

Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources



Cover:

Illustration representing women engaged in artisanal fishing of the clam *Venus antiqua* in southern Chile. Emanuela D'Antoni.

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by

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PREPARATION OF THIS DOCUMENT

This document has been prepared as part of the regular programme activities of the FAO Marine Resources Service, Fishery Resources Division, aimed at promoting improved practices for the assessment and management of fisheries through the production of background documents, technical guidelines and handbooks. In several parts of the world, the productivity of natural populations of marine invertebrates have come under excessive pressure, as rising demand and prices for these generally high-value species lead to their overexploitation. Environmental changes to nearshore environments due to other human activities have on occasions contributed to damaging nearshore stock productivity further. A partial solution has been to enhance or restore populations of nearshore areas, using techniques that range from those resembling extensive aquaculture, to the scientific management of stocks as used for finfish populations. This document reviews the scientific knowledge derived from enhancement activities in shellfish and other invertebrate populations, and attempts to extend the concept of “enhancement” to include any activity which increases the productivity of a marine resource, whether this is by controlled harvesting, stock additions or habitat/environmental manipulation. Multidisciplinary guidelines and operational criteria for conducting and assessing invertebrate stock management programmes are also provided.

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ABSTRACT

A broad review is provided of factors relevant to enhancing populations of invertebrate resources and methods promoting their recovery by natural recruitment, restocking or habitat restoration. The review focuses on the biological, technical, environmental, economic and biological factors affecting the feasibility of restoring or enhancing productivity of commercially valuable local invertebrate populations. Three categories of enhancement activity are recognized: restoring or enhancing stocks by conventional management methods, transplanting or seeding, and the use of juveniles produced from collectors in the wild or from hatcheries. Some guidelines are provided on issues related to enhancing recruitment, site selection, experimental closures, ecosystem considerations including predator control, as part of a stock management and enhancement programme. Ownership and co-management issues, and the necessary decisional rules for successful management are discussed, as well as how to reconcile the enhancement programme with other uses of the coastline. Spatial and geographical considerations are addressed, including allocation of areas for enhancement, rotational harvest schemes, use of refugia for protecting juveniles and the spawning stock, and the impact of the use of coastal zones for other human activities.

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INTRODUCTION

This study focuses on issues related to the scientific management and the feasibility of enhancement or recovery of stocks of commercial marine invertebrates. The review touches on a taxonomically wide range of resources, with inevitably special emphasis placed on those edible species colloquially referred to in English as shellfish. These include both molluscs and crustaceans, as it is here where much of the practical experience in invertebrate management and enhancement is to be found, but we have extended the review to include other invertebrate resources such as echinoderms which are now of importance for inshore fisheries.

Productive natural populations of invertebrate resources are coming under pressure as rising demand and prices for these generally high-value species leads to their overexploitation (Castilla and Defeo, 2001). A decreasing trend in global catch rates and landings from overfishing in the absence of proper management has on occasions led to stock collapse. Nonetheless, in comparison with marine finfish populations where stock enhancement methods are still controversial and limited in success, more positive results have been achieved in enhancing or restoring shellfish populations of nearshore areas. In fact, shellfish culture has been suggested for other purposes in addition to food production, namely, ameliorating nutrient-rich effluents and suspended materials coming from fish farming, and reducing algal densities (e.g. Folke and Kautsky, 1989). In other areas and for other species, shellfish populations suffer negative population impacts from human activities other than fishing and thus may serve as indicators of nearshore ecosystem health. Although we do not enter into this subject area in detail, issues related to consumer health may result from the effects of coastal pollution on shellfish beds, and shellfish monitoring may be used to monitor chemical and bacterial pollutants resulting from other human usages of coastal waters.

Although questioning whether enhancement activities represent a reality or what he calls “techno-arrogance”, Grimes (1998) notes that in the decade from 1986 to 1996, there have been major conferences on roughly a biennial basis on the theme of the practice and evaluation of marine stock enhancement, reflecting an increasing enthusiasm by managers with this theme. But he asks whether our state of knowledge is adequate to make this more than just an interesting concept? The answer for finfish stocks is certainly ambiguous in many cases and for macrocrustacea also, despite some interesting developments that will be mentioned in this text. For molluscs and some echinoderms however, the accumulation of experience suggests that in many cases, stock enhancement activities have been successful when viewed from a commercial perspective, if the necessary habitat carrying capacity was available (Castilla, 1988; Andrew *et al.*, 2002). In fact, most failures stem from a lack of prior evaluation of the availability of suitable habitat. In this respect, Grimes (1998) notes that aspects of the ecology of juveniles in their actual or potential nursery habitats, have become research priorities for enhancement activities. Experience in Japan, the country which has made most efforts to apply these technologies, were summarized by Nakata (1995), and seem generally to reflect some important successes, especially where technology and ecological intuition are applied hand in hand with a knowledge of species biology. In the final instance, success must be evaluated economically, but even here a case can be made for leniency, if it involves the reintroduction of a species to its original habitat (especially if after this has been accomplished successfully, enhancement can be terminated). In the case of some sports fisheries where incidental expenditures by enthusiasts generate considerable revenues outside the fishery sector, Grimes (1998) documents cases where cost-benefit analyses (in the case of sports fish) have shown a positive return even if less than one percent of the stocked animals are recaptured.

As for fish resources, conventional management measures such as minimum size limits and reductions in catch or in fishing effort have their role in stock enhancement of shellfish, by reducing fishing mortality and increasing survival of spawning stocks. Classical methods of stock assessment (e.g. Beverton and Holt, 1957), often will need to be reviewed and adapted however, to take into account the very varied shellfish life histories of invertebrates, and this effort began in the 1970s (see e.g. Caddy, 1975; Conan, 1984; Fogarty and Murawski, 1986; Orensanz and Jamieson, 1998; Smith and Botsford, 1998). Stock assessment methods applied to crustacean populations were discussed by Cobb and Caddy (1989), and more recently widely applied, e.g. in workshops of FAO Regional Bodies, such as WECAFC (2000) for shrimp and groundfish fisheries, and WECAFC (2001) for spiny lobsters. Specific studies on diverse topics of stock assessment methodologies have been published on crustaceans (Arena Barea and Defeo, 1994; Rugolo *et al.*, 1998), molluscs (Rueda and Urban, 1998; Palacios, Orensanz and Armstrong, 1994, 2000; Orensanz *et al.*, 2003) and echinoderms (Andrew *et al.*, 2002; Chen and Hunter, 2003). As for finfish stocks, uncertainties in stock estimates, and major but often hidden changes in fishing power, coupled with risk-prone management, have led to collapses of some stocks. Although this text does not enter into detail on stock assessment methods, which are dealt with elsewhere in FAO publications (e.g. Sparre and Venema, 1992), inevitably we touch upon some of the issues involved in the routine management of these resources. Even with a previously successful management scenario, pressures from new entrants may lead to stock declines if there is an effectively open access regime, so that stock assessment alone without a linkage to management decision-making will of course prove ineffective.

Cowx and Welcomme (1998) provide an extensive review of some methodologies used for finfish enhancement in freshwaters, and some of their conclusions undoubtedly apply to marine invertebrates also (see also Welcomme, 1996). They concluded that limits to production had already been reached in most freshwater systems, and that environmental conditions continue to deteriorate as a result of human activities in watersheds. That production from many shellfish populations has declined under inadequate management regimes was documented by various authors in the review of invertebrate fisheries assessments by Caddy (1989a, b); not only by overfishing, but because nearshore resources are also susceptible to environmental degradation, as are the fishery resources of enclosed marine systems (e.g. Caddy, 1993a; de Leiva Moreno *et al.*, 2000). Hence, it would be difficult to discuss shellfish management issues separately from the environmental management of coastal waters, lagoons and estuaries. In fact, in many situations, the health and productivity of invertebrate populations is the best indicator of environmental integrity: see, for example, “mussel watch” programmes for monitoring coastal pollution (O'Connor, 2002). The use of habitat restoration to improve yields of marine coastal species does occur locally, and important actions of this kind can be subsumed under the establishment of marine parks or marine protected areas (MPA's). Shellfish restoration cannot be considered independent of other activities to restore the coastal environment, but projects principally aimed at restoring ecosystems such as seagrasses and other vegetation (e.g. Dennison *et al.*, 1993), may incidentally consolidate bottom sediments and provide settlement substrates for shellfish such as bay scallops and juvenile penaeid shrimps (Coles *et al.*, 1987).

Other actions which have affected productivity of invertebrate populations have generally occurred at a much larger scale and have rarely been considered under the heading of fisheries management methodologies. For example, the reduction of nutrient runoff, primarily with the intention of improving water quality first in estuaries and river runoff (e.g. the Rhine - Boddeke and Hagel, 1995) and only later in receiving basins (e.g. in Dutch coastal waters – Boddeke,

1989), has nonetheless had impacts on shellfish production in estuarine and adjacent coastal areas. As noted by Cowx and Welcomme (1998), the main objective of ecosystem interventions in developed countries, rather than increasing the fishery productivity, is the more ecologically motivated one of restoring degraded marine environments. In some cases this may also affect shellfish production. Improving inshore water quality should not be discounted as an important mechanism, or precondition, for shellfish stock enhancement, in ensuring that the product meets health requirements for human consumption. In North America, polluted inshore shellfish grounds may be closed due to sewage runoff and health impacts, but such areas may still play an important role as spawning refugia seeding adjacent open grounds (Estevez, 2002). In some case however (e.g. Boddeke and Hagel, 1995), the reduction of nutrient runoff by pollution abatement in order to reduce eutrophic effects in coastal waters, may actually reduce productivity of shellfish stocks, although what the net effect of eutrophication is on all human activities in the coastal zone remains a controversial question. Nonetheless, control of runoff of nutrients, sediments and especially disease vectors affecting shellfish grounds (Klinck *et al.*, 2001), the smothering of shell and gravel habitats, and the need for their restoration, are all important considerations in a successful stock enhancement programme. This might include for example the replanting of sea grass beds and restoration of coastal wetlands for reasons other than stock enhancement *per se*, such as for the conservation of biodiversity. The linkage between environmental manipulation and shellfish production is a very sensitive one, as illustrated by Figure 1, which shows the synergistic effect of three common anthropogenic effects on estuaries: increased outflow of nutrients, of sediments, and reduced water outflow due to irrigation and flow manipulation.

