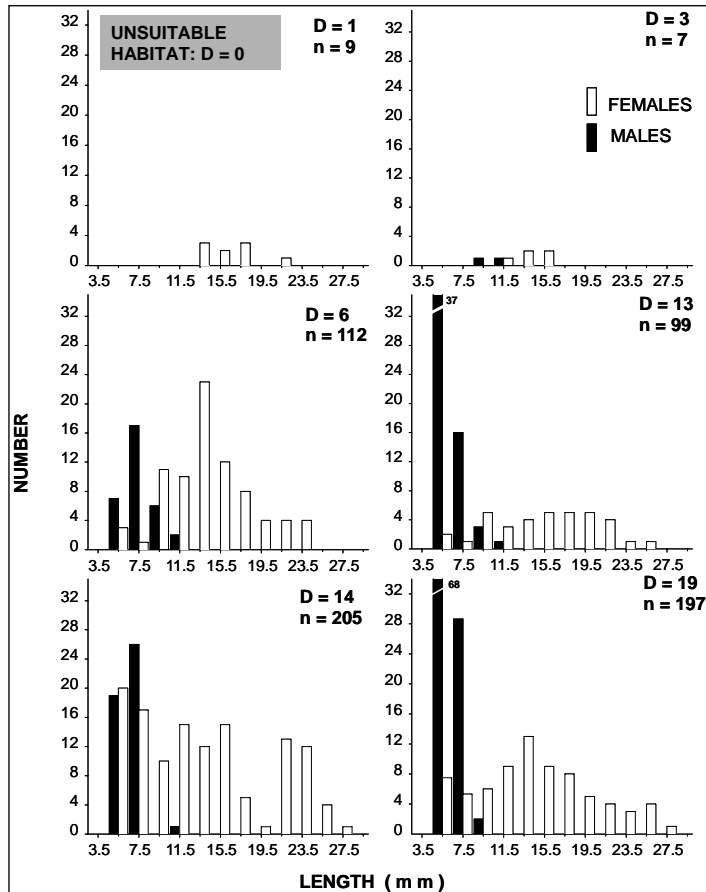


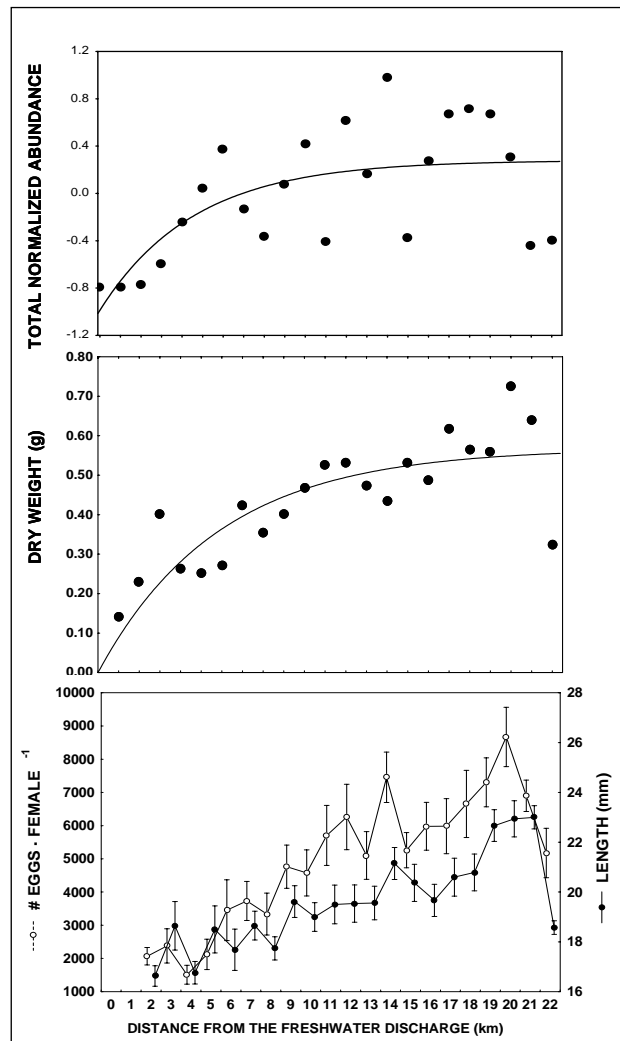
Figure 3.5 Length frequency distributions of the mole crab (Uruguay) discriminated by sex at different distances (D , in km) from the unsuitable habitat, defined by the presence of a human-made freshwater canal. Note the absence of smallest and largest sizes close to the freshwater discharge (see Lercari and Defeo, 1999 for details).

3.3 Linking natural restocking and spatially explicit management tools

3.3.1 MPAs and ad hoc area closures

The recognition of spatial patterns in population demography and dynamics is of utmost importance when planning stock enhancement activities through natural restocking and ad hoc spatial closures or direct seeding. The failure and growing disillusionment with conventional management procedures which assume a single “dynamic pool”, when applied to sedentary invertebrate populations, has led to widespread interest in spatially based management tools for stock enhancement purposes. Indeed, the concept of natural restocking as illustrated by the above example, has led to a search for spatially explicit tools for shellfish management. The most obvious spatially oriented tool advocated for management and conservation efforts is the Marine Protected Area (MPA). A MPA is any intertidal or subtidal area reserved by law for the protection of a component of the ecosystem (see IUCN, 1988). In the current context, a MPA is a management or conservation tool by which all or part of an invertebrate (or fish) stock may be closed to fishing within the boundaries of the MPA. The

Figure 3.6 Effect of habitat unsuitability, measured as the distance from a freshwater discharge, in abundance, individual weight and fecundity of the marine mole crab *Emerita brasiliensis*. See the local effect produced by a minor freshwater discharge at km 22.



design and location of a MPA can in fact be seen as a natural experiment in the effectiveness of protective management and stock enhancement (Alcala and Russ, 1990, Russ and Alcala, 1998). Long-term closures of portions of the habitat, rather than closure of the whole fishing ground, may itself ensure that those areas adjacent to the closed area are replenished by larvae coming from this source of larval production to replenish populations in the open fishing areas. Other area-based tools include sanctuaries, reproductive refugia, ad hoc area closures and rotating harvesting zones; thus incorporating both temporary and permanent area closures (Davis, 1989). These strategies for stock rebuilding have gained increasing attention for managing stocks with strong and persistent spatial structure (Orensanz and Jamieson, 1998) such as sessile and sedentary invertebrates (Caddy, 1999a; Peterson, 2002).

Designation of effective marine reserves requires careful attention to metapopulation dynamics and recruitment processes. The concept of the metapopulation has led to new ways of managing natural populations through, for example, the use of linked ecological reserves and corridors from wildlife conservation practice on land and the recommendation to institute special reserves for overexploited species (Lauck, 1996; Lauck *et al.*, 1998). In this context, management could consist of controls on total removals of individuals mainly from source populations and/or a control on removal of specific age groups. In open populations, the primary target for protection is the source area of larvae, or those aggregations of mature animals that

make up a source of recruitment. This led to the concept of the “spawning refugium” (Anthony and Caddy, 1980), which for macrocrustacea and for demersal finfish is an underused concept with important management implications. Spawner sanctuaries were suggested by Peterson (2002) to restore and protect spawning stock biomass of the overfished *Mercenaria mercenaria* in North Carolina. Other population characteristics, such as site-specific mortality and individual growth patterns, could be also evaluated to determine the effectiveness of site selection for stock rebuilding purposes. The number and dimension of these “refugia” will differ among species, according to life cycle characteristics (e.g. life span, reproduction mode and magnitude of larval dispersal), location of the fishery and ability of these areas to supply recruits to harvested areas and to maintain a sustainable fishing activity (Carr and Reed, 1993). Local and large scale hydrographic features will determine the rate and direction of larval dispersal and replenishment, so that potential refugia should also be taken into account when designing management experiments. Lipcius, Stockhausen and Eggleston (2001) used field data on spiny-lobster (*Panulirus argus*) abundance, habitat quality, and hydrodynamic transport patterns for a reserve and three exploited sites, to evaluate reserve success as a tool for reducing fishing mortality and increasing metapopulation recruitment. Using a circulation model, these authors theoretically assessed the effectiveness of the actual reserve and nominal reserves at the exploited sites in augmenting recruitment through redistribution of larvae to all sites. Only two sites, one at the unexploited site and only one of the three exploited grounds, would be suitable for metapopulation recruitment as receptive areas for settlement. They also highlighted the need to consider information on transport processes to determine the location of a marine reserve, which yielded much more information than information on habitat quality or adult density. In this sense, Palumbi (2003) highlighted that designs of marine reserves requires an understanding of larval transport in and out of reserves, i.e. whether reserves will be self-seeding, or whether they will accumulate recruits from surrounding exploited areas, and whether reserve networks can exchange recruits (see also Botsford, Micheli and Hastings, 2003; Gaines, Gaylord and Largier, 2003; Hastings and Botsford, 2003; Largier, 2003).

Acosta (2002) showed through a logistic model that relatively minor changes (increases) in refuge area and boundary conditions can determine major population-level responses by the exploited spiny lobster and queen conch in Belize, depending also on habitat availability (see also Acosta and Butler, 1997). Eggleston and Dahlgren (2001) showed that relatively small MPAs (30-150 ha) may be too small to protect the population structure of the spiny lobster *Panulirus argus*. Because most MPAs are limited in space, stock rebuilding initiatives for mobile shellfish (e.g. lobsters) will be influenced by the size and boundary conditions of the reserve, with longer larval dispersal distance for these species requiring larger reserves to meet the objectives of sustainability (Acosta, 2002; Botsford, Micheli and Hastings, 2003).

The above discussion implies that marked variations in life history traits of shellfish populations are of utmost importance when designing a MPA. Information about the life history is necessary to investigate the possible reasons for the recent failures of MPAs in increasing shellfish abundance, focusing especially on: (1) the duration of the planktonic stage, larval dispersal, and rates of diffusion of the individuals into and outside the marine reserves (Carr and Reed, 1993; Allison, Lubchenco and Carr, 1998); (2) the role of near-shore hydrodynamics in the settlement process; (3) recruitment patterns among habitats and between years in intertidal zones; (4) habitat preferences, including some intra-and interspecific interactions that may affect habitat use, and (5) intraspecific interactions that may affect survival (Fernández and Castilla, 2000).

Elucidation of points (1) and (2) will determine the spatial scales over which the population dynamics is to be considered a closed or an open process, i.e. if it is more related to the arrival rates of larvae than to post-settlement processes. Retention or dispersion of larvae from LPs has been identified as one of the key processes influencing recruitment success in shellfish stocks. In spite of this, very little is usually known about dispersive abilities of meroplanktonic larval phases of most shellfish, and the mechanisms influencing larval distribution are still poorly understood (however, see Poulin *et al.*, 2002a, b). Alternative hypotheses should be tested to determine whether the population(s) to be enhanced by this operational management tool could be considered as self-sustaining, with relative isolation from the rest of the species distribution. In the specific case of metapopulations, the design of a MPA should seek to preserve the connectivity patterns between LPs. Indeed, the lower the connectivity, the more conservative the management should be in order to avoid the serial overfishing of population sub-units, such as for Pacific crab populations (Orensanz *et al.*, 1998). In cases with a single source, the closure of an area for stock enhancement is straightforward: this source of recruits should take priority in conservation for future replenishment of surrounding sink areas. The case of long distance dispersal with a multiple source pattern is more complicated and difficult to manage, as a result of high uncertainty about the relative contribution of each subpopulation to a common larval pool. While it could be suggested to close areas within each subpopulation in order to minimize the risk of losing the spawning population due to an unexpected disturbance or even adverse hydrographic effects (Carr and Reed, 1993), the information supporting such a complex objective is rarely available. Priority must be given to the major source of larvae, in order to increase the probabilities of ensuring supply, or to collect larvae and enhance contiguous subpopulations through transplanting.

One advantage of MPAs is that they may enhance populations independently of catch and effort control, or the collection of detailed information resulting from routine fishing. At the same time, it is rare that objective data allows an evaluation of the effectiveness of MPAs. In fact, few MPAs to date have established a scientific basis concerning size, location, boundaries and the inherent characteristics of the life history of the species to be protected, and rarely are prior observations taken, or controls used to establish effects quantitatively through well-designed ecological experiments (Castilla, 2000; Hilborn, 2002). A summary of the characteristics of MPAs from a conservation perspective is given in Figure 3.7. One positive example may be mentioned: Bertelsen and Cox (2001) found that the Dry Tortugas National Park served as a breeding sanctuary for Caribbean spiny lobsters: egg-bearing females there, being larger, producing approximately 2.6 times the number of eggs per clutch than lobsters outside the park.

Short-term area closures, as opposed to permanently established MPAs, may be used to protect areas which historically have had high probabilities of successful recolonization (Polacheck, 1990). Spatial reproductive refuges are considered a particular form of MPAs: creating *sanctuaries* where spawning adults could be protected and allowed to perform natural restocking. This could be more feasible for crustaceans (e.g. lobsters), as large egg-bearing females are easily distinguished from males and can be returned to the water if egg-bearing, or marked in some way. Thus, spawning/breeding zones can be specially protected and males can be selectively harvested (Addison and Bannister, 1994). Monitoring yields and sex ratio in these sanctuaries and in adjoining control areas could help to evaluate the performance of long-term enhancement of the sanctuary stock. Saving the juveniles from premature exploitation, but also ensuring low fishing pressure on the spawners, constitutes non-exclusive operational management tools could be jointly considered. Protection of juveniles is particularly important

where fisheries operate mainly on juveniles with unselective fishing gears (from trawling to handgathering techniques: Caddy, 2000a).

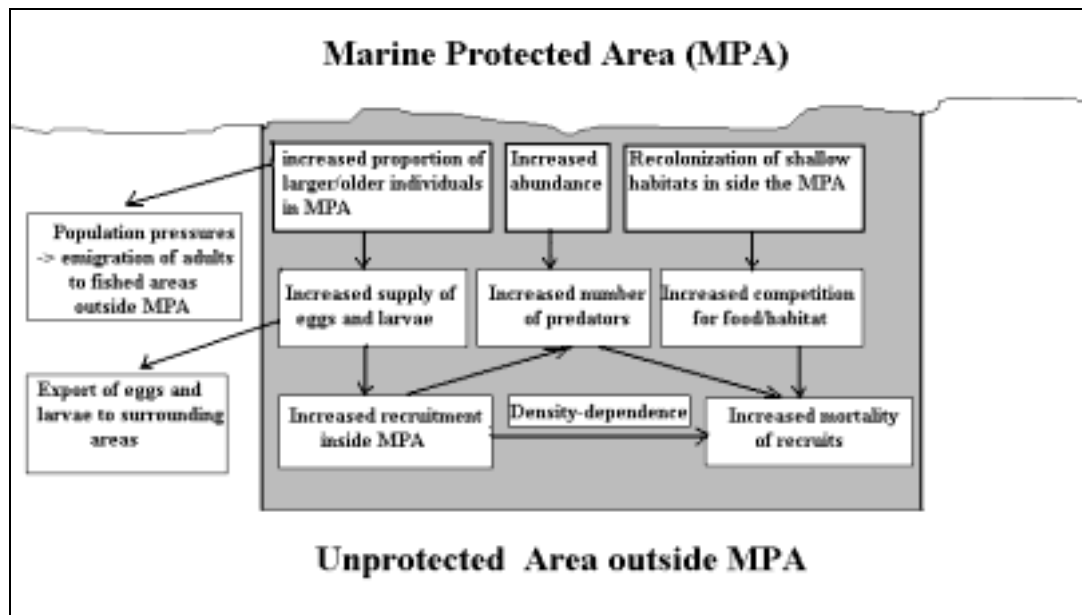


Figure 3.7 Some characteristics of MPAs, particularly with respect to recruitment and density dependence, and their potential contributions to fisheries in surrounding areas. Modified from Planes *et al.* (2000).