In tropical environments, the intensive stocking of coastal ponds and lagoons for penaeid shrimps and other shellfish resources has become economically important, but raises controversial issues relating to the incidental effects of shrimp culture on local communities and coastal fisheries for the wild stocks (Primavera, 1991). For example, the social conflicts between intensive pond culture and the rights of local fishers has become a heated issue in coastal waters around the tropics in recent years (James, 1999). In fact, the excessive proliferation of shrimp ponds at the expense of the natural barrier of mangrove forests, may affect an important nursery area for coastal fishers, as well as reducing protection to coastal lands from storm surges. Thus, some questions related to aquaculture and restoring inshore shellfish resources fall directly under the provisions of integrated coastal area planning (Chua, 1997). Deforestation of mangrove areas for pond culture not only impacts the use of coastal mangrove forests as a nursery area for natural fishery stocks (Robertson and Duke, 1987), for firewood production, and as noted, protection against storm surges (Jagtap *et al.*, 1993). Another issue that falls within the context of interactions of invertebrate enhancement activities with other uses of coastal waters, relates to the practice of using the voluminous bycatch of shrimp trawling, consisting of juveniles of commercial species and trash fish and invertebrates, to feed pond/raised fish and shrimp (Naylor *et al.*, 2001). Although this practice avoids waste, it is also likely to negatively affect supplies of low-priced fish for food security. The end products of intensive aquaculture may often be exported, without a large share of the benefits necessarily returning to the coastal community, and intensive development of pond-culture may impinge on traditional access rights to harvest shellfish and other resources. All of these issues are ancillary, but form part of the larger picture that has to be taken into account when planning a fishery enhancement activity.

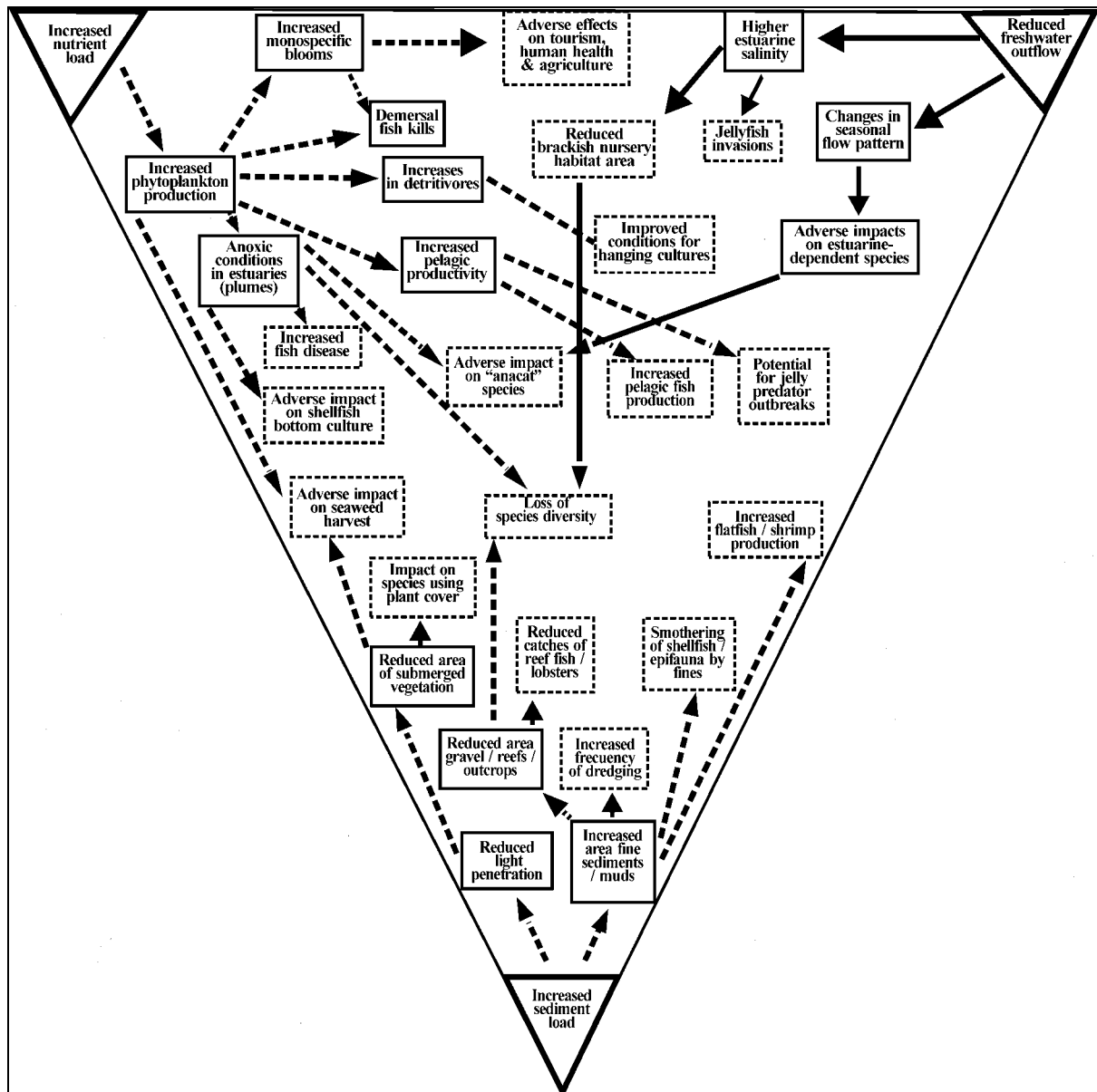


Figure 1 Diagrammatic representation of some linkages between three human impacts on estuarine fisheries and shellfish culture: increased nutrient loading, increased outflow of sediments and reduced freshwater inflow, typical of rivers subject to irrigation or blockage by barrages or dams (from Caddy and Bakun, 1995).

Many developed and some developing countries have implemented restocking programmes in order to restore threatened or endangered resources, such as for example, pearl oysters. As noted by Sims (1993), if animals are transplanted into, and grown successfully in their transplanted environment, and are allowed to mature and spawn, it may not be necessary to repeat an enhancement exercise annually. In such cases, the benefit/cost ratio for this approach over time is almost certain to be positive in light of the train of benefits a healthy invertebrate population should yield into the indefinite future. The potential for enhancement activities appears to have increased with the ratification of the 200-mile Exclusive Economic Zone, especially for those countries (see Kitada, Taga and Kishino, 1992) which have ceded some managerial

responsibility for coastal resources to local government or fishers' cooperatives. Although earlier enhancement activities using large-scale release of very young organisms were of doubtful success, some new small-scale developments provide a more promising picture, but one where careful consideration of the ecological, social and economic context is needed. In many countries, legislation does not permit the exclusive access rights to a marine area that these methodologies require if enhancement is to be implemented by the private sector, or local municipal agencies, and this emerges as a major constraint on the creation of productive employment in coastal economies. Hence, over-centralized governmental decision-making is probably one of the major handicaps to coastal shellfish management, while devolvement of decision-making over local resources provides a favourable climate and support to local initiatives. Under favourable circumstances, stock enhancement using seeded organisms may be a viable alternative management strategy for shellfish stocks, but one where a number of problems are not always evident prior to commencing such a programme, as will be discussed in the following sections.

In the specific case of shellfisheries, some intrinsic characteristics of stocks impose additional problems and constraints to the implementation of enhancement programmes. Benthic invertebrate populations are usually spatially structured resources with patchy distributions (e.g. Caddy, 1975; Orensanz and Jamieson, 1998). Their population dynamics are extremely labile, and sensitive to variations in environmental conditions, even on a reduced scale of meters. This may generate spatial gradients in growth rate, recruitment and mortality (Caddy, 1989b, c; Schoeman and Richardson, 2003). Marked preferences for habitats and other environmental factors often show up this way, and highlight the need to consider spatial distribution patterns carefully when planning stock enhancement programmes. Another factor of utmost importance for sessile and sedentary stocks is the occurrence of density-dependent (DD) mechanisms controlling growth, mortality and recruitment at small operational scales. The effect these processes have on recruitment, however, may show up at varying spatial scales depending on whether DD occurs before or after dispersal of eggs and larvae. Pre-dispersal DD processes include reduction of growth and fecundity at high density due to competition for space or food, and the DD of fertilization rate in broadcast spawners. Typical post-dispersal DD processes involve settlement or recruitment inhibition, or post settlement mortality due to high densities of local adult residents, where gregarious settlement of larvae in the neighbourhood of adult conspecifics occurs (Orensanz *et al.*, 2003). The markedly different spatial scales at which these processes operate vary according to the life cycle of each species, their mobility, the speed of larval development, and larval life stage duration (e.g. Perry, Walters and Boutillier, 1999). Castilla and Defeo (2001) call for a detailed species-specific analysis when planning stock enhancement programmes.

In this document we analyse several different techniques for promoting the active enhancement of productivity in shellfishes. Some guidelines and criteria for conducting and assessing enhancement programmes are also provided. The book is presented in eight main Chapters. Chapter 1 describes the functional categories of invertebrates and how this leads to differing management and enhancement modalities. The basic mechanisms for shellfish enhancement are defined, namely natural stock regeneration, experimental cultivation and seeding, and habitat restoration issues. Chapter 2 provides some broad generalizations on stock assessment methodologies, as well as suggesting information requirements for monitoring stock condition and recovery. Management guidelines are discussed, including the development of some specific indicators useful for evaluating stock status, the relative merits of different management tools, the organizational requirements for management, and the implications of harvest control laws for restoring shellfisheries. This Chapter also deals with some biological

features of invertebrate stocks that impose additional problems and constraints to the implementation of enhancement programmes, notably the extremely labile population dynamics and high sensitive to variations in environmental conditions, even on a reduced scale of meters. The effects of spatial gradients in growth rate, recruitment and mortality, as well as intense density-dependent mechanisms controlling these processes, are discussed. The role of life histories is highlighted in order to plan and implement enhancement programmes and to perform natural restocking experiments, suggesting the need to address the question of adequate spatio-temporal scales for carrying out enhancement exercises. Chapter 3 discusses concepts related to metapopulation theory and their relevance when planning natural stock regeneration programmes. The examples provided include a comparative synthesis of alternative spatially explicit management tools under a framework of management redundancy, especially where metapopulations are concerned. Some case studies derived from large-scale natural restocking experiments are also provided, including the role they are beginning to play in the evaluation of alternative management policies for benthic invertebrates is described. Apart from standard management methods described involving enhancement of stocks by reduction of fishing intensity, Chapter 4 addresses two main strategies of stock enhancement for sessile invertebrates: (a) transplanting juveniles or adults from areas of recurrently successful settlement; and (b) seeding with spat previously reared in the laboratory or field hatcheries, or caught in collectors placed in the natural habitat. Chapter 5 analyses ecosystem issues relevant to enhancement exercises, notably the pros and cons of control of predators or culling of a dominant competitive species as a way to enhance a targeted population. Chapter 6 pays special attention to habitat issues, because it is our view that reducing exploitation alone on the stock being restored will not be effective if critical habitat has disappeared. In Chapter 7 we suggest some guidelines for conducting and evaluating stock enhancement programmes, ranging from consideration of experimental design to economic projections on the success of this type of activity, and the need to incorporate risk and uncertainty in a formal decision analysis of enhancement programmes. It is important to mitigate the undesired effects of rent dissipation in open access systems, and Chapter 8 emphasizes the need to allocate property rights, including institutionalizing co-ownership authority between local government and coastal communities and the role of territorial use rights under a collaborative/voluntary community framework in enforcing enhancement programmes. The cross-linkage between experimental enhancement protocols and the active participation of fishers is suggested as the strategy to be followed in order to conduct enhancement programmes and improve the status of small-scale shellfisheries.