McCall (1990, p. 7) cites an anecdotal report from the clam fishery in Narragansett Bay, Rhode I., USA. Clams occur throughout the estuary, but the fishery was closed in the reaches upstream due to pollution. The fishery normally operated on the downstream beds, and has maintained consistently high yields over many years. At one point, however, the upstream beds were declared safe and opened to harvesting. Overall production declined subsequently. When the upstream beds were once again closed, the fishery returned to its previous high levels of downstream production.

Early on, Castilla and Schmiede (1979) used the concept of metapopulation dynamics in designing a shellfishery restocking strategy along the Chilean coast. The existence of refugia (or *de facto* natural preserves) allowed natural restocking of adjacent overfished grounds, where these refugia areas could be protected from fishing. The control of fishing effort and its effective exclusion from spatial refuges has been demonstrated to enhance yields of marine resources. Some benthic stocks show a great capacity for population recovery or “compensation” following human perturbations (such as excess fishing pressure), and natural restocking of depleted areas may then occur (see Castilla and Defeo, 2001 and references therein). For other species such as abalone, however, this is not the case. In this connection, closed seasons/areas are very useful for detecting population patterns and processes, which until the closure of an area, are usually unknown. For example, natural restocking has produced positive effects on the fishery, landings and economic performance of the *Concholepas concholepas* fishery in Chile; a valuable species which previously had been fished to low levels (see example below).

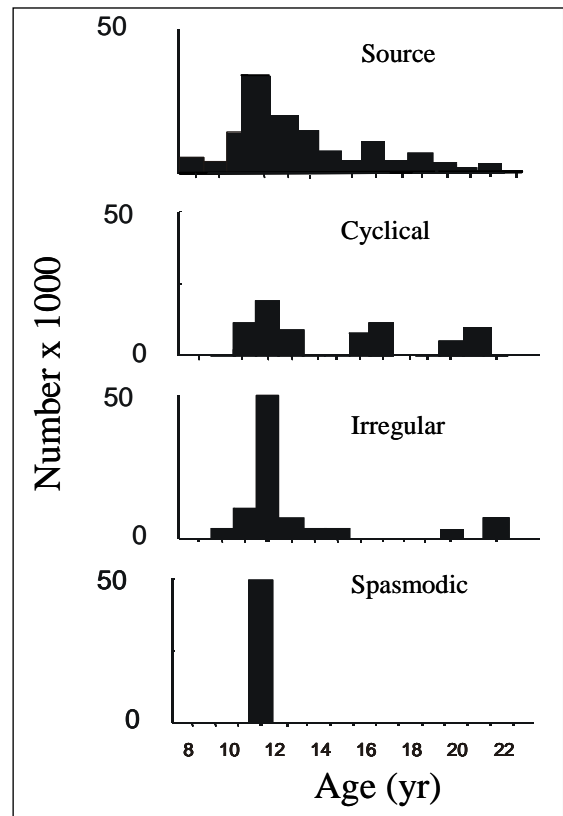
3.3.2 The source-sink hypothesis for stock replenishment and the siting of MPAs

In many cases, the hydrography of the area and its effects on larval dispersal will not be easily determined, although we may expect the siting of release points in relation to prevailing currents to be important for some species. As mentioned earlier in this Chapter, source populations are characterized by frequent successful annual recruitments, and hence the age structure contains a good representation of different age classes. Contrariwise, populations scattered thinly with one or few age classes, occurring irregularly in time, may be considered sink populations (Figure 3.8). Thus, the age structure of the population is probably a good index of the local degree of retention of the larvae for the local population, and hence the probability that their offspring will return to the parental grounds. In this context, the population structure in Figure 3.8, upper panel, could be considered the main source area, because of the presence of all potential year classes in the sample. Subsequent subpopulations represent recruitment events of different periodicity that could categorize, respectively, as cyclical, irregular and spasmodic.

Figure 3.8 The “source-sink hypothesis” and population structure. Sources (upper panel) and Sinks (three last panels) in sedentary invertebrate populations, and the expected age structure as a result of larval dispersal and retention to the parental spawning area and differential post-settlement mortality rates.

We suggest therefore a simple Index of Recruitment Recurrence (*IRR*), based on the population structure in each sampling site. This *IRR* can be obtained if an unselective sampling method is based on samples of (say) 100 animals:

$$IRR = \frac{N_{ages}}{M_{age}}$$



where *Nages* defines the number of year classes in a sample and *Mage* the maximum observed age. The *IRR* ranges between 1 if all ages are present, suggesting an annual recruitment pattern; but will approach 0 where recruitment tends to be spasmodic. Some useful remarks could be extracted from this *IRR*:

1. The areas where $IRR \rightarrow 1$ are those that are most suitable for enhancement if the chosen technique is to artificially increase spawning stock size.
2. Restocking this area with individuals from adjacent areas or unmarketable individuals that are too small to keep, may be a worthwhile strategy.

3. The areas of irregular recruitment are suitable for harvesting, and if the hypothesis is correct, may be harvested without restriction.
4. If the purpose of restocking is merely for harvest purposes, then these sink areas may also be suitable for restocking, but may not contribute greatly to future stock replenishment.

As some kind of spatial autocorrelation should be expected in *IRR* values as a function of distance from the main sources, geostatistical tools (Conan, 1985; Warren, 1998) could be used in order to account for the spatial correlation between successive values of *IRR* and also for purposes of mapping. This could be easily obtained if there is a fixed grid of sampling units throughout the study area. A critical *IRR* value such as e.g. 0.7, could be defined, and mapped areas enclosed by this value could be protected as the main sources of recruitment. Thus, this strategy could be relevant to design and allocation of MPAs.

This hypothesis of source and sink areas leads to harvesting strategies that are very different from the conventional dynamic pool approach. Thus, it would be good to take a precautionary approach, at least initially, and ensure that some fraction of the sink populations is not totally depleted. More importantly, conservation efforts should be focused on source areas to ensure that abundance does not fall below threshold values for successful spawning.

In order to reduce uncertainty in enhancement, passive enhancement could be a "risk averse" strategy to use in the preliminary stages of the restocking process while studies are carried out to assess the technical and economic feasibility of active enhancement. A benefit-cost analysis should be conducted to evaluate the trade-offs among alternatives. Economic analyses are important prior to full scale implementation of an MPA for stock enhancement purposes (Hannesson, 1998). Site selection is evidently a delicate issue, and at least a proportion of the source population should ideally be included. This may not be possible for practical reasons, and Caddy and Carocci (1999) suggest that siting an MPA between two adjacent ports could provide a useful buffer zone with recruitment outwelling from the closed zone to both adjacent open fishing areas. An example of this on a macro-scale is the suggestion by McGarvey and Willison (1995) to situate a buffer zone along the maritime boundary between U.S. and Canadian waters of Georges Bank as a source of recruits to scallop fisheries on both side of the international boundary.

3.3.3 *Rotational harvesting schemes*

Enhancement operations in shellfishes could be particularly useful when used together with other spatially explicit management tools such as the rotation of harvestable areas. Rotating harvesting strategies have considerable advantages over quota management schemes, particularly for sessile or sedentary populations distributed as geographically isolated substocks, where the option exists to harvest different subareas separately (Brand *et al.*, 1991; Caddy, 1993b). Both strategies, enhancement and rotation harvesting, should consider site-specific differences in carrying capacity, recruitment, growth and mortality, and attempt to ensure that each area has more or less the same carrying capacity. Economic factors (especially market demand and prices for preferred sizes) are critical to choosing rotation periods for rotating harvest schemes, especially where larger sizes command a higher price, or where there is the need to ensure that a reasonable proportion of larger fecund animals survive to spawning. Unit prices reflecting different market preferences and discount rates should also be considered when planning rotation and enhancement as a mixed strategy.

Brand *et al.* (1991) showed that a combination of culture and restocking initiatives, coupled with rotational closure of the seabed, is potentially useful for stock enhancement in pectinid fisheries. This application benefited from the rapid growth rates and the remarkably consistent occurrence of recruitment on inshore scallop grounds in the Isle of Man. They also proposed the closure of small areas to assess the potential benefits both of the rotational harvest approach, and stock enhancement. Their conclusion was that the success of this mixed management system strategy is only possible in a community-based context: the cooperation of the local fishers is essential. Experimental results obtained on a local scale were used to demonstrate the potential advantages of the procedure once executed on a larger, commercial scale.

Bull (1994) documented a successful example of enhancement for New Zealand's "southern scallop" *Pecten novaezelandiae*. Seeding techniques were applied under rotational fishing, in which local beds were fished down in a mining strategy to economic extinction. Seeding methods involved a dual strategy of seeding spat previously caught inside Japanese collector bags, and dredging up and transplanting juveniles from collectors. He demonstrated that seeded stock contributes significantly to fishing yields, with an estimated 40-50 percent of the 1992 landings (ca. 700-ton meat weight) being of seeded origin. The 3-year rotational fishing system allowed each fishing sector to be harvested down to its minimum economic density and subsequently reseeded through an enhancement programme. Fishing rights were also imposed as a means of securing rights for existing fishers.

Caddy and Seijo (1998) determined optimal rotation periods for species with different rates of growth and natural mortality and harvesting levels, and noted that the choice of rotation period can be set to approximately correspond to whole population optimal levels of fishing mortality and exploitation rate that have been suggested by independent yield/recruit analysis (Table 3.1).

As noted by Myers, Fuller and Kehler (2000), the result is a simple and efficient means of regulating for optimal exploitation rate. Optimal rotation periods for sedentary stocks were determined by Caddy and Seijo (1998) by also investigating the effect of varying the ratio of natural mortality to individual growth rate (the M/K ratio). This appears to allow an important management tool, not only for sessile and sedentary resources, to be applied for a range of resources with low motility or territorial behaviour. The socio-economic context for its successful application is a management context incorporating territorial user rights for fishing (TURFs), and the possibility of separating the stock into subunits of comparable size between which migration is limited. Indeed, rotation of fishing areas (Pfister and Bradbury, 1996) and the granting of TURFs, together with stock enhancement activities through natural restocking, seeding and transplanting (Castilla, 1988; 2000) constitute another useful way of providing redundancy to management regulations (Caddy, 1999a). Spatially explicit management tools are not mutually exclusive but when simultaneously used, should diminish the risk of overexploitation (Seijo, Caddy and Euan, 1994).

Table 3.1 Identification of key questions on the existing management context when considering a rotating harvesting scheme (after Caddy and Seijo, 1998).

Management questions	Applicability of rotating harvest schemes
1. Do de facto exclusive harvesting rights exist?	If not, rotating harvesting schemes are difficult to enforce
2. Is preventing poaching in closed areas/seasons feasible, cost effective, and supported by fishers?	If not, rotating harvesting schemes are infeasible
3. Is there a management authority with the authority to allocate fishing rights by area to individual participants?	If not, rotating harvesting schemes are infeasible
4. Are there a discrete number of population subunits for the resource?	If not, rotating harvesting schemes are infeasible
5. Can the stock be separated into subunits of comparable size, between which migration is limited?	If not, rotating harvesting schemes are infeasible
6. Is the number of subunits equal or greater than a calculated optimum period of harvest rotation?	If not, a suboptimal rotating harvest scheme may still be feasible and desirable
7. Are there alternative means of employment for local fishers and/or processors if a local resource area is closed for a number of years?	If not, rotating harvesting schemes are problematical
8. In each year of the scheme, do fishers have access to other stocks?	If not, rotating harvesting schemes are problematical
9. Is the method of harvesting selective for the species and sizes most desired?	If not, rotating harvesting schemes are problematical

One feature of rotating harvest schemes for longer-lived species (such as precious red corals) was described by Caddy (1993b), who stressed the importance of concentrating Monitoring, Control and Surveillance (MCS) resources on the protection of those sub-areas shortly to be opened, which contain the highest densities of exploitable stock. Caddy and Seijo (1998), Myers, Fuller and Kehler (2000) and Hart (2002) all analysed the potential of rotating harvest schemes for sea scallops and other resources; noting that sedentary resources violate the assumptions of the dynamic pool models often used for finfish management. Rotating harvest schemes could both increase biomass and yield, and make it less easy to fall into growth or recruitment overfishing than when all areas are fished simultaneously.

Rotational harvesting, enforcement and economic factors. Caddy (1993b) outlined criteria for setting time periods for rotating closures in sessile or sedentary resources, together with some guidelines for enforcement of rotational closures. He defined an open season as consisting of two periods: a “useful” one, when net economic revenues are positive and a “wasteful” period when stock abundance and expected economical benefits are too low to justify exerting effort in that area (Figure 3.9a). During this “wasteful” period, surveillance can be less intense, especially in areas recently closed because there is less incentive for illegal fishing. Figure 3.9b shows the monthly mean CPUE values for seven fishing seasons (1981-1985, 1988 and 1989) between July and February for the spiny lobster (*Panulirus argus*) at Punta Allen, Yucatan Peninsula (Mexico). This fishery is managed by the local community, and thus fishing operations are

limited only to members of the cooperative. This area is also inserted within the range of a Biosphere Reserve, which assures low human intervention levels. Here poaching is minimal and operational management regulations (e.g. a closed season between March and June and a minimum legal size of ca. eight cm of cephalothorax length \approx 14.5 cm of tail length) are respected (Figure 3.9b). CPUE values (kg/boat/day) recorded through the 1981-1990 fishing seasons showed a maximum at the start (July) and a minimum at the end (February) of the fishing season (see Castilla and Defeo, 2001 for review). The conceptual MCS model provided in Figure 3.9a could apply here, particularly because unit prices remain constant throughout the period.

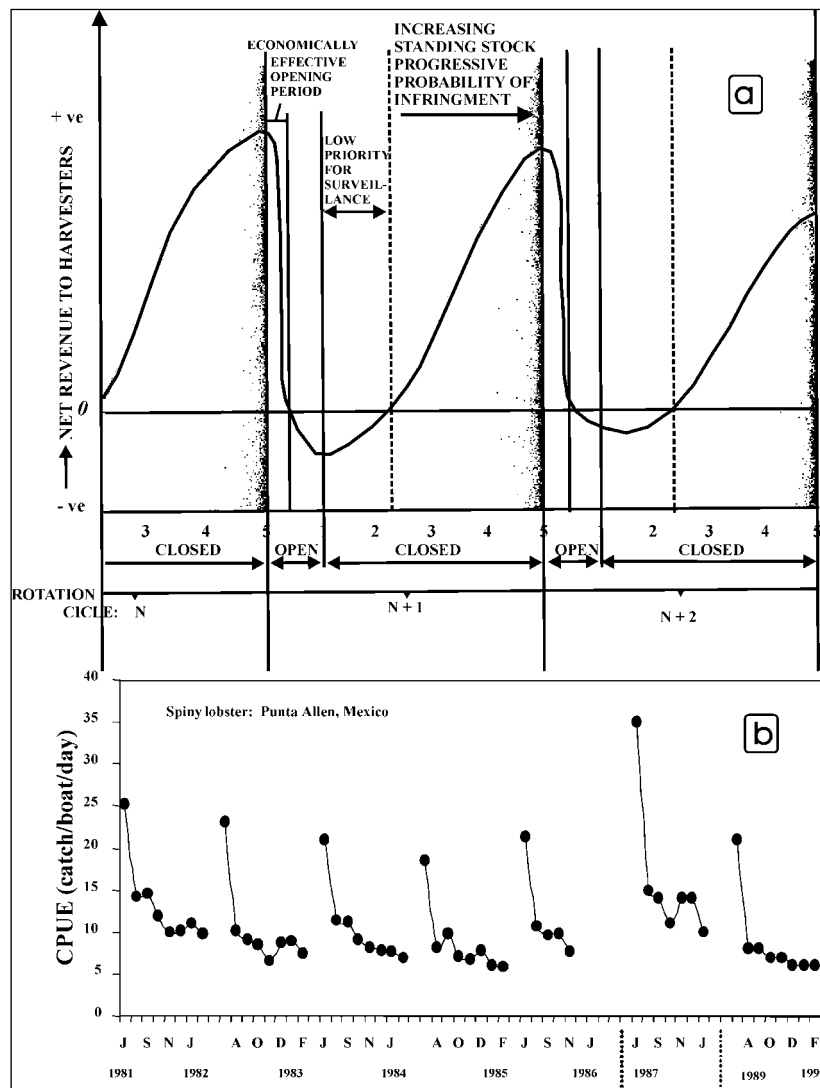


Figure 3.9 (a) Some features of a rotating harvesting framework, include a perspective on control and surveillance of fishers' adherence to the rotating closure under the assumption of constant unit stock prices (after Caddy, 1993b). (b) Monthly mean CPUE values for the spiny lobster (*Panulirus argus*) in Punta Allen, Yucatan Peninsula, Mexico, during seven fishing seasons (1981-1985, 1988 and 1989) between July and February (after Castilla and Defeo, 2001). See similarity of the long-term pattern with Caddy's rotating harvesting scheme in Figure 3.9a.