1. THE CONTEXT FOR ENHANCEMENT OF INVERTEBRATE STOCKS

1.1 Functional categories of invertebrate marine resources

Orensanz and Jamieson (1998) classify invertebrate species into four categories as shown in Table 1.1, with particular attention to their habit, the likelihood of metapopulations, and the spatial scales important for their management.

A similar but more detailed classification of shellfish fisheries is given in Hancock (1979). A remark could be added to this classification, that some slow-growing species with particular habitat requirements can be classified as *k*-selected species (bold in the above Table) requiring more care in management, while others (in italics) may be classified as invasive or *r*-selected species (see e.g. Caddy and Sharp, 1986). These latter are likely to be more resistant to overfishing, or likely to profit from ecological disturbances, but will be difficult to

manage for sustainable yield given characteristically large population fluctuations. With respect to the concept that species in category 4 above consist of single large stocks, this may generally be true, but evidence suggests for some squid species and perhaps other cephalopod resources, that “temporal metapopulations” exist, whereby sequential microcohorts may replace each other over time within the same season.

Table 1.1 A practical classification of commercial invertebrates based on a classification by Orensanz and Jamieson (1998).

	Examples	Resource type	Probability of Metapopulations	Spatial scale
1	Corals	Sessile	High	Small
2	Scallops, abalone , <i>sea urchins</i> , clams, barnacles, <i>mussels</i> , sea cucumbers	Sedentary benthic	Intermediate	Intermediate
3	Crabs, lobsters, octopus, king crabs , conch , other gastropods	Mobile benthic/demersal	Intermediate	Intermediate
4	<i>Squid</i> , <i>euphausids</i> , <i>shrimps</i>	Highly mobile demersal or pelagic	Low	Large

The above characterization of resources logically, leads to quite different management modalities, taking into account particularly the degree of motility and the duration of life histories, as shown in Figure 1.1.

	Short-lived	Multi-annual	Long-lived
Pelagic/schooling	Size limits, seasonal closures, control F/capacity, quotas <i>(e.g. krill, squids)</i>		
Motile/demersal	Seasonal closures, control F/capacity, MPAs/access rights <i>(e.g. cuttlefish, loliginid/reef squid, octopus)</i>	Control F/capacity, maintain age structure/ spawning potential/MPAs, quotas <i>(e.g. lobsters, large/deepwater crabs)</i>	
Sessile or semi-sessile, high dispersal	Spatially differentiated access rights (e.g. rotating harvests), density control <i>(e.g. thinning and transplanting), stock enhancement, predator control?</i> <i>(e.g. tellinids, bait worms) (e.g. clams, sea urchins/cucumbers) (Giant clams, red coral)</i>		
Sessile or semi-sessile, low dispersal	Rigorously enforced access rights, refugia/MPAs <i>(e.g. abalone)</i>		

Figure 1.1 Various modalities of management frameworks and techniques used for invertebrate management, as a function of: (a) life history duration, and (b) motility.

1.2 The context for shellfish enhancement and restoration

Historically, shellfish harvesting was arguably the first and easiest way early humans harvested food resources from the sea, and the numerous shell middens scattered along the shores of the Americas and elsewhere attests to the importance shellfish and other invertebrates had for earlier hunter-gatherer communities. Shellfish were harvested by hand or with simple equipment, from the shore, by diving, and from small inshore craft, and these modes of harvesting have persisted to this day. The first steps to cultivation of these resources also probably occurred early on, simply as a way of storing small specimens and surpluses to immediate needs, and later on observing that growth had occurred. Whatever the mechanism, traditional approaches to extensive or intensive cultivation of invertebrates were and are common along sheltered marine coastlines, and are still an important source of wealth to coastal communities, to whom shellfish resources provide food, employment and income.

Table 1.2 summarizes the range of mechanisms for stock enhancement considered in this document, ranked by increased density of cultivation and degree of intervention. Even though offshore invertebrate resources are now also exploited by industrial scale operations (and these will also be discussed), management and conservation of near-shore shellfish resources is still largely a community-based activity. Given that local communities in developing countries generally have limited skills and resources to invest in the infrastructure required for intensive aquaculture techniques, the importance and potential for managing natural stocks, and its transition through exclusive use rights to extensive cultivation of inshore shellfish resources, becomes evident. There may exist traditional methods locally of holding stock live prior to marketing as a means of market timing to increase prices received for wild-collected animals. It would be a logical step to develop holding methods further, as a stage between gathering and holding animals live, to simple techniques of grow-on. Particularly for molluscan shellfish and other plankton feeders, the advantage of not having to provide supplementary feeding becomes evident. A wide range of traditional and modern approaches to shellfish enhancement with or without extensive cultivation exist, and these go hand in hand with traditional user rights over the tidal and subtidal zones, and could be introduced elsewhere as a further means of providing extra income within coastal communities. Although not discussed in detail here, the holding and grow-on of products such as bait worms, marine organisms of importance for pharmacological purposes, or as curios (see Wells, 1989), are other supplementary income sources that can be explored by local communities or lease owners. The use of zoned management and the extensive culture of shellfish may be regarded as compatible modalities, and may be contrasted with intensive and large-scale aquaculture, where the high commodity value of invertebrate products attracts investments coming from outside the local community, and where the high value product is often exported. The high cost of land and facilities for onshore hatchery or pond culture in fact often requires outside investments, and this is likely to mean that intensive aquaculture may not help much to solve local problems of food security. The technical requirements for intensive aquaculture development, and the financial bottleneck to be overcome with the rearing of larval stages and juveniles under controlled conditions, all point to the need for simpler more extensive approaches to shellfish enhancement, and provide possible avenues for future small-scale development. A major emphasis on improving natural shellfish restocking, especially in developing countries is indicated, but small-scale rearing techniques for seed have recently been developed that could be readily transplanted to developing countries.

The natural social context for enhancement of invertebrate populations therefore, is in rational exploitation of inshore shellfish resources by some form of harvest allocation to a limited number of participants, using methodologies of extensive cultivation using simple and low-cost technologies. These activities fit well within a community-based decisional hierarchy, and should be especially favoured if mechanisms exist for controlled or exclusive access to the local population through licensing or leasing of intertidal or subtidal areas.

1.3 Possible approaches to resource manipulation: some working definitions

Three feasible approaches to enhancing invertebrate populations emerge from the marine literature:

1. Natural restocking (stock regeneration: Table 1.2) as a passive process. This essentially is an extension of standard methods of resource management used for other fisheries resources, although specific features of invertebrate life histories need to be taken into account (see Caddy, 1989a for some examples of fishery management approaches for invertebrate stocks).
2. Direct seeding of early benthic stages or adults collected from other places. This is usually referred as “transplanting”.
3. Introduction of animals either reared in the laboratory, in field hatcheries or on shellfish concessions in the sea, or caught in collectors placed in close proximity to traditional areas of recurrent settlement.

We first clarify what is intended by the term “stock enhancement” as used in this document. Bannister (1991) defined **enhancement** as the “releasing activity of a stock for the public good without the intention of directly benefiting an exclusive user group”. He sees this concept as differing from “**sea ranching**”, where the production from aquaculture techniques is released into a sea area with exclusive access confined to a limited number of harvesters. In other words, following this definition, where access is not limited, “enhancement” is essentially a government-sponsored activity. We will be using the term “enhancement” in a wider sense however, as any intervention that improves the productivity of a shellfish resource and renders the productive activity more sustainable, and do not exclude a role of private individuals, companies, cooperatives or coastal communities in this activity, where the legislative framework allows for this.

We accept that “sea ranching” is an activity that only makes economic sense given the high investments in aquaculture needed for production of juveniles, if those who have made the investment have exclusive harvesting rights to the product. However, an alternative objective might be the restoration of a stock that has been seriously depleted, and such a restoration scheme may have to be in part at least, financed and carried out with government assistance. In this second case, if successful, the future train of benefits from the resource over time may justify such activities, which may also receive an ecological justification in terms of restoring a damaged ecosystem. It is notable that government-sponsored hatcheries for lobsters, oysters and other resources were in operation in a number of western countries in the early twentieth century (e.g. Rice, Valliere and Caporelli, 2000), but public access to the resource, prior to limited licensing schemes being introduced, was not at the time restricted. More importantly, there was almost no attempt made at the time to evaluate the effectiveness of these hatcheries, and this historical background has made for justifiable caution in promoting similar enterprises in the public sector.

Table 1.2 Range of mechanisms for stock enhancement considered in the paper, ranked by increased density of cultivation and degree of intervention.

Mechanism	Activity	Habitat/ environment control or improvement	Social Context	Comments
Natural stock regeneration	Control access/fishing effort/or catch. Assess growth and exploitation rate	Harvest gear does not damage habitat	Rights not necessarily assigned geographically	Fisheries management measures and infrastructure needed for “wild” fishery.
Seasonal closures	Control seasonal access	Ensure harvesting gear does not damage habitat (e.g. ban of use of hydraulic harvesting for clams in hypoxic environments) Avoid fishing in periods of settlement or when oxygen of bottom waters is low	Usually assign access rights to the whole fishing area, but only in certain months or for certain days of the week	Fisheries management measures and infrastructure needed for “wild” fishery
Rotating harvesting schemes	Restrict access annually to specified sub-areas	Fishing area divided into subareas, each containing approximately the same share of the population Ensure harvest gear does not damage habitat	Access rights only assigned to a specified part of whole fishing area, and this sub-area is changed annually	Local management
Extensive cultivation on open coasts or in estuaries	Natural stocking of grounds, habitat improvement, predator control, thinning	Preparation of “beds” for enhanced spatfall; enhance substrates for larval settlement; possibly thin-out juveniles or transplant them elsewhere for grow out. Consider land-based effects	Community, cooperative, company or individual rights	Local or private management: (leases or ownership of grounds)
Intensive cultivation in hatchery, ponds etc. Transplant into lagoons, intertidal, or subtidal zones	Stocking of grounds from hatcheries or upwellers. Reseeding, predator control, habitat improvement, fertilization, broodstock improvement, thinning	Consider and respond to land-based effects and nutrient, pollutant or sediment runoff	Company or individual rights	Private management: (leases or ownership)

We would assert however that there is still a tightly definable role for enhancement activities, whether or not they can be strictly referred to as “sea ranching” following the Bannister (1991) definition, or whether they fall under the heading of “enhancement” using our wider definition (as would “sea ranching” itself). The closure of many government hatcheries for shellfish, was in part because of high costs, and because no evidence of the survival to harvest of the released juveniles was available to justify their continuation. Any mechanism which involves what is effectively a central government payment to a small group of citizens accorded exclusive access to a national resource raises the question of subsidies, an issue currently being addressed in the case of fishing capacity. One can envisage some municipal or local government support, or

support from international funding agencies, to get such potentially profitable activities underway, but as soon as possible, they should return to the private sector under regular governmental review. Enhancement activities might also be envisaged for restoration of formerly valuable, but now rare or endangered species, through interventions assisted by local or national governments. The focus of shellfish restoration technologies and approaches, at least for inshore resources where enhancement activities are practiced, should ideally remain in the local or private context. Such activities are beginning to provide benefits with relatively low start-up costs in some countries, especially the Americas, from some new developments in small scale management approaches, and from new, low-cost methods of rearing shellfish spat.

In practical terms, for finfish, there is a continuous spectrum of activities from intensive cage culture with feeding, through hatchery release of juveniles onto public grounds, to marine ranching, where supplementary feeding is provided on local artificial reefs. Effectively, for motile invertebrates a similar transition occurs. In this document where use of artificially produced seed is concerned, we are mainly interested in activities referred to in Figure 1.2 as “release of spat or juveniles”, which does not exclude sea ranching, but we consider this (other than the aspect of supplementary feeding) as differing largely in terms of the social and ownership context within which it occurs. Sea ranching and other methods for molluscan culture, such as the release spat and juveniles into nearshore areas, by preserving the natural food web, avoid some of the organoleptic problems encountered when consuming aquaculture-raised fish fed on artificial diets, (hence the mention of “good taste” in Figure 1.2). In conclusion then, while retaining Bannister’s definition of “sea ranching”, we feel it is helpful to extend the concept of “enhancement” to include any activity which enhances the productivity from a marine resource, whether this is by controlled harvesting, stock additions or habitat/environmental manipulation.

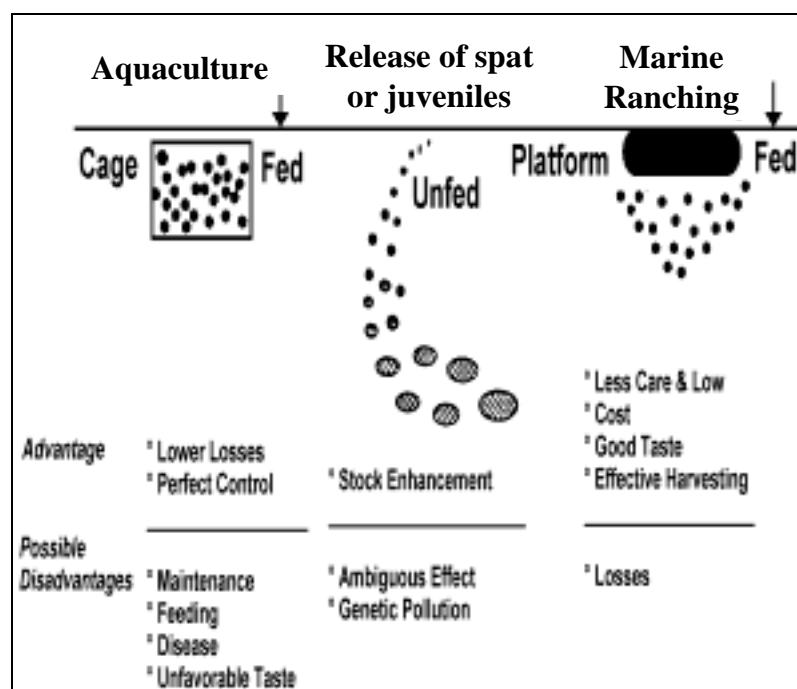


Figure 1.2 Illustrating the functional transition between cage culture (aquaculture) through stocking of public waters by releasing juveniles collected in the wild or produced in hatcheries, to marine ranching within exclusive access (after Masuda and Tsukamoto, 1998).

We note that this wider usage of the term “enhancement” respects the common usage of the term, and allows us to consider different interventions under the sub-headings “recruitment enhancement”, “genetic enhancement”, “habitat enhancement”, “environmental enhancement”, etc. Although such a subclassification is usually impractical so far for lack of data, in theory, one should in future be able to look at the potential cost-benefit of these different approaches to enhancement prior to initiation of any enhancement activity.

The artificial rearing in hatcheries of juvenile invertebrates (often referred to as “spat” or “seed” in this document, though this is strictly speaking correct, only where molluscan bivalves are referred to), for release into the wild, is only one aspect of shellfish enhancement, even though it is the one most often thought of when this subject is discussed. Figure 1.3 shows that successful use of hatchery seed for enhancement has often failed because of an inadequate “upstream” knowledge of the genetic characteristics of the broodstock used, and/or the “downstream” factors affecting life history completion once released in the wild, as well as inadequate attention to monitoring the fate of released animals.

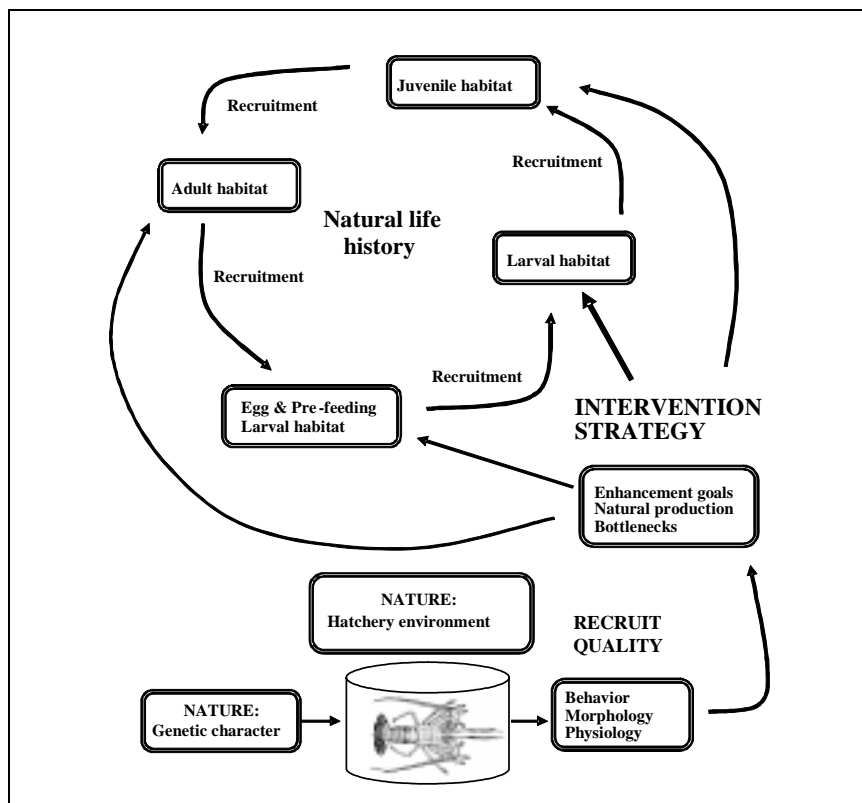


Figure 1.3 A generalized scheme for invertebrate stock enhancement using hatcheries (after Olla, Davis and Ryer, 1998).

Terms closely related to enhancement are “**mitigation**”: meaning “to make milder or less severe”, which could be a frequent objective where there have been some negative impacts of human activities on shellfish production, and “**remediation**” which implies improving to the extent possible after some sort of negative impact, particularly to the capacity of the ground to produce the resource. Examples are attempts to remediate the effects on the resource from harbour extension or other coastal modifications, or to reduce them in severity. Less obviously, we often meet situations where the resource has been depleted over time due to overfishing or

habitat change. Although we should strictly speak of “**stock restoration**” in this case, the distinction between this and “**enhancement**” depends largely on the status of the stock at the start of human exploitation, and in both cases the methods applied are similar. Although in theory restoration is not strictly identical with enhancement, the fact is that many shellfish grounds have been progressively declining in productivity over the last century or more. Thus, what appears to be an “enhancement programme” to one person with a short historical memory, is identical to what may be called a “restoration programme” by another having a historical record of a former productive situation, if records have been conserved.

It is in any case important to investigate historical records of past productivity to ascertain what was the original sustainable harvest from an area, even though there is no guarantee that possibly major and irreversible changes caused by anthropogenic impacts on habitats, or climatic effects, will allow complete “restoration” *sensu strictu*. Hence we will be considering both of these alternative activities in the report, making the distinction where possible that an apparent enhancement may in fact be a partial or complete population restoration, but noting that it will not always be possible to make a hard and fast distinction. More pessimistically, the best that will be achieved in some cases is “mitigation” of anthropogenic effects.

Two other uses of the term “enhancement” that need to be distinguished, are where the species in question is being introduced to an area where it never existed previously, such as the apparently unsuccessful American lobster *Homarus americanus* cultivation and release programme on the west coast of Canada (Boothroyd and Ennis, 1992), and more successfully, the introduction of *Crassostrea gigas* to Europe and North America (Shatkin, Shumway and Hawes, 1997). An extension of the previous geographical range of a species is also possible, because of climate change (see e.g. Frank, Perry and Drinkwater, 1990), or because a hardier strain allows an extension of the species range, or due to habitat manipulation. These all will be considered as aspects of enhancement activities in this document. “**Restocking**” is another term often used, defined as the act of adding individuals to a stock that has been partially or totally depleted (see also Addison and Bannister, 1994), although this term has come to acquire an ecologically rather negative connotation in fresh water fisheries, of the replacement, partially or totally, of the native stock and its supplanting by hatchery animals, often with a distinct genetic component. This is generally not to be recommended, though does frequently occur in an irreversible fashion due to introduction of species in ship ballast water, or with unwisely planned stocking exercises. A related term “**stock addition**” describes the process of colonization of new areas (Castilla, 1988; Bannister, 1991); in many cases by accidental introductions. Re-introduction of a species to a part of its former range where it has become extinct is another possible situation, and here hatchery activities may be required, as in attempts to seed Caribbean islands with conch populations (Stoner and Davis, 1994; Iversen and Jory, 1997). Here, the dangers are of introducing a common conch strain to different islands with distinct habitats and hydrological conditions. This may be a short-sighted solution however, since local stocks will have developed different adaptations to varying local conditions on the different island shelves. “Restocking” activities may simply require harvesting and transplanting, but are more likely to require hatchery production of sufficient numbers to ensure an adequate start; hence they may have a number of features in common with “sea ranching”.