Another picture arises when fishing is recognized to be economically productive even following closure, because of intra-annual price variations inversely related with stock abundance. This is clearly shown in Figure 3.10 for the artisanal *Octopus mimus* fishery in Caleta Coloso, Antofagasta (Chile). This is a typical shoreline cove where all fishing activities are performed by divers at depths of between 5-20 m. The fishery is regulated only by a closed season from 15 December to 15 March, and it can be defined as an open-access fishery outside these dates. Defeo and Castilla (1998) showed a clear intra-annual pattern in five of the six years analysed (daily data), with catches peaking at the start of the fishing season (March-April: Figure 3.10a).

Catches showed an overall downward trend until September-October, at which point they rose slowly, before dropping down to their lowest level at the end of the fishing season. However, unlike the lobster example, the average price paid per tonne of octopus increased from the beginning to the end of the season (Figure 3.10b). The inverse relationship between intra-annual fluctuations in catch or CPUE and those of price suggest short-term changes in price according to resource availability, but also suggest the desirability of reducing early exploitation rates early in the season.

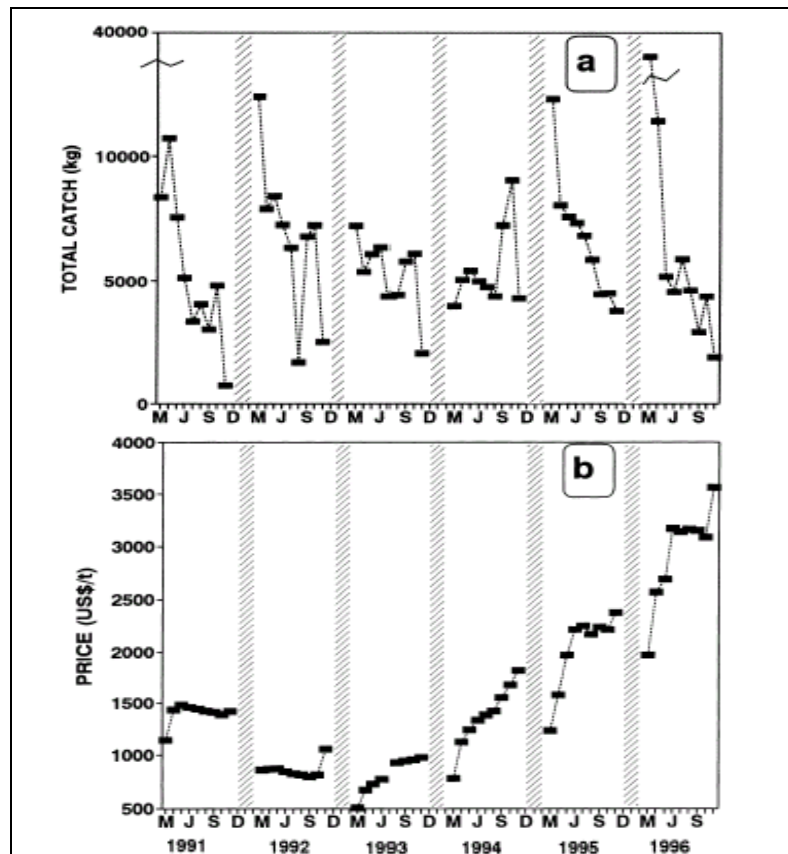


Figure 3.10 Monthly values of (a) catch and (b) mean prices paid to the fishers for the *Octopus mimus* fishery of Caleta Coloso (Antofagasta, Chile) between 1991 and 1996. See the marked inverse relationship between catches and unit prices within seasons (after Defeo and Castilla, 1998).

These considerations have a strong impact in open access systems such as the one being discussed here i.e. when the price paid to fishers varies with supply, uncertainty in future stock levels will promote a high inter-temporal preference in the pattern of octopus harvesting (Defeo and Castilla, 1998). This could promote high exploitation rates, over-exploitation and economic rent dissipation in the short-run. In this case, a high priority for surveillance is needed throughout the period, including after closure. Thus, a closed season or a rotational management scheme is not adequate on its own to manage the fishery, but imposes its particular control and surveillance requirements and impacts on access rights that will require strong adherence by fishers to the concept. Other measures (e.g. minimum legal size, catch quotas, marine harvest refugia) and the allocation of territorial property rights may need to be considered together with rotating harvest schemes, in order that a precautionary approach results (FAO, 1995).

3.3.4 *Average meat count regulations*

An average meat count regulation was agreed under ICNAF for scallop fisheries of Georges Bank in the 1970s, and required that the number of scallop meats in any randomly sampled part of the catch did not exceed a certain value (which initially was 70 meats/lb in Canadian catches in the early 1970s, but was gradually decreased to 30-40/lb over more than a decade). This type of regulation of course allowed a small proportion of small scallops to be legally landed, but the fleet was obliged to fish outside the main concentrations composed of young scallops in order to maintain the count below the regulated level, with penalties if more than a certain proportion of samples exceeded the limit by a given tolerance. Although this management measure has been criticized as not strictly corresponding to a minimum size limit because “mixing” of catches from small and large patches undoubtedly occurred, it imposed a degree of control over the rate of harvesting of dense patches consisting mainly of newly recruited year classes. As such, in a situation where good recruitment is irregular, it provided some protection to patches of juveniles such that irregular peaks of good year classes have an opportunity to support the fishery for several years, and a significant number of animals in the high density patch could reach mature ages before capture.

3.4 **Controlled field experimentation and natural stock regeneration**

Improved understanding of invertebrate population dynamics should come from experimental manipulation of populations and fishing effort (Jamieson and Caddy, 1986; Cobb and Caddy, 1989). This would allow testing patterns of resource response to fishing pressure and the linkages and strengths of ecological interactions (Defeo, 1998). Larkin (1978, 1984) highlighted early on the need to perform field experiments to obtain empirical information on the consequences and effectiveness of alternative management schemes. One way to perceive experimental management is by observing the response of fisheries to different levels of fishing effort or different management scenarios. In fact, a change in harvesting rates derived from the implementation of any management strategy is a perturbation experiment whose outcome is uncertain due to the influence of exogenous variables (e.g. environment) and to the intrinsic characteristics of the stock. Field experimentation could also be achieved by closing large areas and comparing the effects of unharvested zones with those in which different levels of fishing effort is exerted (Alcala and Russ, 1990; Castilla, 1993, 1994; Russ and Alcala, 1998).

Controlled field experimentation has unfortunately played a minor role in developing fisheries management theory (Caddy, 1999a), and shellfish fisheries offer a unique opportunity to conduct management experiments. Their null or low mobility and their heterogeneous distributions, lend themselves to experimentation in alternative management practices, much more so than for finfish (Hancock and Urquhart, 1965). The reasons for this could be summarized as follows:

1. The sedentary nature of shellfish populations offers definite advantages for small-medium scale experimental studies in the field is localized, relatively small pilot-scale experiments (e.g. those involving one or very few, beds, patches, or subpopulations) can be carried out. The effects of different levels of fishing effort can also be evaluated, and the response of a stock subunit to a specific level of disturbance observed. A proper evaluation of the relative importance of spatial factors on stock enhancement however, ideally requires the closure of significant areas of ground over a medium to long-term perspective. Temporary closures of the whole area, or initiation of a single small MPA for

example, may not provide unambiguous results. In practice of course, experimental studies large enough to provide unambiguous results may be difficult or impossible for socio-economic reasons.

2. Stock enhancement experiments should be adequately designed; acknowledging the particular characteristics of the spatial structure of the invertebrate stock in question. This implies a proper replication scheme at the relevant spatial scales of analysis according to the addressed question. The misleading use of the experimental approach in order to promote MPAs has gained space in the primary journals (Castilla, 2000; Castilla and Defeo, 2001; Wickstrom, 2002). Specifically, several experimental designs directed to show that the effects of “no fishing zones” beyond the boundaries of an MPA have been conceptually weak in the sense that there were usually no controls in the study and no strong evidence of an effect of the experimental treatment (Hilborn, 2002). Moreover, the use of too small a spatial scale in the experimental format as judged from the life cycle of the species (e.g. too small MPAs used in experimental treatments), can lead to over-optimistic or overreaching conclusions. Temporal scales directed to assessing the outcomes of stock-rebuilding experiments should also be consistent with the characteristics of the life cycle of the species involved, and the controls in this case could be surveys of the area believed to be affected before and after the intervention.
3. In the case of the stocks of littoral zones, measurement and estimation errors for density and fishing effort could be minimized, as both quantities can be estimated *in situ* and by individual fishing ground. This reduces uncertainties in the possible outcomes of any intervention. When using catch rate (CPUE) to estimate effects of an intervention, naturally occurring spatial distributions in density should be taken into account and experiments conducted on a spatial scale relevant to match the classical assumption of proportionality between CPUE and abundance (Prince, 1989). Discrete homogeneous areas in which catch rates accurately reflect the true abundance of a shellfish population should be established before an experimental intervention. Reductions in harvest rates cannot always be spatially replicated however, where for example, a strong gradient in environmental factors is present. Indeed, one of the main problems in conducting this kind of experiment is the control of access to large areas, and the ability to distinguish the relative contribution of experimentally induced stock variations, and those resulting from large-scale natural environmental and oceanographic processes.
4. As in any experiment, a limited range of credible hypotheses should be defined, followed by the use of proper statistical tools to decide whether significant changes are occurring over time. The application of the scientific method is straightforward in sessile species, because of the easy implementation of controls and treatments. McAllister and Peterman (1992) concluded that most of the approaches to fishery management have been non-experimental. The results (unexpected or expected) resulting from fishery management actions often lead to confusion, since management manipulations are not originally designed to distinguish rigorously between alternative hypotheses (see also Larkin 1978, 1984). The adaptive management approach, originally proposed by Holling (1978) and later implemented by Walters (1986) and co-workers (i.e. Walters and Holling 1990, Walters, 1997 and references therein) is worth considering in designing such interventions. Adaptive management can be defined as a structured process of “learning by doing” involving a modeling exercise and the implementation of large-scale management experiments, hand in hand (Walters, 1997).

5. In fast growing, short-lived invertebrates, management experiments are especially useful for evaluating the rate of stock rebuilding and in setting appropriate precautionary target reference points. Imposing a closed season is de facto a management experiment which is particularly useful for evaluating the capacity of a stock for population recovery following human perturbation.
6. Experimental enhancement procedures in shellfish should ideally be carried out in a community-based context in order to be effective; i.e. fishers must be familiar with, and agreeable to the nature and scope of the experiment; have accepted the necessary sacrifices involved and understand the potential benefits that realistically might be achieved from it in the medium/long-term. The implementation of large-scale experiments (on areas of 50 to 70 ha of intertidal and shallow subtidal) in cooperation with artisanal fishers in South American coastal waters has allowed the testing of specific hypotheses on natural re-stocking of overexploited invertebrates, including the economical viability of these operations (Castilla *et al.*, 1998).
7. Experimental management has also been suggested as a useful approach in newly developed shellfisheries, in which little or no information on stock dynamics is available (Jamieson and Caddy, 1986; Perry, Walters and Boutillier, 1999). At the beginning of fishery development, a precautionary approach could be implemented by setting precautionary management options, i.e. obviously suboptimally low effort levels. This approach is particularly important in coastal invertebrate fisheries in developing countries, in which an overall increase in fishing activity has not been accompanied by a corresponding increase in scientific and fishery information, and where the absence of demographic and fisheries studies has led to inadequate management.

Castilla and Defeo (2001) showed that fortunately, large-scale fishery experiments do play an important role in the evaluation of alternative stock rebuilding strategies in Latin American benthic shellfisheries, especially when they explicitly involve the participation of fishers in field experimentation (Castilla *et al.* 1998; Castilla, 2000). The exclusion of humans from Reserves on rocky shores in Chile, allowed the testing of the effects of handpicking and diving on shellfish abundance, and the evaluation of community elasticity (Moreno, Sutherland and Jara, 1984; Moreno *et al.*, 1987; Castilla and Durán, 1985; Castilla and Bustamante, 1989). Unreplicated experiments in Central and Southern Chile demonstrated that humans as specialized top predators constitute the key factor (Moreno, Sutherland and Jara, 1984; or "capstone" *sensu* Castilla, 1993), altering exploited and unexploited benthic coastal populations. This generates ecologically cascading effects that affect the structure and functioning of benthic or intertidal communities (Castilla, 1999). Varying rates of extraction of species at different trophic levels may translate into different community structures, thus enhancing the identification of linkages and strengths of ecological interactions. This information has been used by scientists to understand system elasticity and to translate ecological knowledge into management strategies.

In Chile, artisanal shellfisheries have served as the flagship guiding the implementation of important, novel and adaptive shellfish management schemes in the country (Castilla, 1994). These include the implementation of new co-management and fisher participatory tools for the extraction of benthic resources, such as Individual Non-Transferable Quotas (INTQ) and the Benthic Regime for Exploitation and Processing (BREP) incorporated into the Chilean Fisheries and Aquaculture Law. This law includes the implementation of regulations on TURFs, exclusively assigned to small-scale benthic shellfish artisanal communities and

linked to formal Marine and Exploitation Areas (MEAs; Castilla, 1994; Minn and Castilla, 1995; Payne and Castilla, 1994; Pino and Castilla, 1995; Castilla and Pino, 1996). Specific results of research on the fishery, ecological and economic context, and on community organization have been reported from studies in several MEAs located along the central Chilean coast (Fernández and Castilla, 1997; Castilla and Fernández, 1998). Key points of these are as follows:

1. The evaluation of benthic invertebrate stocks within the MEAs was carried out jointly by fishers and scientists, increasing the credibility of results, and strengthening the linkages between fishers, scientists and managers.
2. A marked increase in stock sizes of several shellfish, such as “loco”, key-hole limpets and sea urchins, was documented within MEAs, and evaluated through a comparative analysis of CPUE and individual sizes between MEAs and open access areas.
3. Collaboration between scientists and fishers within MEAs have facilitated the joint planning of biological, ecological and fishery studies, experiments, and fishery ecosystem approaches. In MEAs, fishers control enhancement and exploitation operations, although co-management of benthic shellfish also applies, and MEAs may be used as experimental fishery units.

The sedentary nature of some invertebrate populations provides a unique opportunity to conduct small-scale, highly localized fishing down experiments in order to evaluate spatial variations in resource use and fishers' attitudes to exploitation (Iribarne *et al.*, 1991). Prince (1989) described fishing-down experiments for the Tasmanian fishery of the abalone *Haliotis rubra* in order to test hypotheses about the relationship between CPUE and species abundance. Hourly catch rates of four individual divers were examined over seven fishing days. He also examined the factors that influence trends in CPUE, notably spatial fluctuations in abundance, as well as variations in abundance estimates as a result of short-term decisions of fishers. Catch and effort data were analysed by individual fishery blocks in order to estimate spatial variations in abundance and catchability. Drastic between-diver variations in catch rates were found to be due to dissimilar behaviour of fishers, as well as individual variations in efficiency (see also Prince, 1992). Prince and Hilborn (1998) and Prince *et al.* (1998) conclude that TURFs offer considerable potential benefits within a regulatory scheme.