Techniques of shellfish enhancement following the wider definition we propose, vary considerably both between species and in the degree to which interventions to manipulate one or more stages of the life cycle are feasible in open marine ecosystems (Larkin, 1991). Hence it may be impossible to draw a strict line between any of the activities given in bold in the above paragraphs, and inconsistencies will undoubtedly arise. It is suggested that the reader

concentrate more on the activities themselves than in attempting to place them in hard or fast categories.

2. ASSESSING THE STATE OF INVERTEBRATE RESOURCES

2.1 Stock assessment methods applied to sedentary and semi-sedentary resources

This paper does not go into detail on stock assessment methodologies (see e.g. Hilborn and Walters, 1992; Sparre and Venema, 1992; Haddon, 2001), but a few sources of information are provided in the following, and some broad generalizations follow. The techniques that will need to be used where a stock assessment is required will depend to a large extent on available data. The following main options seem to exist:

2.1.1 Biomass estimates and distribution

Estimates of biomass and densities are important to evaluating the performance of a stock enhancement initiative, especially in experiments carried out at large spatial scales (see e.g. Hancock and Urquhart, 1965; Defeo, 1996a; Castilla *et al.*, 1998). Abundance estimates of shellfish need to be expressed as a total quantity by stock, shellfish bed or management area, with some measure of the associated variance. Two approaches are distinguishable: design-based and model-based. In the former, abundance or density estimates (B) are classically estimated by the swept area method (Caddy, 1979a) as $B=c/(a \cdot e)$, where c is the total catch in each haul, a is the area swept by the gear and e is gear efficiency, defined as the fraction of organisms in the path of the gear that are actually caught, and this parameter could be experimentally estimated (see e.g. Lasta and Iribarne, 1997). The swept area method detailed above is based on variance estimates, which assume that the error terms of the samples are stochastically independent of one another (Simard *et al.*, 1992).

The above approach, which relies on random sampling theory, allows calculations to be done ignoring the spatial autocorrelation or small-scale dependence between consecutive sampling units (SUs) (Legendre, 1993). This condition is not met by most sessile and sedentary invertebrate populations, which are spatially autocorrelated (Conan, 1985). Indeed, invertebrate populations present strong and persistent (*sensu* Orensanz and Jamieson, 1998) spatial distribution patterns, mainly as a response to an environment that is spatially and temporally structured by sharp, small-scale gradients. Aggregations persist in time, and, especially in sessile species, in space, with relative positions of patches across the gradients (e.g. latitude, depth) varying according to the different susceptibility of each species to variations in environmental conditions. For this reason, the spatial dimension of population processes and patterns has received considerable attention in invertebrate ecology, bearing in mind the paradigm of spatial structuring, a critical determinant of how ecosystems function (Legendre, 1993). Given the strongly aggregated patterns, model-based estimates (e.g. geostatistics) are relevant when interpolating abundance between SUs across a given grid with fixed coordinates (Conan, 1985). Geostatistics explicitly consider the shape of the spatial autocorrelation in density of consecutive SUs, together with their spatial organization and location on regular grids (surface or volume) or at fixed stations (e.g. single-dimensional transects) (Petitgas, 1993, 2001; Legendre and Legendre, 1998). The fact that mean abundance estimates and their variances are expressed in terms of this structure has made model-based approaches very relevant for crustaceans (Conan, 1985; Simard *et al.*, 1992; Maynou, Sardà and Conan, 1998; Roa and Tapia, 2000) and bivalves (see e.g. Thrush, Hewitt and Pridmore, 1989;

Hewitt *et al.*, 1997; Orensanz *et al.*, 1998; Defeo and Rueda, 2002; Gutiérrez and Defeo, 2003). The relative merits of both design- and model-based estimators have been a source of controversy, and variances obtained from these alternative approaches cannot be properly compared with one another because of conceptual and methodological differences (Warren, 1998). Thus, our main focus is not to point out crude differences between estimates, but to highlight the definite benefits of applying model-based estimates (geostatistics, kriging) in the light of the spatially structured nature of shellfish and other invertebrate marine resources.

Numbers or biomasses and size compositions in the annual population from surveys may also be used as the basis for e.g. Thompson-Bell calculations (Ricker, 1975), to establish yield per recruit or fecundity per recruit optima, as a basis for deciding on exploitation strategies (see Sanders and Beinssen, 1998 for a shellfish example).

2.1.2 Growth

A major concern in enhancement programmes is to optimize stocking densities, concurrently with the corresponding growth and survival rates that determine the relative success of the initiative. The identification of factors limiting growth (e.g. food, space, density) is also a critical step in enhancement protocols, because a precise knowledge of these factors should avoid economic losses derived from low growth and high mortalities caused by density-dependent mechanisms. Some techniques directed to estimate growth and mortality are briefly presented in the following sections.

In the context of an enhancement programme, shell growth patterns are useful to reconstruct the effect of environmental and ontogenetic events after they have taken place and to obtain age data critical for estimating growth rate, recruitment, and survivorship, as well as information on physiological processes (Palacios, Orensanz and Armstrong, 1994; Cerrato, 2000). Age reading in molluscs is relatively simple in species from temperate waters, in which macroscopic growth bands are formed in valves with annual periodicity. Annual rings, usually determined by external reading or acetate peels and validated by e.g. stable isotope analysis, give sufficient information for most stock assessment (see e.g. Lutz and Rhoads, 1980; Ropes and Jearld, 1987). Shell growth patterns have been shown to have subdaily and daily increments and irregular microgrowth patterns at low temperatures, especially in bivalve larvae (Cerrato, 2000). Thin sections of the hinge region of *Mya arenaria* also revealed tidal and seasonal patterns (Cerrato, Wallace and Lightfoot, 1991).

In crustaceans, life history processes are integrated with moulting schedules (see e.g. McGarvey, Levings and Matthews, 2002). In higher latitudes, seasonal cycles are also linked to temperature, physiological processes and maturity, in that egg bearing may influence intermoult time of mature females. Macrocrustaceans usually show fairly regular slowing trends in moulting with age. It also appears to be a function of the age at a given point in the life history, and programmed slowing of moult frequency with age and size leads to multi-year intermoult periods in some crustaceans. Moulting schedules of macro-crustaceans through life may even offer insights into the appropriate scaling of time units for other developmental processes. Caddy (2003) showed that subdividing a life history into progressively longer intervals by a constant proportion between successive intermoult intervals is a useful way of modelling crustacean moulting schedules. Intermoult duration throughout life for a variety of crustaceans were compared with a geometric series of time intervals increasing from an initial “seed” interval by a constant proportion at each successive interval: a strategy of time division referred to as gnomonic. The geometric progression of

time intervals, and Hiatt's model for size increments which also tends to a geometric progression, suggest a discrete gnomonic growth function for crustaceans. This proposed growth function can be made compatible with von Bertalanffy growth but provides a wider range of growth forms. This strategy for simulating intermoult intervals can be modified to account for seasonal environmental and life history deviations.

Size-at-age and number-at-age data obtained using lipofuscin (the "aging" pigment left over from the breakdown and digestion of damaged blood cells) was demonstrated useful for bivalves (Lomovasky *et al.*, 2002). The authors showed that lipofuscin concentration in the connective tissue around the intestine and in other tissues of *Eurhomalea exalbida* was better related with individual age as determined from stable isotope-validated shell growth bands, than with any morphometric parameter. Age appears to be accurately predicted from lipofuscin concentration in the connective tissue by a von Bertalanffy model, suggesting that this concentration is a function of individual age. If this holds true for bivalves in general, lipofuscin may be a suitable proxy for age in species with less clear shell growth band patterns. This technique was shown to be useful for estimating growth and mortality in lobster populations (Sheehy *et al.*, 1996), in which sampling nerve tissue containing lipofuscin from the eyestalk has the advantage of leaving the lobsters in marketable condition. Ju, Secor and Harvey (2001) showed that the lipofuscin level in pond-reared crabs (*Callinectes sapidus*) was significantly correlated with size (carapace width), but it was more closely correlated with chronological age. The constancy of normalized-lipofuscin accumulation rates of blue crabs across seasons and environmental conditions suggests that lipofuscin concentration can be a more robust indicator of age than carapace width alone. Sheehy and Bannister (2002) analysed the age composition of a *Homarus gammarus* population off the northeast coast of England by using age-dependent in situ deposits of neurolipofuscin in the eyestalk as an age index. An approach is presented that accounts and (or) corrects for the two most important potential sources of error in age determinations by this technique, namely environmental temperature variation and unexplained individual variation. This approach yielded for the first time in clawed lobsters, reproducible catch age structures with year-class resolution. The method has shown to be generally applicable to crustaceans.

Profiles of strontium/calcium ratios (Sr/Ca) constitute a useful ancillary criterion for age validation. Palacios, Orensanz and Armstrong (1994) assessed the use of Sr/Ca as an objective criterion for age estimation in extinct and extant populations of *Mya arenaria*. Peaks in the Sr/Ca ratio, measured across thin sections of shell chondrophores, always corresponded with translucent bands in shells from the two populations. Cycles of high and low Sr/Ca ratios matched seasonality in the environment (temperature), allowing validation of ages. The positive significant correlation between mean Sr/Ca ratio and estimated age at the time of shell formation is perceived as an ontogenetic trend related to age, growth rate or both.

Where age reading is infeasible or too costly in time and manpower, length frequency distributions (LFDs) from catch monitoring and survey data can be analysed for stock units using catch curves to estimate overall mortality rate (e.g. Fournier and Breen, 1983; Defeo, Ortiz and Castilla, 1992; Smith and Botsford, 1998), as well as size selectivity of the gear (Sparre and Venema, 1992). Alternatively, variations on the Jones (1984) method of cohort analysis by sizes may be used (if estimates of natural mortality rate M are available). Modal analysis using methods such as e.g. NORMSEP (Hasselblad, 1996), Bhattacharya (1967), or others (e.g. MacDonald and Pitcher, 1979), some of them contained in well-developed

software (Gayanilo and Pauly, 1997), can be used to identify cohorts and determine their relative abundance – and from this information overall mortality rates (Z) can also be derived. Relevant methods from the literature for these methodologies are included in the compilations by Pauly and Morgan (1987) and Sparre and Venema (1992). Since LFDs are relatively easy to obtain in enhancement exercises, between-cohort variations in growth rates could be quantified in different treatments (e.g. densities, food, depth, productivity) of a stock enhancement research and then subject to classical Analysis of Variance (ANOVA) procedures to test the null hypothesis of absence of differences in growth rates between treatments, or, alternatively, using Analysis of Covariance (ANCOVA) with individual size as covariate, in cases where individual were not controlled at the start of the experiment.

2.1.3 Mortality

The instantaneous rate of total (Z) and natural mortality (M) are critical parameters in assessing the success of stock enhancement programmes. Because of the logarithmic relationship between mortality rates and the cost to enhancement initiatives, a realistic understanding of mortality processes and effects and to optimize culture and release strategies for highest possible survival is critical in this context (Stoner and Glazer, 1998).

M and Z could be calculated by the age-length key provided by the reading of growth marks, or, alternatively, by length-converted catch curves (Pauly, Moreau and Abad, 1995). Methodologies using size structure of samples are of particular relevance, since except for certain bivalve species, and daily rings in squids and cuttlefish otoliths and pens, age structure is not readily obtained from hard skeletal structures. The overall mortality rate is also obtained from tag and recapture experiments, particularly for macrocrustaceans (see examples in Caddy, 1987, 1996). Reliable estimates of M -at-age are difficult to obtain in exploited molluscs, in which a simultaneous effect of fishing and incidental mortality may also be involved. For many invertebrates which are exploited early in life, the problem of deciding an appropriate level of natural mortality occurs, and where this has been studied (Appeldoorn, 1988; Caddy, 1991; Pérez-Castañeda and Defeo, 2003) this typically decreases with age, one approach to modelling suggesting the use of a reciprocal relationship for M with age (Caddy 1991, 1996). Modelling natural death rates of juveniles is important in mollusc stocks with complex life cycles, where an early planktonic phase is affected by mortality agents on a variety of spatial and temporal scales. Subsequent variations in mortality arise from settlement to recruitment to the fishery, depending on a variety of abiotic and biotic (density-dependent) factors. The relevance of spatial and temporal fluctuations in M has been highlighted in a variety of studies (e.g. Orensanz, 1986; Shepherd and Breen, 1992). Density-dependent effects on mortality and age-specific survival rates usually found in molluscs suggest that intraspecific competition could importantly affect population dynamics (Brazeiro and Defeo, 1999; Lima, Brazeiro and Defeo, 2000), which in turn will affect the outcome of enhancement programmes.

Caddy (1991) postulated a continuous mathematical function for the change in M with age as an extension to the "constant adult M " axiom:

$$M_t = M_\infty + b \cdot \frac{1}{t}$$

where M_t is the age-specific mortality rate, M_∞ is the asymptotic mortality at some hypothetical maximum age, restricted to values of t such that $b/t > M_\infty$. M_∞ is generally below the constant

adult M observed for the species. This model, as applied to short-lived invertebrate populations (Caddy, 1996), can be used to generate different trajectories of M according to variations in the mean individual fecundity and mean parental age, under the assumption of "steady-state population replacement", that is, given one female with mean fecundity, a steady mortality rate should result in an average survival by the critical or mean parental age of at least two survivors at the age of spawning: one male and one female. High b and low M_{∞} values might correspond to a high larval and low adult M values, whereas moderate values of both parameters could occur in cases with lower M values for early stages of the life cycle and higher adult M . In a similar way, the relationship between M and age t can be modelled using a Weibull hazard function of the form (Appeldoorn, 1988):

$$M = d \cdot t^{c-1}$$

where c and d are constants. Both models appear to be well-suited to reproduce variations in natural mortality at age, as exemplified in Figure 2.1 for the queen conch *Strombus gigas*.

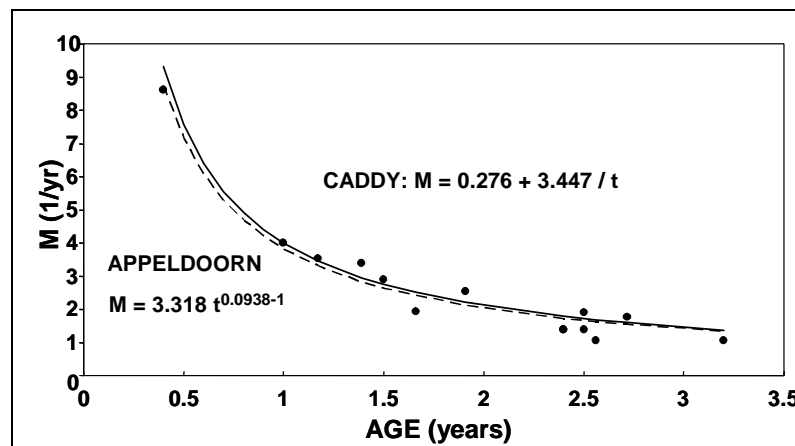


Figure 2.1 Appeldoorn (1988) and Caddy (1991) models fitted by non-linear least squares to M -at-age data for the queen conch *Strombus gigas*. Data in Appeldoorn (1988).

The fact that natural mortality widely varies with age and also between-years is critical from a stock enhancement perspective. Long-term investigations carried out by Stoner and Glazer (1998) showed that mortality and predation in *Strombus gigas* indicate that M in nursery grounds in the Bahamas and the Florida Keys is often higher and more variable than recognized earlier, with seasonal, interannual, and site-specific sources of variation. For example, in the Florida Keys, M rates for 200-mm conch in summer varied interannually from <2.0 to 12.0 year⁻¹. M rates for 100-mm conch, often considered ideal in size for field releases, varied from 0.5 to 12.0 year⁻¹, depending on site, season, conch density, and deficits in behaviour and shell form associated with hatchery rearing. The authors showed inverse density-dependence in mortality.

Following a similar reasoning, Pérez-Castañeda and Defeo (2003) showed that mortality rates of juvenile shrimps *Farfantepenaeus duorarum* in a coastal lagoon of Mexico decrease as the individual size increases. The size-dependent mortality, modelled by a reciprocal function of length, provided a more reasonable prediction from a biological point of view than the conventional exponential decay model, which tends to underestimate mortality at smaller sizes. Figure 2.2a shows the detailed procedure of estimation of Z :

1. Identification of normal components in the length frequency distributions (LFDs).
2. Separation of normal components (assumed cohorts) in the LFDs, using NORMSEP (maximum likelihood) or Bhattacharya methods.
3. Estimation of mean carapace length (CL), its standard deviation, and the size (N) of each cohort.
4. Evaluation of a separation index (SI) higher than 2, as criterion to separate contiguous normal components in each LFD (Sparre and Venema, 1992).
5. Tracking of cohorts through time by linking mean CL's of consecutive sampling dates.
6. Estimation of mortality by monthly changes in shrimp abundance (N) of each cohort over the monthly intervals.

Afterwards, the relationship between Z and age can be evaluated (Figure 2.2b).

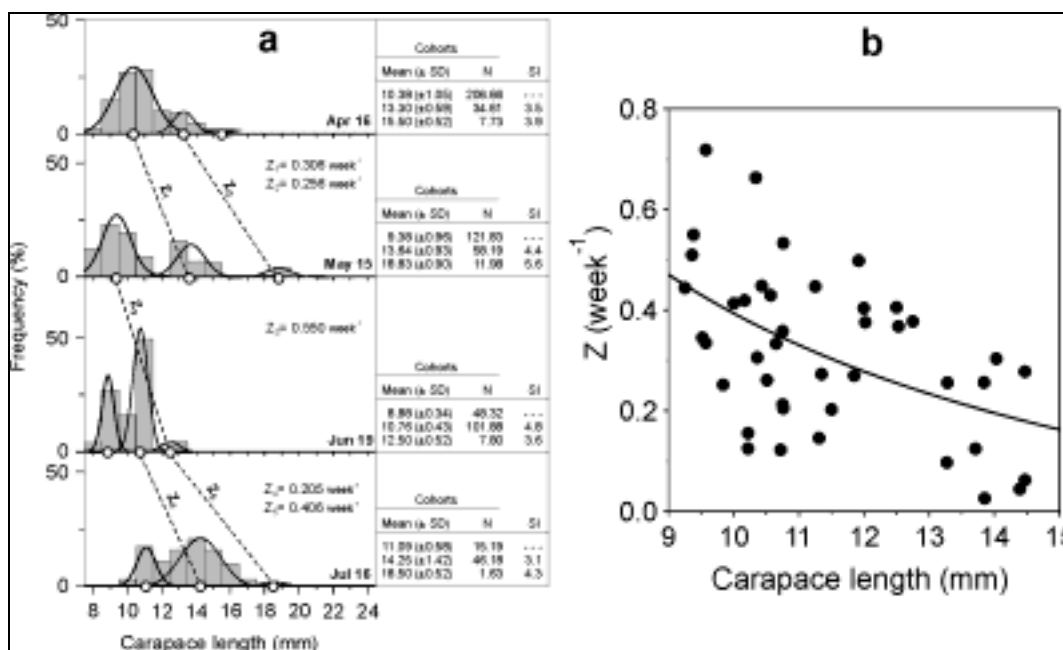


Figure 2.2 (a) LFDs of selected sampling dates (April-July 1997) for *Farfantepenaeus brasiliensis* of Celestun lagoon (Mexico), with separation of cohorts by NORMSEP. Mean (\pm SD) carapace length (CL), cohort size (N) and the separation index (SI) of contiguous cohorts are shown. Dashed lines link mean CLs of identified cohorts (O) used for Z estimations. (b) Size-dependent mortality predicted by the reciprocal model (after Pérez-Castañeda and Defeo, 2003).

The effects of density-dependence and habitat quality in mortality estimates could be experimentally assessed. The sedentary/sessile nature of the species, especially intertidal bivalves with negligible migratory movements and complete accessibility at low tides, favours the development of accurate experimental designs such as those utilized in agricultural sciences. The experimental approach could also be carried out by the closure of large areas for prolonged time periods, in order to evaluate the long term effects of different mortality sources, including incidental effects in exploited and unexploited population fractions and also in untargeted sympatric species, by means of direct (shell damage) and indirect (sediment disturbance) agents (Cobb and Caddy, 1989; Defeo and de Alava, 1995; Blaber *et al.*, 2000).

The experimental approach allows separation of M from F , and to distinguish and calibrate the relative importance of the main components of M , as well as damage and loss as a result of harvesting methods. Hancock and Urquhart (1965) carried out large-scale, long-term (1958-1963) covered mesh experiments, in order to separate M into its components (e.g. predation, diseases, parasites, senescence, and environmental conditions) in an exploited population of cockles (*Cerastoderma (Cardium) edule*). M was estimated by fencing off a series of squares and sampling inside them (unaffected by harvesting), whereas additional samples were taken outside as controls ($F + M$). In order to estimate M , the natural logarithm of the number of organisms per square metre was related to time according to a simple linear regression. The effect of predation by e.g. oystercatchers was also observed by examining changes in natural logarithms of numbers·m⁻² in areas completely protected by netting and in control samples. This was a particularly important and innovative study approach that could be repeated for other littoral resources, in which most predation occurs at high tide and where indirect mortality caused by the activities of human fishers may strand clams on the surface where they are vulnerable to various sources of mortality. Hall (1983) estimated different sources of mortality according to variations in tidal levels for the Manila clam *Tapes philippinarum*: (a) a genetically determined "background value" (M_0), related only to senescence, was assumed to be constant throughout the beach; (b) a predation component given by aquatic and aerial predators (M_{AP}); and (c) a stress component, determined by the relation of organisms to exposure (M_{TS}). Since only experimental evidence could distinguish between (b) and (c), Hall (1983) modelled them as a single process and expressed these sources of mortality in additive form:

$$M_T = M_0 + M_{AP} + M_{TS}$$

Figure 2.3 shows the function fitted by non-linear least squares to field data. The function and defined parameters can to some extent be interpreted biologically. The noticeable deviation at intermediate values and the bimodal distribution suggests that the impact of the predation component could be explained by a sum of two normal components (Hall, 1983). The author suggested that this model could be generalized for mollusc populations inhabiting intertidal gradients. Estimates of differential mortality across an intertidal gradient could be important when siting enhancement initiatives. To test whether natural mortality differ between sites or cohorts, an ANCOVA could be performed with log (density) as the predicted variable, age (in years) as the covariate, and sites or year classes as main factors.