4. EXPERIMENTAL CULTIVATION AND SEEDING

Apart from standard management methods described earlier which involve enhancement of stocks by reduction of fishing intensity, two main strategies of stock enhancement for sessile invertebrates are: (a) transplanting juveniles or adults from areas of recurrently successful settlement; and (b) seeding with spat previously reared in the laboratory or caught in collectors placed in the natural habitat.

4.1 A brief historical overview of shellfish hatcheries

Hatcheries for shellfish such as clams, scallops, oysters, and lobsters have operated in North America, Japan and elsewhere, starting as early as the late 1800s (see e.g. Rice, Valliere and Caporelli, 2000) with the intention of providing spat for public or private reseeded grounds. Most of these establishments, funded by local or national governments, were closed

around the mid-twentieth century or earlier, largely due to a general failure to demonstrate any effects of their operation on commercial fishery landings.

Earlier hatchery operations tended to release larvae into the wild fairly soon after hatching, and the general impression, confirmed by more recent studies, was that survival was low. The problem of demonstrating their contribution to the wild stock remains a major issue, but a lack of data has prevented any realistic cost-benefit evaluation. This is not surprising since under the open access conditions that generally prevailed, collecting adequate data to evaluate even the state of the stock was not a simple matter. More recent research on European lobsters, conch and other species described later, indicates that rearing to a later juvenile stage improves survival, but also drives up costs. The use of microwire tags or other means of identification of released juveniles also allows identification of recaptured hatchery progeny that is not easily accomplished with larval release.

Although revival of large-scale hatchery facilities is not a reasonable option, it is worth noting that at the time these operations were carried out, natural populations were generally fairly healthy, so that density-dependent mortality of releases may have been accentuated. The idea of using natural colour variants, especially where stocks are very depleted, might have been worth further consideration to test possible contributions from shore-based rearing facilities. For example, naturally blue lobsters occasionally occur in the wild, and the release of unusually coloured offspring might be easily detected in the wild as a natural tagging experiment – similar colour variants might be used for other invertebrate species. However, with respect to hatchery and release operations, the emphasis nowadays has switched to the use of relatively low cost equipment for local rearing that can be installed at the end of a wharf for example, and mainly involves bivalve resources. The use of variants of the “upweller” technology (see below and Figure 4.2), has shortened considerably the holding period, which is now effectively confined to the larval life in vitro, and has reduced the costs of hatchery operations. This has allowed local entities and organizations to rear shellfish seed with minimal plant or investment. This appropriate-scale technology appears to have made small-scale molluscan shellfish relaying a commercially feasible proposition, and in theory, the methodology might be extended to other invertebrate resources.

Due to degraded habitats and overharvesting, replanting schemes for clams is an operational methodology (Rice, Valliere and Caporelli, 2000). A common procedure has been relaying shellfish from natural populations in contaminated bays, to allow their depuration on clean private leases. Rice, Valliere and Caporelli (2000) describe the history of shellfish management and restoration efforts in Rhode Island, which began in the late 19th century, and these provide a general perspective on the evolution of shellfish enhancement activities.

1. From the late 1890s up to the Second World War, the Rhode Island Fisheries Commission operated a lobster hatchery in response to a decline in local lobster catches. Eggs were collected from wild broodstock, hatched, and larvae reared to fifth stage juveniles before being released. The project was terminated mainly for cost considerations, but also due to the failure to demonstrate any improvement in lobster catches. Currently there is an effort underway to restore lobsters to artificial reefs using settlement funds provided in compensation for an oil spill in Narragansett Bay in 1989.
2. From the 1930s to the 1980s, hatcheries were used to produce bivalve spat for public and private culture, but these efforts were not economically viable. The programme of longest duration was for relaying *Mercenaria mercenaria*, from dense beds in waters

closed to shellfishing due to pollution problems. Large-scale operations began in the 1950s, but were terminated in the 1960s when power dredging for shellfish was banned in Narragansett Bay. Since the late 1970s a small-scale programme pays a small fee to hand-diggers who transplant quahogs under supervision, from closed waters into clean, managed areas for harvest after depuration. Since 1997, dredge boats have again been hired to relay shellfish into management areas. A calculation based on maximum sustainable yield (MSY) considerations, restricts annual relays to not more than 10.3 percent of the standing crop. Finally, the Rhode Island Public Benefit Aquaculture Project, a joint educational effort with commercial fisheries involvement, is involving secondary level students in the nursery culture of shellfish (though marina-based upwellers) for seeding of public shellfish beds.

In conclusion, shellfish hatcheries have had an uncertain history as government-run institutions, but still operate locally in response to a growing demand for seed, especially for clam and oyster fisheries.

Experiments with New Zealand littleneck clams by Stewart and Creese (2002) showed that growth was highest but that mortality was also high, when transplanted low in the intertidal zone, and vice versa, high in the intertidal. A best compromise was to transplant to mid-tide level: this gave a high recovery rate of 60-90 percent, and clams tended to remain in the transplanted area. Transplanting would seem therefore feasible, although season of transplant and densities of transplanting need to be tested carefully.

Declines in wild production of soft-shell clams in Maine have led to a revival of interest in enhancing stocks from hatchery-grown seed, but predation is a serious problem (Beal and Krouse, 2002). In one experiment, seed were transplanted into boxes with mesh covers, which showed a 13 percent greater survival than uncovered boxes. Interestingly, survival was independent of density in the unprotected boxes, but inversely density-dependent in protected boxes. The strategy proposed is to transplant juveniles from the hatchery to near or below mid-tide levels, and to cover them with a flexible netting (6.4 mm aperture) raised several cm above the sediment surface, to protect them from predation. This can be removed before seasonal storm conditions ensue. By this time, (which precedes winter in Maine), lengths of 25-30 mm have been reached, and clams can burrow to escape predators. For soft-shell clams, growth to harvest will then take another 2-4 year depending on temperature, but will be considerably faster for other species in less extreme climatic conditions.

An example of the use of hatchery-produced spat in upwellers was the evaluation by Heasman *et al.* (2002) of two alternative nursery-rearing protocols for hatchery-produced *Pecten fumatus* larvae. This provides an example of possible pilot scale and experimental approaches using hatchery-reared spat and their grow-on in upwellers. Larvae were initially settled and on-grown on mesh downweller screens in a conventional hatchery. Two experimental protocols were then followed:

1. Spat were retained on downweller screens until large enough to transfer to a field nursery consisting of stacks of mesh screens located in an upwelling system. Stocking density per unit surface area of screen was critical in determining growth rate of *P. fumatus* spat in field upwellers. Irrespective of growth-limiting factors such as food, the stocking rate at which maximum growth rate was maintained was approximately 70 percent screen coverage.

2. An alternative nursery-rearing protocol settled spat on mesh screens using cheap nylon curtain material and retained these in the hatchery for 1-5 weeks post-settlement, before the mesh was removed from each screen, cut into sections, and placed in spat collector bags filled with coarse plastic netting before being deployed in the field for grow-on.
3. Subsequent survival after 30 days depended on spat size at deployment and on handling methods. Some 25-30 percent of 500-750 µm spat at 2-3 weeks post-settlement, were recovered at a size of >5 mm, suitable for transfer to grow-out facilities and comparable with that from tiered upweller nurseries. Screen to collector bag transfer required less capital and was less labour-intensive than tiered upweller systems.

The operations just described may best be described as aquaculture operations, but also form useful procedures before field seeding during enhancement.

4.2 Viability of stocked organisms

The use of hatchery recruits to enhance a stock will need to take into account the existence of natural bottlenecks in the habitat which could prevent the enhanced recruits contributing effectively to the population (Figure 4.1). This requires knowledge of constraints that operate in the wild, and the failure of many enhancement procedures appears to stem from inadequate knowledge of these natural factors. The genetic makeup of the seed used for enhancement should reflect the range of genotypes in the local population, since although it may be advantageous over the short term to add faster-growing strains, this risks creating an “enhanced” stock that is not well adapted to the environmental changes that will certainly occur, which the local stock through behaviour or hardiness may have adapted to overcome.

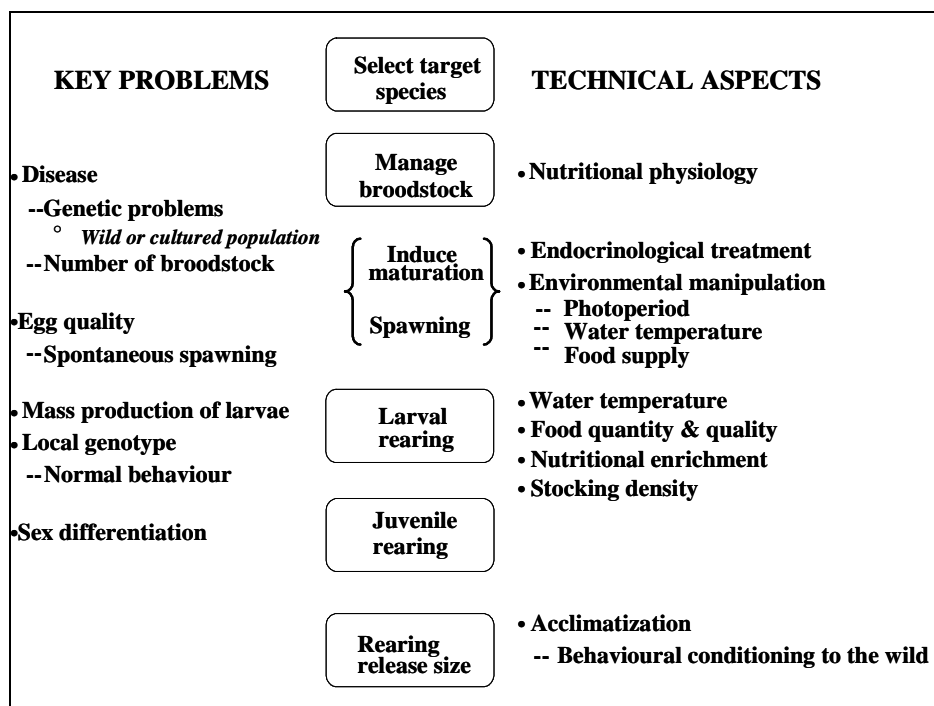


Figure 4.1 A listing of some of the key problems to be faced in a shellfish enhancement programme (after Tanaka, Seikai and Furuta, 1998).

The ideal size for stocking, as well as the likely size-dependence of predation mortality, may be tested by tethering animals of different sizes in the grow-out environment. This approach revealed a very high mortality for stocked conch (*Strombus gigas*) compared with juveniles from the native stock. This suggests that predation will be a difficult and costly obstacle to overcome (Ray, Stoner and O'Connell, 1994), since it requires cultivating conch to a minimum release size of 75-90 mm, which is a costly operation. Predation may also occur through the effects of a wide range of micro-predators on small settling shellfish (see e.g. Ray-Culp, Davis and Stoner, 1997). These include crabs, shrimps, lobsters and a variety of polychaete worms, and emphasize the importance of releasing juveniles at about a centimeter or more in size.

The re-stocking or enhancement of Homarid populations has been the focus of several research projects in the last decades. However, despite being able to successfully rear lobsters in captivity, there are few reports of newly settled European lobsters (*Homarus gammarus*) in the wild (Linnane *et al.*, 2001). One of the few well-documented enhancement experiments for crustaceans was conducted by Bannister, Addison and Lovewell (1994) on the European lobster, *Homarus gammarus*, using over 50 000 hatchery reared juveniles released at an age of three months; released animals being identified by microwire tags and conventional T-bar tags. Lobsters showed a considerable "site fidelity", remaining within six km of release sites. They survived in the wild up to six years, to be caught at legal size of 85 mm 4-5 year after release in the commercial fishery, and some animals already were egg bearing on recapture. An independent experiment with T-bar tagged animals allowed the fishery exploitation rate to be determined independently. Using this information, estimates of survival from release to recapture averaged between 50 and 84 percent, depending on assumptions made about tagging mortality and tag shedding during the experiments. This experiment seems to suggest that hatchery operations may be useful, at least for stock restoration of lobsters in depleted areas, if the problems of conserving the wild genotype can be avoided through use of brood stock from local populations. Bannister and Addison (1998) describe the associated lobster research programme on enhancement from the technical perspective of ensuring survival to commercial size of up to 50 percent of microwire wire tagged lobsters released. They concluded however that stock enhancement of this slow-growing species is unlikely to be economically worthwhile when the cost of running a hatchery is taken into consideration. They note however that a programme aimed at enhancing the natural breeding stock, or for tourism purposes associated with public visits to the lobster hatchery, may still be viable. Bannister and Addison (1998) emphasise that experimental testing is needed of whether hatchery-reared juveniles supplement or replace naturally settled shellfish before assessing the biological and economic benefits of enhancement programmes. Again, experiments must be designed to answer ecological questions and to make predictions about how stocking density of natural stock will affect survival and recapture rate. This is of serious concern for managers when trying to ascertain if restocking or enhancement programmes are going to be successful at the fishery level (Linnane *et al.*, 2001).

Site-fidelity following colonization is an important issue where private or local resource users are considering such an operation. Site fidelity was observed by Jensen *et al.* (1994) after colonization by European lobsters of an artificial reef erected on a flat sandy bottom some three km from the nearest natural reef. Colonization occurred after several weeks, and 48 percent of the 114 tagged individuals were recaptured at least once on the reef. "Vagrants" tagged on the reef were captured elsewhere, but generally less than 16 km away from the reef.

An experiment described by Shiota and Kitada (1992) involved the release of tagged individuals of a more mobile swimming crab, *Portunus trituberculatus*, in different seasons in shallow coastal waters of Japan, where the species is confined within the 30 m isobath. This gave recoveries of between 11–46 percent; 90 percent of which were recaptured less than 20 km from the release site, despite a spawning migration to shallow water from a hibernation area at 20–30 m depth. Again, this shows that restocking, even of mobile crustaceans, may be a practical proposition, although the economic effectiveness of this operation was not evaluated. A better documented experiment for a tagged inshore flatfish, hatchery-reared flounder can be mentioned in this connection, in the same waters, which was supported by a 2-stage random sampling survey described by Kitada, Kishino and Taga (1993), who found the operation to be profitable, even with a recovery rate as low as 15 percent.

Beal, Mercer and O’Conghaile (2002) note that success is uncertain when releasing large number of lobster larvae from a hatchery; however, costs are high for grow-on of post-settlement stages to a larger size before release. A strategy they found to be cost-effective, was a field-based nursery system for rearing cultured lobster juveniles in cages deployed on the bottom. Feeding was on the plankton, or by foraging on the fouling community in the cages. Rates of recovery in on-bottom growth cages were site-specific, but of the order of 25–40 percent to 5–7 mm carapace length. Presumably these juveniles might then be used for transplanting to favourable juvenile habitats as described by Bannister and colleagues, but doubts as to the economic viability of the whole operation stem from the slow growth rate of European lobsters.

In the tropics, the stocking of lagoons for harvest by artisanal fisheries has been practiced. Davenport *et al.* (1999) describe the stocking of a lagoon in Sri Lanka with *Penaeus indicus*: a species which does not breed in the lagoon, where the outlet of the lagoon is blocked seasonally by a sand bar. Over the winter to spring months the shrimp stock in the lagoon is almost entirely harvested. Previous twice-annual stocking with larvae and post-larvae could therefore be linked to subsequent catches, which corresponded to roughly 3.5 percent of the post-larvae released: catches were enhanced by some 1 400 percent over previous levels. Bioeconomic calculations demonstrated this to be ecologically and economically sustainable.