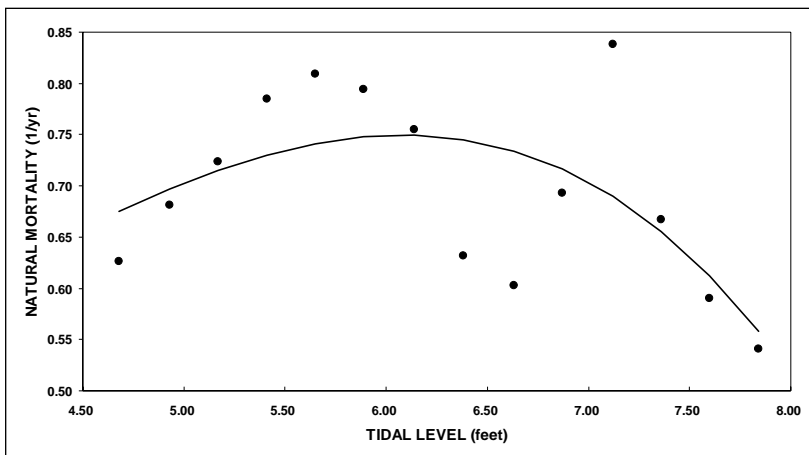


Figure 2.3 Bivariate distribution of M and the corresponding tidal level for the manila clam *Tapes philippinarum* in Puget Sound, Washington (after Hall, 1983).

Other significant sources of mortality, especially for younger clams, may include the scouring effects of winter storms, vehicle traffic on beaches, flood events and siltation (Hancock and Urquhart, 1965; see review by McLachlan *et al.*, 1996). Short and long-term climatic events, accumulation of toxins from algal blooms and viral diseases produce massive mortalities that could also affect the outcome of enhancement programmes (Arntz *et al.*, 1987; Raimondi *et al.*, 2002; Defeo, 2003). The identification of meaningful spatial and temporal scales of variability in population regulation mechanisms and processes is relevant in these cases.

2.1.4 Merging growth and mortality for stock enhancement: cohort projections

Joint estimates of growth and mortality rates allowed cohort projections to be made in order to optimize harvesting yields from a stock enhancement programme. Figure 2.4a shows a hypothetical biomass projection based on: (i) monthly predicted lengths estimated by seasonal growth curves of the generalized von Bertalanffy model; and (ii) a length-weight relationship, natural and fishery mortality rates; and (iii) an initial number of 1000 individuals. It is now possible to calculate biomass at age for a range of growth and mortality rates, and to estimate when biomass is maximal, which occurs when the increase due to growth compensates for losses due to natural and fishing deaths (Caddy, 1993b).

Figure 2.4b illustrates the projections of biomass for three cohorts of the yellow clam *Mesodesma mactroides* in different periods representing dissimilar harvesting scenarios, including one (1988 cohort) in which a management experiment was carried out over 32 months (Defeo, Ortiz and Castilla, 1992). The maximum cohort biomass was observed in the first austral summer, when the yellow clam reached the mean length of sexual maturity. The cohort of 1983 (young-of-the-year), growing under low adult densities, achieved high growth rates and attained the spawning and exploited sizes (i.e. 50 mm) some weeks before the 1984 year class. Further, the unexploited cohort of 1988, showed similar abundance of recruits as for the 1984 cohort, and reached spawning size at the same time. All three cohorts reached a harvestable size during the winter. The growth pattern observed for *M. mactroides* means that individuals reach a length of 50 mm during the winter period. Projections of biomass show that a cohort should be ideally harvested during the second spring and summer (i.e. second peak observed in Figure 2.4) in order to maximize yield and assure an important contribution of recruits to the fishery under normal conditions.

Density-dependence processes could play a role in limiting growth (intraspecific competition for food) and recruitment magnitude (adult-larval interactions at the time of settlement) in this population. Hence these factors could affect the stock component available for exploitation, as well as the outcomes of stock enhancement programmes under different stocking densities.

The use of EXCEL or other spreadsheet software's is widespread, and the Thompson-Bell procedure for example is well adapted for carrying out simple simulations of different fishing strategies under a variety of assumptions as to growth, natural mortality and selectivity at size and age (see Sanders and Beinssen, 1998, who extends the use of this procedure to bioeconomic calculations on an abalone population). In addition to the standard data on catch per unit effort, size (and if possible) age structure, broken down by subarea, special data requirements may be evident for invertebrate resources.

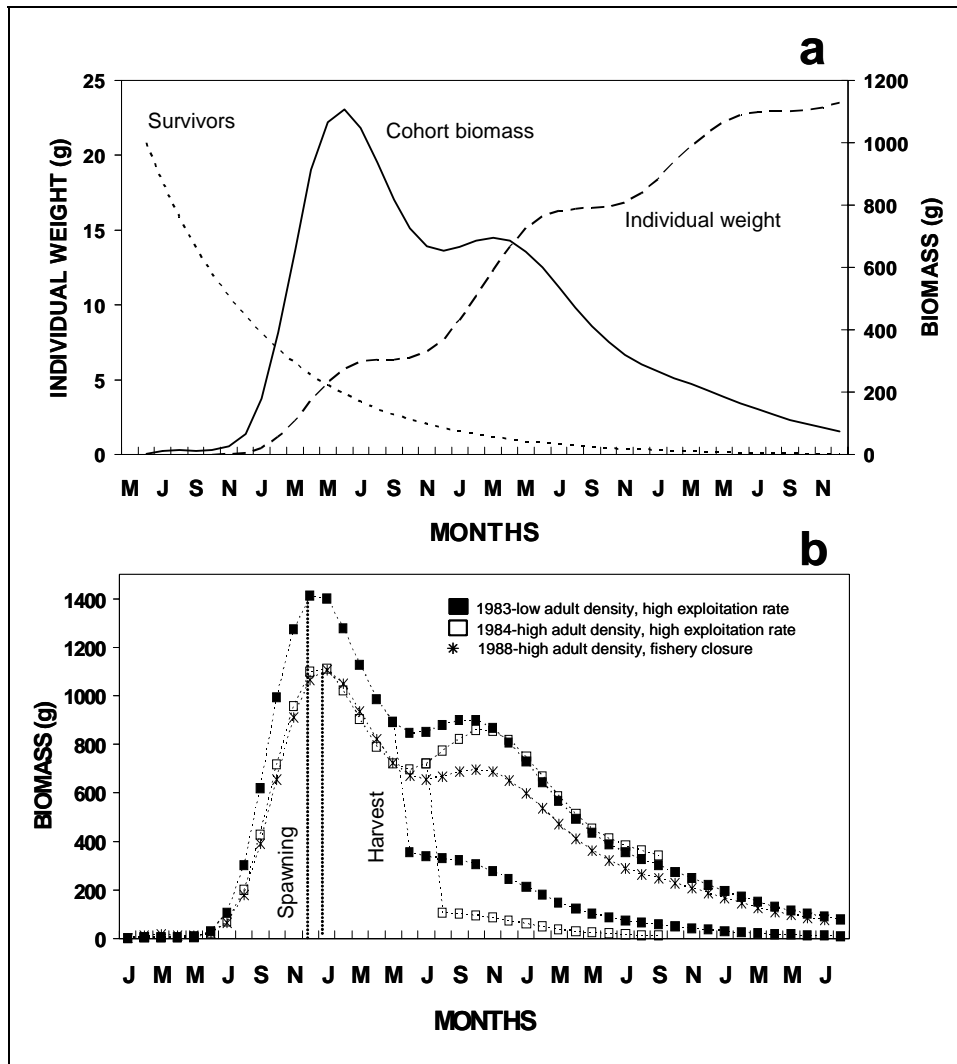


Figure 2.4 (a) Monthly trajectories of growth in weight, decline in numbers and biomass projections for an idealized biomass projection based on monthly predicted lengths estimated by seasonal growth curves of the generalized von Bertalanffy model, a length-weight relationship, natural and fishery mortality rates, and an initial number of 1000 individuals. (b) Biomass projections for three cohorts (young-of-the-year) under contrasting harvesting scenarios and adult densities. The cohorts of 1983 and 1984 show biomass trends with (lower lines: $Z = F+M$) and without (upper lines: $Z = M$) fishing activity and the time at which the yellow clam reached spawning and commercial sizes (after Defeo, Ortiz and Castilla, 1992).

2.1.5 Production/area estimates

A comparison of productivity (e.g. tonnes/km² of grounds) with fishing intensity, defined as effort exerted per unit area and expressed as effort or fleet capacity exerted per km² of grounds (Caddy, 1975), can form the basis for a composite production modelling approach following the method of Caddy and Garcia (1983). It has seldom been used in shellfish resource assessment (Caddy, 1986b), because of the widely employed but inaccurate assumption that a production model applied to the whole sedentary population is the best approach to modelling. The dynamic pool assumption that the local effects of fishing effort applied anywhere in a sedentary population are “mixed” over time in a sedentary resource is misleading, and although an overall effort-yield model can be fitted, it would also be useful to consider spatially discriminated estimations of fishing effort and catches by subareas of the whole population range, and fit individual production models for each sub-area for which catch and effort data can be discriminated. "Production-intensity" curves may be derived by multiplying effort and catch by the area of the individual grounds, even in different or similar time periods (Caddy and Garcia, 1983; Caddy, 1986b). For example, a modified Fox (1970) exponential model in this context can be expressed by:

$$Y_i / A_i = (f_i / A_i) CPUE_{\infty} e^{-b(f_i / A_i)}$$

where A_i is the area of each fishing ground, f_i is the fishing effort exerted on ground i and Y_i is the mean annual catch per fishing ground.