The possibility of using hatchery-reared queen conch to rehabilitate overfished Florida populations was evaluated by Stoner and Davis (1994) through a 15-month field experiment in the Bahamas, comparing hatchery-reared and wild juveniles of 85–120 mm shell length at two experimental sites; one with a wild population, the other without. Survival of hatchery reared conch after seven months was low (nine percent) compared with wild stock (28 percent), and thin shells, short spines and low burrowing frequency may have increased the vulnerability of hatchery stock to predation, and their growth rate was half that of the wild stock. Survival was somewhat higher where resident populations provided some density-dependent protection for introduced individuals. In an experiment with tethered animals, hatchery conch showed twice the mortality to predation of wild individuals, confirming their higher vulnerability. Despite this, the authors considered this a possible method of rehabilitation, noting that this approach to enhancement requires release of large numbers of high-quality large juveniles into appropriate habitats.

Successful enhancement programmes for conch, as for other species of invertebrate, will have to consider habitat requirements and how they shift during ontogeny. Sandt and Stoner (1993) found juvenile conch (35–54 mm shell length) to remain buried in clean sand during the day.

At 1-2 years they moved into seagrass and coral rubble habitats where growth rates were much higher. This movement may be in response to food requirements or predator avoidance, but needs to be taken into account in stock enhancement programmes. A further complication noted by Stoner and Ray (1993), is that juveniles remain aggregated within only a small fraction of the vegetated habitat, in an area where tethered individuals showed lower mortalities. Evidently, the requirements for survival of transplanted individuals vary on a local scale for reasons that are not clear, suggesting that experiments with tethered animals (or for other species, pilot-scale trials with juveniles grow-out in cages), in different habitats, could usefully precede any large scale transplantation.

4.3 Transplanting and thinning

Biological pollution of habitats containing significant shellfish biomasses has given rise to replanting schemes for clams in a number of localities. Relaying shellfish from populations in contaminated bays allows their natural depuration on clean private leases prior to marketing (Rice, Valliere and Caporelli, 2000). Such operations may allow the local management authority to charge a modest fee to private shellfish diggers transplanting stock – digging often being facilitated by the use of mechanical harvesters. A best compromise was to transplant to mid-tide level: this gave a high recovery rate of 60-90 percent, and clams tended to remain in the transplanted area. Transplanting would seem therefore feasible, although season of transplant and densities of transplanting need to be tested carefully.

Transplantation is intended to maintain or improve depleted or overexploited populations, or even to extend distribution areas to new grounds in order to establish new fisheries. Different approaches to transplanting are (a) relocation of seed or juveniles from dense beds to depleted areas; (b) collection and culture of local and imported seeds from e.g. long-lines or seed collectors, after which they are transplanted in a habitat suitable for species development (see e.g. Kristensen and Hoffmann, 1991); and (c) transplanting subadults or adults to supplement reproduction of natural populations, or in the case of “empty” habitats, in the hope of developing new self-sustaining populations (Peterson, Summerson and Luettich Jr., 1996).

There are many examples of the gathering of juveniles (oysters, mussels, clams) from one area and their transfer for on-growing to another (Quayle and Newkirk, 1989; Brand *et al.*, 1991). For example, juveniles of the New Zealand scallop *Pecten novaezelandiae* which settled on the outside of collector bags were redistributed to areas where natural settlement had been unsuccessful (Bull, 1994). Alternatively, juveniles can be transplanted on grounds that may be unsuitable for releasing very small spat because of predators, or adverse hydrographic conditions (see Tegner, 1989 and references therein for examples on sea-urchins). Kristensen and Hoffman (1991) transplanted seed of *Mytilus edulis* dredged from natural beds to 3000 m² culture plots, in order to evaluate individual growth rates and production within the period of transplantation. The effects of wave action and starfish and shore crab predation were mentioned as factors limiting success of their enhancement operations.

Addition/colonization experiments by transplanting adults from high-density sites to new areas are poorly documented for molluscs. Peterson, Summerson and Luettich Jr. (1996) reported a successful transplantation experiment with adult scallops *Argopecten irradians concentricus* from an abundant site to four receiver sites where the species had been virtually eliminated by a red tide outbreak. Transplanted sites enhanced local adult densities from 1-3 to 15 scallops m⁻² in two years, and local recruitment was up to five times greater than in years when no transplantation had occurred. However, settlement indices, as estimated from spat collectors,

did not confirm that the transplants succeeded through the enhancement of larval abundance. Despite this partial success story, local transplantations have usually been conducted on a trial and error basis, without evaluating the implications of such introductions in the colonized area. Active restocking should also be conducted carefully in order to avoid further unexpected ecological damage (Peterson, Summerson and Luettich Jr., 1996).

On larger spatial scales, experimental restocking trials from other sea areas (Brand *et al.*, 1991) or even from one ocean to another, have on occasions had at least temporary success (Larkin, 1991). For instance, a long distance extension of the distributional range of high-valued species has been achieved (e.g. for Japanese oyster *Crassostrea gigas*), and this species in many cases has replaced native oysters which have been decimated by disease or environmental change (see also Chapter 5 for additional information on invasions and species introductions).

As noted by Hannesson (1986), thinning of a population subject to density-dependent growth influences increases the potential growth rate of the survivors, and in the case of shellfish, small, young individuals may command a separate market price, making this two-stage harvesting a close to optimal strategy. One of the characteristics of harvesting by dredges or towed gear is the inevitable presence of small individuals in the catch, which ideally should be returned to the sea, but may not be since they command a market price. Fishers have ways of reducing the proportion of small individuals in the catch if there is a legislative incentive to do so. A scheme was introduced for the Georges Bank scallop fishery in the 1970s which did not rely on a minimum size limit (which would be difficult to apply where the animal was “shucked” from the shell prior to landing).

4.4 Recruitment enhancement and population seeding

Enhancement of wild shellfish stocks with hatchery-raised seed has been seen as a useful and, in some cases, economic way of restoring depleted stocks (Saito, 1984; Schiel, 1993), although on occasions its economic validity has been questioned, especially where large hatcheries are used. Natural production can be augmented through the use of collectors to catch spat in their natural habitat, or by inducing spawning and rearing larvae in the laboratory. In fact, due to the decreasing trend in landings of most important species, the number of spat released from enhancement programmes in some countries is continually increasing. For example, Kitada, Taga and Kishino (1992) documented a considerable increase in the number of spats of scallops and abalones released in Japan between 1983 and 1989 where scallops are one of the most important species used in stock enhancement programmes (*ca.* 3 231 million fingerlings were released in 1989). Although hatcheries may achieve economies of scale by providing spat to growers over a wide area, there are significant advantages in small local spat production, which conserves local genotypes. A new technological development, the “upweller” is now being used to produce seed or spat for local growers.

Despite a growing demand for entry into small-scale hard clam aquaculture in the USA, this has been limited by the cost of hatchery seed ready to replant at a suitable planting size (usually eight mm SL or larger) and formerly it was necessary to grow-on small seed to this size in a nursery. Ponds or impoundment facilities are other alternatives for grow-on, but often lack access to ready supplies of clean seawater and suffer from seasonal algal blooms. The use of floating trays for cultivation of spat led to an “upwelling system” located in a sheltered impoundment (Bayes, 1981: in Hadley *et al.*, 1999). Nurseries on land give high survival and rapid growth, but require expensive waterfront property and are energy- and

labour-intensive to operate. Field-based nurseries are inexpensive, but seed survival is often very low and success is site-specific. Hadley *et al.* (1999) described a floating upwelling system (FLUPSY) which has the advantages of land-based hatcheries, such as good survival and growth, with the low-cost operation of field-based systems. This approach can avoid high real estate costs by for example, being incorporated into a dock or floating pontoons on a wharf. The system described by Hadley *et al.* (1999) cost US\$ 4 500 to construct, with operating costs below US\$ 5 000 annually, suitable for small-scale growers.

Currently, small scale upwelling systems may be powered by a pump, airlift or water wheel, to ensure an upward flow of seawater through the facility, using the natural plankton therein to feed spat in stacked or side-by-side trays in the facility. Hadley *et al.* (1999) describe a tidally powered unit (Figure 4.2). Using this system, after larval rearing to settlement in a relatively limited facility, animals can be grown to a size where they are more resistant to predation at relatively low cost. Upwellers have proven to be extremely effective as bivalve nursery units and their use is steadily increasing in North America (Appleyard and Dealeris, 2002). Another variant of small-scale spat production is the wave-operated nursery system was developed by Hickman *et al.* (1999) for growing hatchery-produced spat of the New Zealand dredge oyster *Tiostrea lutaria* through to 20 mm, suitable for on-growing using conventional oyster farming techniques.

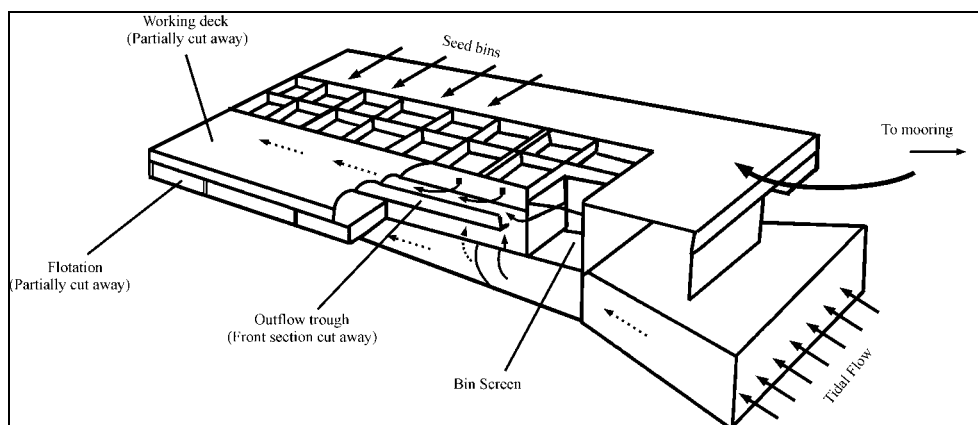


Figure 4.2 Representation of a tidal-powered upwelling system for spat rearing (redrawn from Hadley *et al.*, 1999).

4.5 Field identification in the wild of stocked invertebrates introduced from hatcheries

Linnane and Mercer (1998) compared five tagging methods to follow survival of juvenile European lobsters after release through multiple moults, and found that implanted coded microwire tags and elastomer implants were more efficient than rostrum ablation; in fact the rostrum was rapidly replaced after three moults. Survival rate, as usual, was higher for somewhat larger juveniles. Abdominal streamer tags showed good retention and survival, though they occasionally interfered with moulting. Branding resulted in somewhat lower survival. This type of comparative study seems advisable prior to any large scale enhancement programme involving restocking.

Studies with another cryptic species, the gastropod *Trochus niloticus*, showed that metal tags of folded aluminium foil can be easily picked up by a metal detector even in complex coral habitats for at least three months, and may have a wider application in following survival of other species of hatchery-released shellfish. From parallel experiments described elsewhere, the suggestion is that survival rate is relatively low in most localities, suggesting the desirability of an experimental approach prior to large scale stocking.

4.6 The use of collectors

Seed collectors are often used as a preliminary stage in transplantation programmes. However, they have also been used to collect early life history stages, which are then either transferred to a controlled environment for faster grow out to a marketable size, or released at the larger size needed to avoid high predation rates (Brand *et al.*, 1991). Kristensen and Hoffmann (1991) described successful transplantation experiments of the blue mussel *Mytilus edulis* in Denmark. The approach was based on transplantation of seeds collected from long lines and from natural mussel beds to bottom culture plots. Individual growth rates, production and biomass were evaluated and compared with natural mussel beds.

Timing and placement of shellfish collectors has to be varied according to life history characteristics of the cultured species for optimal results. Spatial and temporal patterns in spat distribution (both vertically and horizontally), duration of the spawning season, and sequences of larval stages, are all information required for spatfall forecasting and timing of collector placement, especially for those species with short duration peaks in settlement within the year. For example, settlement of the puerulus stage of the palinurid *Jasus edwardsii* was determined by crevice collectors at sites along the east coast of the North Island of New Zealand (Booth *et al.*, 1991). Depth of greatest settlement found on collectors varied with locality and time, but was within the upper 12 m. The ability of *J. edwardsii* to settle over a wide depth range may improve its chances of recruitment. The authors also described a device (closing crevice collector) for measuring puerulus settlement of *J. edwardsii* at depth. Phillips *et al.* (2001) tested different collector designs for the rock lobster *Panulirus cygnus* at different depths and distances offshore; they also examined the effect of collector size, and tested the effect of frequency of servicing the collectors. Five collector designs were set in shallow waters < five m, and were checked over four lunar months during peak settlement. Sandwich collectors had significantly better catch rates than others, and settlement rates were highly correlated with collector dimensions. Daily servicing for seven days around the time of new moon yielded catches 170 percent higher than those from a single monthly servicing.

In some cases collectors failed to reveal enhancement following adult transplantation. In fact, Peterson, Summerson and Luetlich Jr. (1996) showed that spat collectors are not a reliable indicator of recruitment enhancement, and this was confirmed by a poor correlation between larval settlement of scallops and subsequent recruitment data on the grounds. This suggests that collectors are not always effective for following natural enhancement of shellfish populations, and results using these techniques are species and site/time-specific. Detailed description of seeding techniques of this type is beyond the scope of this review but interested readers are referred to Quayle and Newkirk (1989) or Shumway (1991).

4.7 Effects of stocking on natural populations

Shellfish culture in Japan using hatchery juveniles to supplement wild stocks of fish and invertebrates has been implemented on a commercial basis for decades, and a review of

programme successes and failures was provided by Masuda and Tsukamoto (1998). Scallop stock enhancement appears particularly successful, with stress on the necessary high quality and viability of seedlings, and habitat improvement. Crop rotational practices may be followed, supporting a steady increase in yield, but for all species, questions of habitat improvement and the preservation of genetic diversity remain priorities.

The effects of scallop culture on total wild plus cultured production from a marine area, has been well documented by the Japanese scallop industry of Hokkaido (Kitada and Fujishima, 1997). The most striking feature is not only the considerable increase in landings following the use of culture techniques, but the reduction in the coefficient of variation of annual landings that has accompanied it. Seed release appears to be economically successful, but the most interesting implication is that a greatly increased level of spawning resulting from the artificially enhanced population has improved overall recruitment in the culture areas, which contrasts interestingly with the earlier mention in this text of the very low minimal %SPR levels for recovery of *Placopecten magellanicus*.

Three approaches to enhancement of estuarine bay scallop populations were tested by Goldberg, Pereira and Clark (2000) in an area where high densities of natural spat are uncommon: (a) collecting and distributing natural spatfall (which for shellfish may occur locally in very high densities reducing growth rates and promoting increased mortality); (b) introduction and overwintering of hatchery-reared stock to serve as spawning stock the following season; and (c) overwintering of the same in suspension culture, to create mobile spawner sanctuaries. The first option, involving planting of hatchery-reared spat at different times in different densities, showed that predation probably is the major factor influencing survival. Time of planting rather than planting density was a key factor, emphasizing the importance of deciding on an optimal season of release. Scallops released in an eelgrass bed had high overwinter survival and spawned the following season, thus contributing to the enhancement programme in two ways. Overwintering in suspension culture gave a 60-80 percent survival to spawning the following year: the advantage of this approach which mimics that just described for Japanese scallops, is that spawners could be transferred to “source” areas where spawning is believed to ensure optimal survival of seed. This seems to illustrate the contention that for shellfish, there is the potential to use a range of methods in areas where recruitment is poor but environmental conditions are not limiting, but that timing of the enhancement intervention is critical.

4.8 Production under controlled conditions

Other stock enhancement programmes are based on the production of larvae or post-larvae under controlled conditions, and their subsequent release onto the fishing grounds (Tong, Moss and Illingworth, 1987; Schiel, 1993). As an alternative to adult rearing, which in almost all cases is economically infeasible, one option is the direct placement of early hatchery-raised benthic stages into natural habitats favourable to survival (Schiel, 1993). This by-passes high predation and density-dependent effects (e.g. competition, cannibalism) and avoids the environmentally induced mortality that occurs in the larval phase.

Over recent decades much research has focussed on the rearing of shellfish spat or juveniles for enhance overfished stocks. Large-scale juvenile production units, and reseedling programmes have been carried out, particularly in Japan (Saito, 1984), but with variable success. Tong, Moss and Illingworth (1987) documented an enhancement strategy of a natural population for the abalone *Haliotis iris* using larvae reared in the laboratory and released after 13 days post-

fertilization. Schiel (1993) detailed a comprehensive enhancement programme for the abalone *Haliotis iris* in which 80 000 hatchery-raised juveniles were placed on rocky boulders at eight sites around Chatham Island, New Zealand. Economic analyses showed that only in three of the eight sites analysed was the internal rate of return positive; high natural mortality rates determined negative returns on the other five sites. Nevertheless, an overall positive financial return was obtained when all sites were combined.

High production costs and high predation on spat released directly into the natural habitat thus appear to be two major bottlenecks to consider when planning such enhancement programmes (Ogawa, 1988; Castilla, 1990; Kristensen and Hoffmann, 1991; Schiel, 1993; Parrish and Polovina, 1994).

4.9 Genetic factors

Genetic factors are now recognized as playing an important role in any enhancement plan. The application of genetic techniques to invertebrates is in many ways essentially similar to that in finfish (Thorpe, Sole-Cava and Watts, 2000). However, relative differences in the life history of shellfishes lead to particular problems in the use of genetic data to study invertebrate species and the potential for enhancement from a genetic perspective. The main role for genetics is the identification of groups of interbreeding individuals as the basis for a fishery or stock enhancement programme (Tringali and Bert, 1998). In the genetic assessment of invertebrate stocks, the large evolutionary range of invertebrates exploited and their widely different life history attributes, notably the mobility and the relative extent of the dispersive larval phase (see Chapters 2 and 3), poses additional problems when compared with finfish, which deserve special consideration .

At high densities of stocking, enhancement programmes can conflict with conservation considerations, and lead to loss of genetic diversity (e.g. Baltic salmon). Genetic differences between possible broodstocks also need to be taken into account (e.g. Kristensen and Hoffmann, 1991). Strains resistant to diseases or capable of faster growth or meat yield may be selected for, but the irony is that continued resistance to environmental changes is likely to be conferred by maintaining a wide range of genetic components in the broodstock population (Gaffney and Bushek, 1996). Slow-growing shellfish for example may be inefficient competitors for food, but live longer and be more resistant to environmental change. Genetic factors also played a significant role during large-scale transplantations (see Brand *et al.*, 1991 and references therein). The way that transplanted individuals affects wild stocks is not clear, although serious concern has been shown in the case of Baltic salmon that genetic “contamination” from escaped cage-reared fish is reducing the ability of natural populations hybridized with them to find their natural spawning grounds. All of these issues deserve more investigation, but in general, selection to improve commercial characteristics of shellfish in culture will inevitably continue.

Stock enhancement programmes should use information on population structure to optimize enhancement strategies (Shaklee and Bentzen, 1998) in such a way that the genetic diversity and character of existing wild stocks is protected. Genetic methods of stock identification allow tests of reproductive isolation and gene flow between populations using naturally occurring marks, thus avoiding the need for physical tagging. Protein electrophoresis has been widely used, but nuclear and mitochondrial DNA-based methods have less stringent tissue sample requirements, and their higher cost appears destined to decline, and relevant data bases are likely to grow as focus is directed at these more recent methods.

Boulding, Boom and Beckenbach (1993) used empirical parameter estimates from coding regions of mitochondrial DNA to assess genetic-variation in one bottlenecked and two wild populations of the Japanese scallop (*Patinopecten yessoensis*). The genetic diversity of a population bred in a small experimental hatchery in British Columbia for three generations was compared with its wild source population at Mutsu Bay (Aomori, Japan) and with a second wild population at Uchiura Bay (Hokkaido, Japan). The three populations were similar in the frequency distributions of the 11 mitochondrial clonal lines. This suggests that the experimental hatchery stock was not severely inbred and that gene flow between the two wild Japanese populations has been sufficient to prevent divergence. Genetic analysis of proteins and/or DNA variation have revealed the existence of multiple isolated stocks in what was formerly treated as a single population, but now must be referred to as a metapopulation, with a requirement to conserve the individual population components (Boulding, Boom and Beckenbach, 1993).

Design of enhancement programmes requires an understanding of larval transport in and out of selected areas reserves, and the understanding of whether selected sites will be self-seeding, and whether recruits from surrounding areas will intermix with the local stock, and hence what is the rate of exchange in recruits. Direct measurements of mean larval dispersal are needed to understand connectivity between members of a metapopulation, but such measurements are extremely difficult. Genetic patterns of isolation by distance have the potential to add to direct measurement of larval dispersal distance and can help set the appropriate geographic scales on which marine reserve systems will function well (Taylor and Hellberg, 2002; Palumbi, 2003). While low connectivity does not imply limited gene flow, the opposite is true: geographic genetic differentiation is strong evidence for low connectivity (Orensanz *et al.*, 2003). Some studies in invertebrates show that the genetic structure of populations, using polymorphic allozymes, revealed an expected congruence between the larval strategies and spatial differences in allele frequencies. For example, allele frequencies for planktotrophic species lack significant spatial heterogeneity over distances of > 1000 km, while there was significant spatial heterogeneity in allele frequencies over distances of as little as 100 km between populations of lecithotrophic species (Lambert, Todd and Thorpe, 2003). This long-term study (1985-1995) corroborated the spatial studies, showing that the population structure for these species is closely related to their realized larval dispersal. The authors show that the scale of larval dispersal and recruitment could be successfully examined in the field by means of transplant experiments between genetically and/or phenotypically different pairs of populations. The results obtained by the authors for two intertidal nudibranchs, however relevant for shellfish and other invertebrates, suggest that small, local populations are not totally open demographically and receive at least a proportion of their recruits from larvae generated within that population, thus increasing the probability of local extinction (Lambert, Todd and Thorpe, 2003).

Thus, the degree of genetic differentiation between locations can provide important indirect evidence, reflecting the pattern and scale of effective larval dispersal. Genetic studies conducted by Heipel *et al.* (1998) and Heipel, Bishop and Brand (1999) also showed that a stock of *Pecten maximus* from a semi-enclosed area (Mulroy Bay, Ireland) differed significantly from open water populations, suggesting that scallop populations in semi-enclosed coastal systems tend to be self-sustaining. The lowest genetic variability was recorded from this enclosed habitat, probably reflecting the relative isolation of Mulroy Bay, whereas dynamic hydrographic conditions in the Irish Sea and the Channel may generally ensure extensive mixing of the planktonic larvae. Lewis and Thorpe (1994) evaluated scallop stock enhancement through transplantation, which could reduce the fitness of receptor local

populations. They found highly significant inter-site genetic heterogeneity in a study of twelve populations of *Aequipecten opercularis* around the British Islands. Preliminary evidences of differentiation though transplant experiments could also be assessed through reproductive ecology studies. Ansell, Dao and Mason (1991) showed that differences in the reproductive ecology of different populations of *Pecten maximus* indicated relative genetic isolation among stocks (see also Mackie and Ansell, 1993). However, results should be contrasted through genetic studies and could not be supported by e.g. allozyme polymorphisms (Wilding, Latchford and Beaumont, 1998; see Orensanz *et al.*, 2003).

As the potential of enhancement of invertebrate stocks through aquaculture becomes increasingly realized, transplanting and introductions are becoming more common. To predict the genetic consequences of transfers, information on genetic differences between source and recipient populations is critical (Beaumont, 2000). This author highlighted that potential risks and consequences of hybridization should be experimentally assessed before introductions of scallops are carried out, because hybridization is unpredictable and can lead to loss of genetic diversity or breakdown of co-adapted gene complexes.

The possible effects of restocking in diluting, through mixing, a relatively small but locally well-adapted genotype, has been referred to as “genetic contamination”. It is now widely recognized that hatchery introductions of genotypes differing from the local population through cross-breeding with the locally adapted stock can negatively affect adaptation of the local race to its particular environment, and we should recognize that hatchery strains selected for fast growth in culture may not be adapted genetically or behaviourally for life in the wild. Tringali and Bert (1998) point out that conservation of a sufficiently large genetically discrete population could be affected by stocking programmes. One hypothetical example could be a project to reintroduce the queen conch, an important commercial mollusc, to island shelves of the Caribbean where populations have declined to low levels. An economically efficient approach would be to use a central hatchery to cultivate conch from one of the remaining abundant populations, and simply to distribute the juvenile conch from a small plane flying over each island shelf. The problem is that isolated conch populations are likely to have adapted to the hydrographic and ecological situation of each individual island shelf, such that the introduced animals would have a limited chance of completing their life history, and thus this enhancement methodology would compromise the possibility of recovery of any remnants of the local native stock.

5. ECOSYSTEM ISSUES

Sharp changes in the abundance of targeted and non-target invertebrate species, and also in the relative species composition of exploited communities, have been detected worldwide, as a result of growing fishing intensity (Orensanz, Parma and Hall, 1998). Overfishing with a progressive decrease in stock size commonly occurs at the highest levels of the trophic chain (Bustamante and Castilla, 1987; Steneck *et al.*, 2002). This has led to the recognition that in practice, harvesting affects incidental or intentionally different species within a community (Caddy and Sharp, 1986; Defeo, 1998; Castilla, 1999; Cabrera and Defeo, 2001). Over the last two decades, fishery scientists have taken a more holistic approach to management (Caddy and Sharp, 1986; Walters, Christensen and Pauly, 1997; Fulton, Smith and Johnson, 2003), and thus research has been directed at evaluating the ecological effects of fishing on invertebrate communities (Thrush *et al.*, 1998; Menge *et al.*, 1999; Tegner and Dayton, 2000).

Direct and indirect effects of fishing have been widely reported on for many marine benthic assemblages (Tegner and Dayton, 1999 and references therein). Much of this work has been focused on industrial shellfisheries with emphasis on mobile fishing gears, whereas little is known about the quantitative effect of small scale fishing gears intensively used in coastal shellfisheries. An understanding of the role of fishing and how it affects ecological functions is needed to place enhancement programmes in an integrated management context. In synthesizing the effects of fishing on estuaries and nearshore systems, Blaber *et al.* (2000) defined eight process-orientated categories according to the nature and extent of the fishing impact: target organisms, non-target organisms, nursery functions, trophic effects, habitat change, reduction of water quality, human environment, and extinctions. The marked decline in commercial catches of top carnivorous species and the general increase in species low in the food chain suggest potential trophic effects of fishing caused by the concurrent increase in fishing technology and effort. This agrees with the “fishing down the food web” hypothesis of Pauly *et al.* (1998, 2001), but it is also clear that changes in fishing technology have played a crucial role (Caddy, 1999a). A number of examples provided strong support to the sequential depletion hypothesis; i.e.: overexploitation of target species first and incidental ones later on. According to Orensanz *et al.* (1998) in their extensive study in the Greater Gulf of Alaska, the pattern of collapse in several shellfisheries is not haphazard but proceeds serially, starting with the most valuable resources.

5.1 Trophic cascades

Trophic cascades are defined by Pinnegar *et al.* (2000) as “predatory interactions involving three trophic levels, whereby primary carnivores, by suppressing herbivores, increase plant abundance” (Figure 5.1). These are also known as “community-level cascades” (*sensu* Polis *et al.*, 2000), where plant biomass is substantially altered throughout the system as a response of predator removals. Examples involving three or more levels in a food web are shown in Figure 5.2. from Pinnegar *et al.* (2000), and may not necessarily involve marine plants. Polis *et al.* (2000) define a “species-level cascade” as a mechanism which can account for changes in a subset of a community, such that changes in predator abundance affect several species, including one or a few plant species. They emphasise that although the definitions of species-level and community-level cascades refer explicitly to the three levels mentioned above, “they also apply to any multilink linear food-web interaction”.

Trophic cascades involving shellfish fisheries have been identified mainly on rocky substrates (Estes and Palmisano, 1974, see review in Tegner and Dayton, 2000; see also Steneck *et al.*, 2002), largely because on particulate sediments and in the water column, the linkages are less obvious. One could model quantitatively the linked species groups shown in Figures 5.1 and 5.2 through softwares such as ECOPATH and its derivatives (Walters, Christensen and Pauly, 1997; Pauly, Christensen and Walters, 2000), but for purposes of management it may be sufficient to be aware that such linkages exist, and avoid destabilizing the ecosystem by excessive removal of a species that is maintaining the ecosystem in balance.

Examples shown in Figure 5.2 (after Pinnegar *et al.* 2000) are: (A) the basic concept of a three-level trophic cascade involving plants, grazers and their predators; and specific examples of trophic cascades for: (B) Northeast Pacific kelp ecosystems, and the sensitivity of algal cover to predation on sea urchins by other food web components; (C) South African mussel and macro-algal equilibria affected by over-harvest of rock lobsters, showing also a reciprocal predator-prey relationship between rock lobsters and whelks (depending on their

relative densities); and (D) a typical Caribbean coral reef ecosystem, where overharvesting of reef fish can lead to urchin explosions and decimation of algae, or where either predation on sea urchins or the disease epidemics they are prone to, can lead to coral overgrowth by algae. From all these examples, one can deduce the facility with which overharvesting of a keystone component (Paine, 1994; Power *et al.*, 1996) of a food web can lead to major changes in productivity and holding capacity, if not to a transition to a quite different assemblage of species.

Figure 5.1 An example redrawn from Pinnegar *et al.* (2000) illustrating how overfishing sea urchins may tip the ecosystem from dominance by large algae to coralline barrens with minimal cover. (+ve implies a reinforcement of the box pointed to).

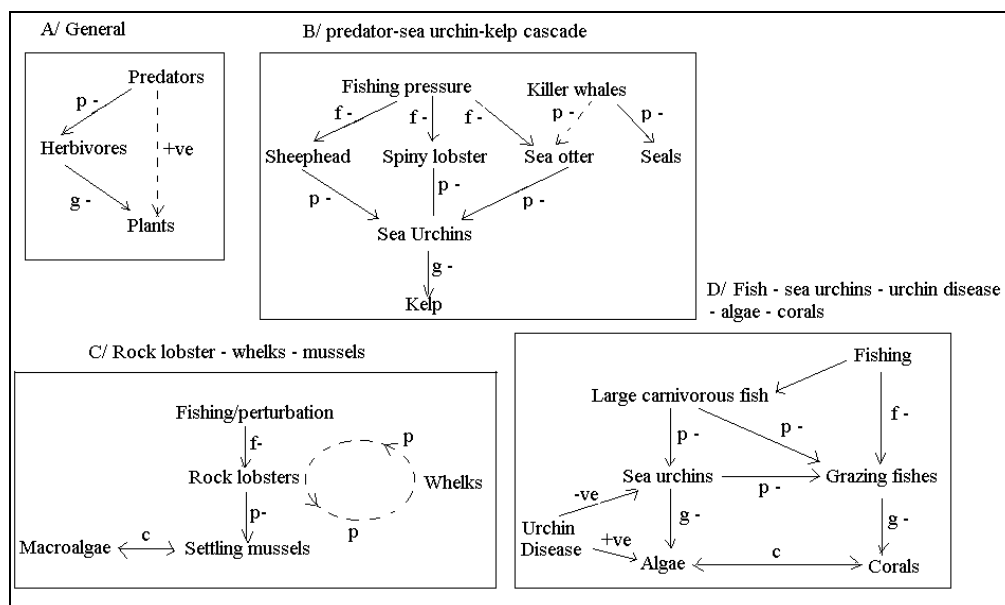
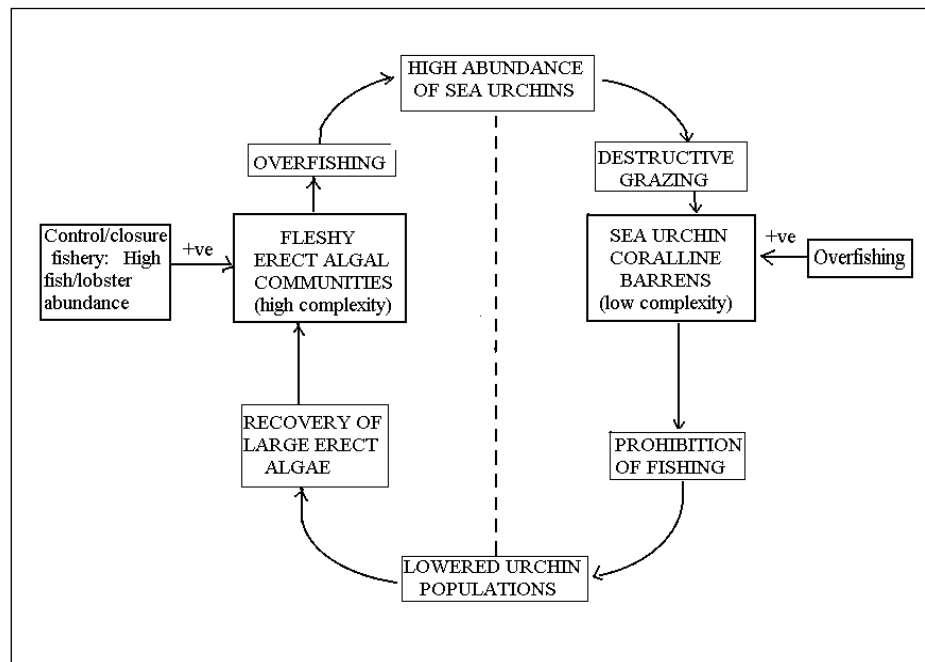


Figure 5.2 Examples of trophic cascades involving invertebrate resources (modified from Pinnegar *et al.*, 2000). [Key: f – negative effect of fishing on population size pointed to; p- similar effect due to predation; g – similar effect due to grazing; +ve and –ve: positive and negative effects of the factor at the base of the arrow on the box pointed to].

Dye, Lasiak and Gabula (1997) noted the difficulties in achieving recovery of depleted stocks of the brown mussel in South Africa resulting from the ever increasing level of exploitation of the species which resulted from “political and logistic problems stemming from law enforcement”. Mussels recruit preferentially to mussel beds, and where these have been depleted, algal cover replaces them. Dye, Lasiak and Gabula (1997) estimate that the rate of natural recruitment of mussels to substrates is very low and recovery may take up to eight years. They suggest that active enhancement be implemented in conjunction with rotational cropping as the best management strategy. Schoeman, McLachland and Dugan (2000) conducted a community-level, short-term and manipulative experiment involving a simulated anthropogenic disturbance, directed to address the potential effects of harvesting *Donax serra* on the macrofauna community of sandy beaches of South Africa. Some evidence suggested harvesting effects on the structure of the macrofauna, although the impacts appeared temporary because of the impossibility of controlling morphodynamic variables such as beach face slope and tidal rhythms. The high dynamics of the intertidal environment obscures the results of this kind of experiments because the effect of harvesting is not easy to assess over the short-term.

From South American experience in experimental shore ecology, Castilla (1999) notes that humans have high impacts on coastal and shore ecosystems through uncontrolled shellfish gathering, and that these impacts often occur in the sequence: (1) habitat transformation, fragmentation or destruction; (2) introduction of exotics or extinction of native species; (3) resource depletion; (4) food web modifications or “trophic cascades” as a result of 1 to 3. Through the institution of experimental “no-take” areas, he was able to observe and quantify some of these transitions. Often impacts from removal of grazing species led to increase algal cover. The exclusion of humans from rocky shores (“Reserves”) in Chile allowed effects of handpicking and fishing (diving) on shellfish abundance and community elasticity to be tested (Moreno, Sutherland and Jara, 1984; Moreno, Lunecke and Lépez, 1986; Moreno *et al.*, 1987; Castilla and Durán, 1985; Oliva and Castilla, 1986; Castilla and Bustamante, 1989; Durán and Castilla, 1989). Experiments in Central and Southern Chile demonstrated that humans, as specialized top predators, constitute the key factor (“capstone” species, *sensu* Castilla, 1993), altering exploited and unexploited benthic coastal populations, and generating ecological cascading effects that affect the structure and functioning of communities (Castilla, 1999, 2000). Varying extraction intensity on species of different trophic levels may translate into different community structures, thus enhancing the identification of linkages and showing the strengths of ecological interactions. This information was used to understand system elasticity and to translate ecological knowledge into management strategies (Castilla and Defeo, 2001).

Tegner and Dayton (2000) reviewed the effects of fishing in kelp forest communities organized around the primary productivity and physical structure provided by members of the Laminariales. This ecosystem supports a variety of fisheries, including harvesting of the kelp itself for alginates. The authors showed that sea-urchin grazing affects the abundance of both urchins and kelps, and the association of exploitation of various urchin predators with destructive levels of urchin grazing usually leads to cascading implications for other species dependent on the productivity and habitat provided by the kelps. Competition between abalones and sea urchins also affects some kelp communities. These ecosystem-structuring processes are also impacted through the ecosystem effects of fisheries for predators, abalones, sea urchins, and kelps. The authors suggested that no-take MPAs may be the only way to determine the true ecosystem effects of fishing.

Steneck *et al.* (2002) also reviewed the conditions in which kelp forests develop globally; and where, why and at what rate they become “deforested”, as well as describing trophic cascades affecting different members of these communities. Overfishing of highly valued vertebrate top predators often lead to increases in herbivore populations and consequent kelp deforestation. This has had profound and lasting impacts, leading to species-depauperate systems in e.g. Alaska and the western North Atlantic. Continued fishing down of coastal food webs has resulted in shifting harvesting targets from apex predators to their invertebrate prey, including kelp-grazing herbivores. The recent global expansion of sea urchin harvesting (Andrew *et al.*, 2002) has allowed kelp forest biomass to increase significantly. Shifts from fish- to crab-dominance caused by the absence of top predators in some places have occurred in coastal zones of the United Kingdom and Japan. Fishing impacts on kelp forest systems have been both profound and much longer in duration than previously thought. In other places, the large-scale removal of predators for export markets increased sea urchin abundances and promoted the decline of kelp forests over vast areas. The authors concluded that management should focus on minimizing fishing impacts and restoring populations of functionally important species in these systems.

Shears and Babcock (2003) reported that between 1978 and 2001 benthic communities in the Leigh Marine Reserve shifted from being dominated by sea urchins *Evechinus chloroticus* to being dominated by macroalgae, as a result of a trophic cascade resulting from increased predator abundance at reserve sites. Reserve sites had lower urchin *E. chloroticus* densities and a reduced extent of urchin barrens habitat, with higher biomass of the two dominant algal species (*Ecklonia radiata* and *Caipophyllum maschalocarpum*). At reserve sites, *E. chloroticus* was completely absent by 2001. Predation of gastropods and limpets on sea urchins at reserve sites are thought to be at least partially responsive for changes in community structure.

5.2 Predators, competitors and their control

Control of predators has been frequently mentioned as part of shellfish management programmes, and could be considered in the development of an enhancement plan. One of the suggested implications for enhancement programmes is that an unutilized niche in the food web or pyramid may exist, that can be filled by enhancement experiments (Figure 5.3). Experimental removal of competitors and predators might then be used to promote stock enhancement and allow time for adaptation if this is feasible and proves cost effective, and could diminish predation effects. The response of the benthic community will depend on the strength of interaction between species, as well as on the functional role of the species to be enhanced. Keeping in mind this multispecies framework, the returns from enhancement operations in theory could be maximized by deliberately overexploiting potential predators/competitors of the target species.

Contrary to this perspective, although control of predators or culling of a dominant competitive species has often been suggested as a way to enhance a targeted population, this strategy has not been a clear success in many cases, though circumstantial evidence from fisheries landings does suggest that in some cases, a decline in predators has had some positive impact on prey landings. The benefits from this operation have usually been moderate however, due to compensatory increases in other predators or competitors. Contrary to this perspective, it has been argued that these experiments be performed to promote stock enhancement under the hypothesis that increasing the availability of limiting resources (e.g. food and space) could promote competitive release or a diminution of predation effects on an economic valuable species (Carr and Reed,

1993). Experimental removal of competitors and predators could be used however, to evaluate the strength of, and better understand the ecological indirect and direct effects on the population dynamics and structure of a harvested population (i.e. side effects and cascade effects).

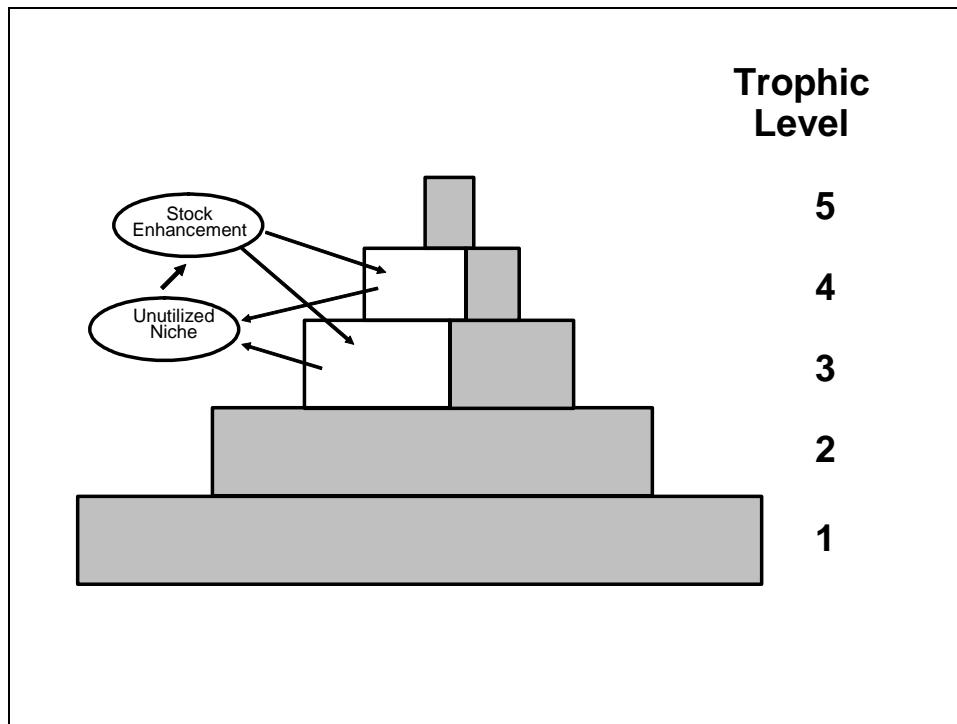


Figure 5.3 One of the suggested justifications for enhancement programmes is that an unutilized niche in the food web or pyramid may exist, that can be filled by enhancement experiments. This diagram (modified from Masuda and Tsukamoto, 1998) illustrates the concept, and may be valid where overexploitation has removed a keystone species from the ecosystem, which risks radical change in its absence. In most cases however, the results of such interventions on destabilized trophic pyramids are likely to be unpredictable.

Experimental and manipulative approaches to ecosystem management have so far not had a high level of success, but seem worth pursuing further where the ecosystem is sufficiently simple to allow some predictions to be made. Such approaches would certainly seem to provide a more reliable means of guiding community structure to a desired state than basing management decisions solely on the predictions of a group of separately viewed single species models (Sainsbury, 1988: p. 361). However, experimental manipulations must be executed first in small experimental units, because the complex dynamics in multispecies assemblages generally precludes a firm forecast of the ecological outcome of a single manipulation of species abundance (Sainsbury *et al.*, 1997; Castilla, 2000). Even in rocky intertidal communities where trophic linkages are among the best understood of any assemblage, relatively little is known about the effects of massive removals.

These alternatives are risky in nature, because ecosystem linkages are not always predictable. Often informal experiments performed on small experimental units are useful, but the complex dynamics in multispecies assemblages usually precludes a synthetic forecast of the ecological outcome of a single manipulation of species abundance. Nevertheless, some positive results

were obtained both for shellfish and finfish concerning competitor and predator control. These provide some cautious support for predator control as an ancillary management tool in some circumstances as an aid to enhancing stocks (see Cowx, 1994; also Northcote, 1995 for examples from finfish populations).

In general, starfishes are commonly identified as keystone species in intertidal invertebrate communities where artisanal shellfisheries take place, because small changes in abundance (growth and survival) of this predator may lead to disproportionately large impacts on community structure. It is thus expected that massive removals of these key species could be useful for stock enhancement. In an experimental and manipulative approach intended to diminish predation rates and favour enhancement. Kristensen and Hoffmann (1991) showed that predation by the starfish *Asteria rubens* on *Mytilus edulis* reduced the density of this mollusc from 3 500 to 1 800 ind·m⁻². Even though the predation was not concentrated in this case on the culture plots, it was clearly a potentially important source of mortality during enhancement operations (see also Orensanz, Parma and Iribarne, 1991). Natural restocking experiments conducted in Chile (Castilla, 1994), and the implementation of natural reserves and the concession of exclusive use of some grounds to fishers, led to predator control of subtidal populations of those organisms which are considered as competitors or predators of those species with the highest market economic value (Castilla *et al.*, 1993). These authors reported the removal of almost seven tonnes of starfishes and omnivorous grazers (e.g. the black sea urchin *Tetrapygus niger*) in a local cove, where they were perceived by fishers as dangerous for early stages of the muricid gastropod *Concholepas concholepas*; one of the most important exploited invertebrates in Chile. This kind of massive removal should be approached with caution however, due to the possibility of other trophic linkages, (such as the release of predatory control on competitors of shellfish for example). The dramatic effects of this kind of disturbances can be unpredictable and even negative for the targeted species in the long-term (see Foerster, 1954 for a well-illustrated case for salmonid populations). Carefully designed field and laboratory experiments are required to rigorously test hypotheses about the effects of predators under realistic conditions, and also to predict how species interaction strengths will change in response to the magnitude of fishing effort exerted (see Castilla *et al.*, 1993 for examples). The same conclusion was reached by Schielbling (1996), who evaluated the effects of predators on the distribution, abundance and behaviour green sea urchin *Strongylocentrotus droebachiensis*: the dominant grazer in the rocky subtidal zone in eastern Canada, whose abundance largely determines the structure and dynamics of the coastal ecosystem. This author also evaluated the potential for predatory control, and concluded that the lack of knowledge about predator-prey interactions in this system precludes any generalizations about the role of predation in regulating sea urchin populations.

Removal of predators has been reported as very successful in protecting restocked juveniles of the Pacific scallop *Platinopecten yessoensis* in Japan (Ventilla, 1982). This strategy has also been used in a large experimental enhancement trial in France with *Pecten maximus*, but requires further investigation (Lake, Jones and Paul, 1987). Removal of predators has been documented by Brand *et al.* (1991) to enhance pectinid populations in the Isle of Man. Potting of lobsters and crabs is permitted within small experimental areas in which the stock is being enhanced by transplantation of spat or cultivated juveniles, since these are potential predators of scallops.

Although proving a direct effect of predator removal is problematic from fisheries landing data, a number of circumstantial cases have been documented where prey species increased in productivity as groundfish have declined. Caddy (1981) documented the increase in octopus landings off West Africa after sparid stocks were fished down, and Caddy and Rodhouse

(1998) suggested similar mechanisms for a number of squid resources following groundfish catch declines. Although a specific linkage has not been documented, the unprecedented increases in lobster landings in the Northwest Atlantic seem to coincide with the collapse of groundfish stocks there. This case is still ambiguous despite a growing amount of circumstantial evidence. Elsewhere, for example, Kruse and Zheng (1999) found little evidence to suggest groundfish predation or competition provides an overriding explanation for crab fluctuations in the eastern Bering Sea.

When considering the effect of the collapse of Canadian groundfish stocks early in the 1990s as it affected Newfoundland waters, and especially invertebrate fisheries, Power and Newlands (1999) found a slow decline in mean trophic level of catches since 1900, but a most marked collapse between a mean trophic level of 3.5 and 2.8 between 1988 and 1995, accompanied by a shifts in targeting from groundfish to a higher proportion of invertebrates in catches. This may in part have been a result of changes in market demand, but the reduction of predation on the invertebrate catch increases observed cannot be discounted. The net result for eastern Canada from collapse of groundfish stocks is that a considerable degree of the resulting shortfall in landed values has been made up by increased landings and the high unit values of invertebrate resources.

Many municipalities in New England, USA, maintain public shellfish stocks, in part by using hatchery seed. A survey of 68 municipal managers responsible for these programmes (Walton and Walton, 2001) estimated annual seed loss averaged 44 percent, but survival to market was between 25 and 49 percent. Predation was viewed as the major source of loss, with the green crab, *Carcinus maenas*, the main threat, but there was a division of opinion on the effectiveness of predator trapping to reduce losses, although further studies were called for. Mark-recapture experiments were used by Shepherd (1998) to estimate survival of ages 2-4 year cohorts of two Australian abalone species. Natural mortality at 2-8 months was density-dependent, but from eight months to four years, was lower, and independent of density. Predators were mostly crabs and wrasses. A related issue is the importance of shellfish for sea birds, and Jennings, Kaiser and Reynolds (2001) described the effect of disturbance by shellfish harvesters on mortality of sea birds such as oystercatchers.

5.3 Interspecific interactions and side effects of fishing on the ecosystem

The large number of overfished shellfish stocks, as well as the indirect negative effects of fishing gear on marine ecosystems, confirm that management has often failed to achieve sustainability. A more holistic approach incorporating interspecific interactions and physical environmental influences would contribute to restoring shellfish populations (Botsford *et al.*, 1993). Potential side effects of introducing hatchery stock to the benthic community may include multispecies interactions for example. Hatchery-raised shellfish, when transplanted to natural habitats, may be more susceptible to predation and show different behaviour patterns from native juveniles (Schiel and Welden, 1987; Schiel, 1993). Increased mortality rates may thus occur before the organisms become established in the natural habitat.

As noted in Chapter 3, drastic declines of the surf clam *Mesodesma donacium* in Peru after an ENSO event enabled the increase in abundance of subordinate competitors for food and space, the suspension feeders *Donax peruvianus* and *Emerita analoga*. This suggests potential interspecific interactions because of competitive release of resources by formerly dominant members of the faunal community becoming depleted or sub-dominant. The fishery closure for 32 consecutive months, from April 1987 to November 1989, in the yellow clam *Mesodesma*

mactroides of Uruguay (see Chapter 3) was also used to investigate the effects of fishing activities on the demography of the yellow clam and on the sympatric suspension feeder, the wedge clam *Donax hanleyanus*. Markedly different effort levels over the long term generated major changes in the abundance and population dynamics of the wedge and yellow clams beyond the effects of exploitation; thus highlighting the ecological impacts of humans in the ecosystem, as extractors and as a source of physical disturbance. Abundance of the sympatric unharvested wedge clam *D. hanleyanus* rose steadily throughout the fishery closure. However, this could be explained as a monotonically decreasing exponential function of yellow clam density, i.e. what was effectively an interspecific stock-recruitment relationship, or in other words, an exclusion effect. In 1989 and 1990, during and immediately after fishery closure, both species occurred at their highest observed densities, suggesting that wedge clam recruitment was affected by the amount of fishing on yellow clam (Defeo and de Alava, 1995; Defeo, 1998). The spatio-temporal abundance of wedge clams was inversely correlated with fishing intensity over *M. mactroides*, suggesting that incidental damage (broken shells) and physical stress produced by sediment disturbance during harvesting were significant causes of mortality. Later information (1993-2002) confirmed the above trends, with an inverse relationship in abundance emerging between the two suspension feeders. In fact, anthropogenic disturbance in soft-sediments can lead to changes in substrate penetrability (Probert, 1984; Peterson and Black, 1988; Wynberg and Branch, 1992, 1994), which restricts the movement of burrowing organisms and increases mortality (Peterson, 1985). Hypotheses tested on the population dynamics and demography of exploited and unexploited bivalves by manipulating fishing effort, showed that human activities and endogenous density-dependent factors play important roles for exploited sandy beach molluscs (Brazeiro and Defeo, 1999; Lima, Brazeiro and Defeo, 2000).

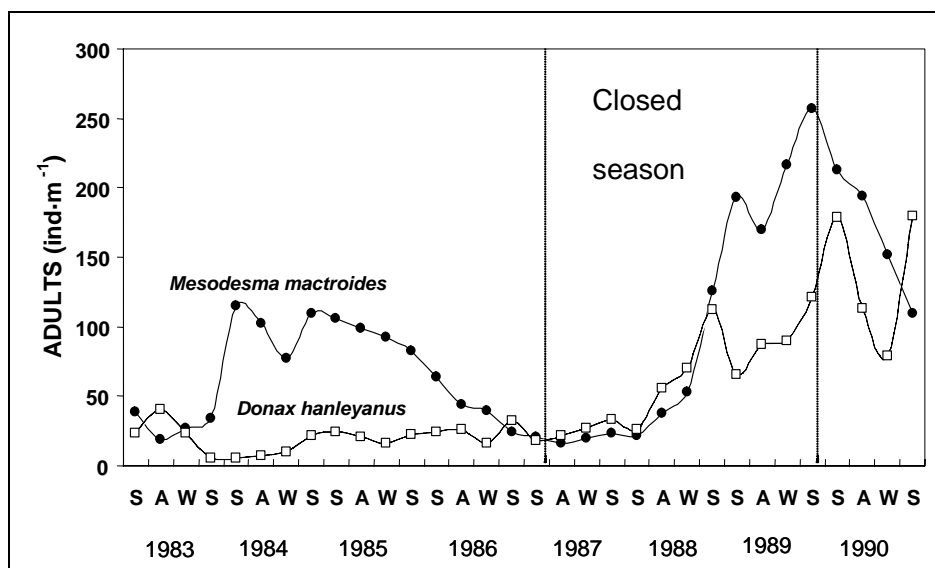


Figure 5.4 Long-term fluctuations in abundance (ind per stripe transect: ind·m⁻¹) of adults of *M. mactroides* (—●—) and *D. hanleyanus* (—□—) in Uruguay.

Positive interactions of associated species on the target species may also occur, and commensalism, mutualism and facilitation were indicated as important processes in soft sediments. Ahn, Malouf and Lopez (1993) showed that dense assemblages of the gem clam *Gemma gemma* enhanced settlement of four to five-day old hatchery-reared larvae of the commercially important bivalve *Mercenaria mercenaria*. A positive interspecific adult-larval interaction was demonstrated, and even the presence of empty shells of *G. gemma* enhanced

settlement of hard clam spat. Peterson and Black (1993) manipulated local densities of two bivalves of *Katelysia* in a Western Australia lagoon characterized by exceptionally high bivalve abundances. They showed that competition occurs only weakly, and that the addition of sufficient numbers of clams and dead shells filled with sand and implanted in the living position in the sediment mitigated mortality at low density. Thus, this particular positive interspecific interaction could be used to enhance settlement by simply scattering empty shells on the sediment to increase the quality of the settlement habitat. Indeed, as a possible alternative to costly restocking/seeding, habitat enhancement using artificial or natural materials added to the habitat may provide additional space for settlement and increase or concentrate stocks, possibly at a lower cost than rearing juveniles onshore (see Chapter 6).

5.4 Invasions, species introductions, massive mortalities and diseases

Introduction of exotics has been criticized from the strict perspective of conservation of ecosystems, and there has been little practical evidence that negative consequences of anthropogenic effects can be reversed, or that the introduction of exotic species, for example in ships ballast, can be easily controlled. The accidental introduction with seed or cultch of a variety of species of exotic predators and troublesome commensal organisms could however have been avoided by careful quarantine procedures, but these procedures have rarely been implemented. An appropriate precautionary approach to species introductions is described in FAO (1996), based in part on the ICES “Code of Practice on the Introduction and Transfer of Marine Organisms 1994”, and is described in Annex A to the above-cited FAO report. Although this text does not enter into detail on this topic, which is dealt with in the above FAO publication, inevitably we touch upon the implications of these processes in enhancement programmes.

A large number of organisms, some useful (such as the Manila clam, *Tapes philippinarum* and the Pacific oyster, *Crassostrea gigas*), but most of them harmful – (such as the slipper limpet *Crepidula fornicata*, various predatory gastropods, and a variety of seaweeds such as Sargassum weed and *Laminaria japonica*), are thought to have been introduced into European waters on shells or cultch during exotic shellfish introductions. The development of predictive models of the impacts of species introductions of commercial importance is a major issue for stock enhancement programmes. Introduced species could strongly affect recruitment of other taxa, and these effects varied between spatial scales and sites and among taxa (e.g. Orensanz *et al.*, 2002 and references therein). This implies that development of predictive models of the effects of similar invaders will require detailed knowledge of the responses of individual species that comprise local assemblages (Holloway and Keough, 2002). Changing climate might facilitate invasions by favoring introduced over native species, thus shifting to dominance by nonnative species (Stachowicz *et al.*, 2002). This has shown for sessile invertebrates, which are of major relevance in the context of this paper.

In the marine environment, apart from some estuarine introductions such as striped bass on the west coast of North America, most cases of introduced species that end up being the subject of enhancement activities were originally introduced accidentally. This is true for example of manila clams introduced with Japanese oysters into west coast environments of North America and elsewhere, and the predatory gastropod *Rapana* sp. which now forms the basis for a significant fishery in the Black Sea. There are relatively few cases where new species have been deliberately introduced, and there is a great reluctance to do so, despite the fact that for some species such introductions could have positive economic repercussions if successful. The repercussions may however be significant: thus the immigration of lizard fish

into the Mediterranean from the Red Sea through the Suez Canal has led to a new Mediterranean fishery off Israel for this species, but has constrained the hake stock in the eastern Mediterranean to a more restricted bathymetric range than formerly.

Another paradoxical application, which is the converse of enhancement, is the use of predators to control unwanted invasions of molluscs such as zebra mussels *Dreissena polymorpha*, which occur in large biomasses and lead to engineering problems in waterworks and pumping infrastructures. Molloy (1998) suggests that microbes represent the most promising biological control agents for these pests, given that predators are often not specific enough in their feeding habits. Practical experience in fact shows that exotic predators introduced for control purposes may consume species of importance to man.

Empty niches generated by kelp deforestation in the western North Atlantic as a result of population increase of herbivore populations were filled by introduced algal competitors, which carpet the substrate and threaten future kelp dominance. Other non-native herbivores and predators became established and are now dominant components of this ecosystem (Steneck *et al.*, 2002).

Harmful algal blooms are more frequent than previously due to high nutrient levels caused by coastal pollution, and while shellfish populations may reduce the density of blooms, the possibility of harmful effects is a real one (see Babaran, Espinosa and Abalos, 1998). In choosing an area for enhancement, any historical records of harmful algal blooms that occurred in the past in the area need to be investigated. Accumulation of toxins resulting from algal blooms and viral diseases may produce massive mortalities that must be addressed. Stock enhancement programmes for beach clams could be constrained by the accumulation of toxins associated with algal blooms and can cause mass mortalities of clams or render them unsafe for human consumption. The increasing short-term occurrence of this phenomenon makes commercialization and immediate consumption highly risky in areas where these blooms regularly occur (McLachlan *et al.*, 1996). In this context, massive mortalities of suspension feeders in South America almost decimated yellow clam populations all along thousands of km of coast during the 1990s (Fiori and Cazzaniga, 1999). The occurrence of cold atmospheric fronts that accumulated high concentrations of dinoflagellates in the surf zone, have been invoked as a cause of massive clam mortalities along the Brazilian coast (Odebrecht *et al.*, 1995), as well as being associated with specific viral diseases.

Arntz *et al.* (1987) demonstrated massive mortalities in the recreationally and commercially harvested sandy beach bivalve *Mesodesma donacium* in Peru, as a response to the strong ENSO climatic phenomenon, and this formerly dominant member of the macrofauna disappeared following ENSO episodes due largely to an increase in sea surface temperature. The intertidal black abalone *Haliotis cracherodii* has experienced mass mortalities along the coast of California, USA, since the mid-1980s due to infection by a pathogen that leads to a fatal wasting disease called “withering syndrome”: the foot of the abalone atrophies until it can no longer adhere to the substratum (Friedman *et al.*, 2000). The presence of the pathogen, and warm water conditions associated with El Niño, may accelerate the development of withering syndrome and the rate of decline of black abalone populations. Anthropogenic disturbances, such as the discharge of heated water or global warming, may thus increase the incidence of this fatal disease (Raimondi *et al.*, 2002).

5.5 Techno-ecological interdependencies

One additional management problem related to the enhancement of stocks relies on the effect of technological externalities produced by contemporary fisheries for other species, or even on interactions between coastal commercial and sport fisheries in the same area. Once again, legislation must be implemented to avoid confrontational competition between fishers for different target species, or with different gears, probably by some form of zonation by gear type usage, possibly in addition to separate zones for fishers and other users of the coastal zone. This is likely to be especially relevant in cases where enhancement is conducted in coastal nursery areas that are also attractive grounds for other fisheries.

Increasing fishing capacity and introducing technological changes aimed at increasing fishing power may have undesirable effects on the habitat used for stock restoration programmes. These interactions have reduced our ability to calibrate effective fishing effort and mortality, and hence, introduced a major uncertainty into estimating population variables. Complementary studies should be carried out on a case-by-case basis to identify less damaging new technologies that have a reduced impact on the environment. Well-designed experiments provide useful information on the impacts of the technologies on particular habitats, as well as on the species being enhanced and its biological community. For example, maximizing the productivity in many scallop fisheries needs to consider the effects of indirect fishing mortality and disturbance of the seabed through dredging (see example by Bull, 1994). This should lead to a regulation of fishing intensity in these areas, and will contribute to establishing an optimal periodicity of a rotational approach. One of the most important artisanal shellfisheries in Argentina since the 1940s is based on the extraction of the clam *Mesodesma mactroides* (Olivier *et al.*, 1971). The fishery collapsed because the use of tractors (instead of manual collection as elsewhere in South America). This markedly increased fishing power and negatively affected the physiographic characteristics of the beach substrate (Olivier and Penchaszadeh, 1968).

In sequential fisheries, in which juveniles and adults are spatially segregated and harvested with different techniques, technological and ecological interdependencies occur, affecting both population components and generating externalities (Seijo, Defeo and Alava, 1994). A typical example is the surf clam *Mesodesma donacium* fishery of the intertidal and shallow subtidal of Chilean sandy beaches (Defeo *et al.*, 1993). Intertidal juveniles are manually harvested during low tides, whereas free and semi-autonomous hookah divers operating from artisanal wooden boats, harvest subtidal adults. In this example, stock enhancement programmes should be carefully planned to minimize potential problems and risks. The most appropriate individual size for restocking should be evaluated, taking into account which population component is easier to handle and transplant and less costly to enhance.

The impact of fishing on the structure of an ecological community might depend also on the number of species that are marketable, and on the corresponding unit prices. For example, the net revenues derived from fishing could be maximized by deliberately overexploiting a less valuable but dominant species, in order to increase production of a subordinate competing species with higher market value. Existing market conditions could also lead to depletion of the most commercially profitable species to such a low population size that the fishery for an interdependent stock becomes economically unfeasible. This suggests that humans behave as generalist predators when closed seasons/areas and other regulatory measures are imposed on harvests of traditional resources (Smith and McKelvey, 1986). This has been frequently observed in shellfisheries (Bustamante and Castilla, 1987; Orensanz *et al.*, 1998; Cabrera and