This approach assumes that: (1) the grounds considered are comparable in productivity; (2) the virgin catch rate $CPUE_{\infty}$ is the same for all areas; (3) differences in fishing intensity are responsible for differences in abundances between grounds, i.e. a proportionality exists between fishing intensity and the resulting fishing mortality, as well as between catch rates and stock abundance in each area; (4) fishing pressure is the only human-induced factor affecting the productivity, and no environmental gradient that could differentially affect the areas exist; (5) the same gear and similar conditions of fishing (e.g. no differences between bait, tow speed, elapsed time of setting traps) apply such that a relative homogenous fishing power applies; otherwise, effort must be standardized; (6) when considering sequential data from only one area, this area must not change in extent, so that a functional stock unit concept remains realistic: i.e. the population may be considered as a self-sustaining discrete identity; (7) when considering a mosaic of areas in the same year, or combinations of different years and different areas (i.e. the “composite production model”), the extent of each fishing ground must be the same during the whole study period, and the assumption of a constant basic productivity in time and space should remain reasonably valid.

The advantage of this method is that it is possible to fit this composite model from only one or few years of data, and thus estimate the maximum yield per area (MYPA) and the optimum level of effort (f_{max}) per unit area (Caddy, 1986b), and the short-term data series used should be relevant in the context of an enhancement programme (Figure 2.5).

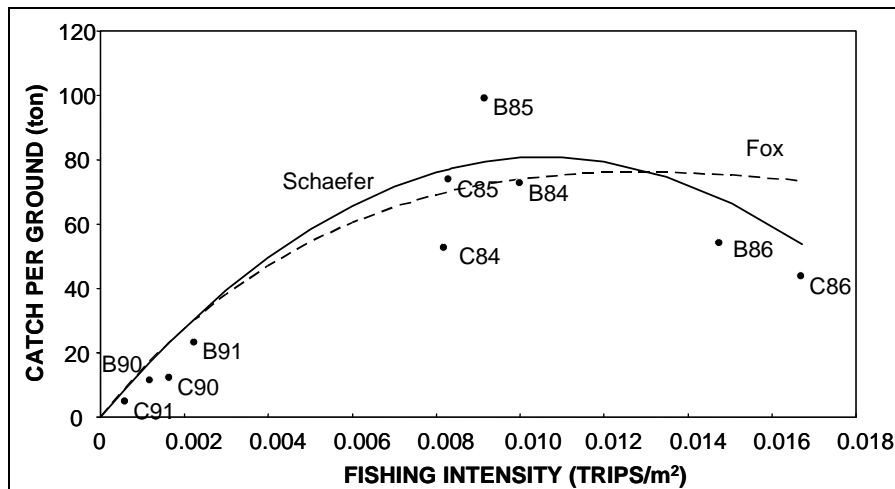


Figure 2.5 Composite production models (Schaefer and Fox) for a clam fishery in Uruguay, from fishing grounds denoted as B and C (comparable in terms of productivity) and years 1984-86 and 1990-91. (Data from Defeo, unpublished).

The model can be fitted by non-linear least squares, or by linearising the above equations; in which case the logarithm of the mean annual catch per unit effort is fitted against the fishing effort per unit area, that is:

$$\ln(CPUE_i) = \ln CPUE_\infty - b(f_i / A_i)$$

and thus:

$$f \max = 1/b$$

$$MYPA = e^{\frac{a-1}{-b}}$$

Using the same reasoning, the classical surplus yield model of Schaefer (1954) can be modified to account for differences in spatial allocation of effort, i.e.:

$$CPUE_i = a - b(f_i / A_i)$$

and then solving for $fmax$ and MYPA as follows:

$$f \max = a / 2b$$

$$MYPA = a^2 / 4b$$

The models may be fitted by a geometric mean regression (Ricker, 1975), which provides more conservative estimates of optimum effort in cases when R^2 is low. In addition, estimates of mean, standard errors and confidence limits for the parameters can be obtained by bootstrap or jackknife techniques, which could easily be performed in EXCEL or other spreadsheet software. This approach fits well with metapopulation statistics where separate data sets for different subunits are available, ideally allowing estimates of the fishing intensity at maximum productivity to be derived, even with only a few years of data.

Stratification of grounds into statistical areas will enable maps to be drawn demonstrating spatial variations in abundance, catch and effort, and these should be analysed together with variations

in stock concentrations (Defeo *et al.*, 1991). A spatial mapping of [survey] results can provide the basis for a stratification scheme, and serve to display information recorded from fisher's reports or log records, which could be particularly useful in the enhancement initiative. It would be preferable if sub-area boundaries coincided with the suspected variability in productivity and other site-specific environmental factors. These kinds of environmental gradients are common, and affect accessibility and availability of the stock, and could be linked to variations in, e.g. depth, sediment, current velocity etc. All factors which could alter the outcome of an enhancement programme.

2.1.6 Production modelling

Conventional production modelling where existing time series of catch and effort exist, can be employed to determine the current state of exploitation in relation to MSY conditions (see Punt and Hilborn, 1996). If however, effort data are not available, but annual estimates of overall mortality rate are, then static or dynamic approaches to production modelling using overall yield and annual estimates of total fishing mortality can be used to estimate MSY conditions and model changes in yield against mortality over time (see Caddy and Defeo, 1996 and Defeo and Caddy, 2001, respectively). The advantages of this last-mentioned approach are evident for invertebrate populations where only annual catch and overall mortality estimated from regularly sampled size frequency data are available, but no data on fishing effort.

In general, there are significant advantages (and often few alternatives) to working with the overall annual mortality rate Z_t , instead of partitioning causes of mortality into for example, natural and fishing mortality rates, and again partitioning M into effects of predation and disease for example. Since sources of shellfish mortality may also vary between years: e.g. from disease, due to density-dependence, or because of variations in predator abundance as well as fishing mortality, assuming a constant natural mortality M may not be realistic. Hence overall estimates of annual mortality Z_t will need to be interpreted with care, and it would be advisable to contrast apparent or actual variations statistically to indicator series for environment, predation and density, where such accompanying data exist. An example of the lack of stability of M over time is given by Ducrottoy *et al.* (1991) for the cockle *Cerastoderma edule*.

2.2 Settlement dynamics and the stock-recruitment relationship

2.2.1 Settlement

A major concern in enhancement programmes is to ensure a steady supply of new recruits. To this end, the peak spawning and settlement periods must be known for collecting, seeding or transplanting organisms. In temperate regions, information on time and intensity of spatfalls is required, and these may be infrequent or episodic. Such precise knowledge should avoid economic losses derived from e.g. excessive or inappropriate economic investment, or the accumulation of fouling on collectors. Similarly, the time and place for successful release of previously collected larvae or juvenile are often site and season-specific, and this must be taken into account to avoid massive mortalities following release. The natural depth distribution of spats must also be known in siting collectors. Similarly, the time and place for successful release of previously collected larvae or juvenile are often site and season-specific, and this must be taken into account in order to avoid massive mortalities following release.

Recruitment variability of benthic organisms is often the main factor leading to fluctuations in stock abundance, with fluctuations in the physical environment apparently outweighing the effects of stock size for many species (Coe, 1953; Hancock, 1973; Connell, 1985; Caputi and Brown, 1986; Phillips and Brown, 1989; Penn, Hall and Caputi, 1989; Holm, 1990; Raimondi, 1990; Caputi, 1993; Botsford, 2001). Life history characteristics such as high fecundity and a sedentary habit inevitably lead to variability in natural recruitment. For example, a comparative study of the cockle *Cerastoderma edule* in Northern Europe (Ducrotoy *et al.*, 1991), showed that typically, four phases in population fluctuations occur: a “crisis condition” with few poor and few classes, followed by a rapid “recovery phase” due to exceptional year classes, and finally, a period of “upholding” at high densities. This is followed by years of “decline”, often motivated by cold winter temperatures. These however free up particulate sediments for recruitment of good spat year classes. In fact, the large fluctuations in abundance observed where planktonic larvae and benthic adult stages are decoupled in time and space, are great when compared to otherwise similar oviparous or viviparous species, where larval stages are reduced in range and duration. This has led to the description of shellfish resources as resurgent populations (Coe, 1956; Ansell, 1983). Large-scale physical, chemical, and biological factors affect long range dispersal of early planktonic stages, and are key determinants of recruitment success and high variability in population size for marine invertebrates (Botsford, 2001; Norkko *et al.*, 2001; Poulin *et al.*, 2002a). However, recent evidence suggests some mechanisms of retention of larvae in nearshore areas. For example, while sampling during a strong coastal upwelling event (produced by strong southwesterly winds), the gastropod *Concholepas concholepas* larvae in Chilean coasts were only found in the upwelled waters between the front and the coast. This unusual pattern contrasts with what would be expected for typical epineustonic larvae, suggesting the existence of a mechanism of transport or retention by which *Concholepas concholepas* larvae stay near coastal settling areas, thus avoiding offshore dispersion (Poulin *et al.*, 2002b). Other studies also suggest that populations can remain demographically closed for generations despite extended larval duration. Genetic analyses of marine population structure often find only slight geographic differentiation in species with a high dispersal potential (Taylor and Hellberg, 2002; Palumbi, 2003). The success of the settlement stage at the point of settlement, by contrast, is a small-scale phenomenon. Because recruitment combines both pre-settlement (i.e. larval dispersal of planktonic stages) and post-settlement survival, the relative importance of each process to the species distribution and abundance, as well as the biotic and abiotic factors involved in such processes, are often unclear. This highlights the need to consider which factors operate at different scales in order to effectively address issues relating to recruitment (Botsford, 2001; Navarrete *et al.*, 2002; Largier, 2003), which is a process having major repercussions on the success of shellfish enhancement activities.

Spat settlement rate can vary greatly even between sites close together. Thus, spatial variations in settlement must be estimated to evaluate the potential success of restocking of areas that are still receiving recruitment from wild populations, and also to optimize spat collection for subsequent seeding. Appropriate scales of sampling must be used in order to characterize the large variation in dispersal dynamics over space and time, and the between-site variation in settlement dynamics of larvae. Single time or “snapshot” studies should be avoided because they generally lead to erroneous conclusions (see Gaines and Bertness, 1993). Mesoscale (local populations) and macro/megascale (geographic) patterns are usually present. These allow one to decide which fishing grounds have a higher probability of sustaining high-density stocks. Life history, and the characteristics of habitat or substrate, when known, helps identify the potential causes of recruitment bottlenecks and density-dependent processes (Peterson, Summerson and Luettich Jr., 1996). Two additional topics deserve consideration here: (a) *gregariousness* i.e. a tendency for larvae to settle more readily on surfaces on which there is already some spat (see

e.g. Ahn, Malouf and Lopez, 1993); and (b) in some species (e.g. *Placopecten* sp., *Mytilus edulis*) movement or dispersal of juveniles may take place after settlement by swimming or passive drift.

2.2.2 *The stock-recruitment relationship*

Closed populations are those in which immigration and emigration processes at any stage of the life cycle can be considered negligible within the management area for the species. Populations characterized by a very restricted degree of dispersal can be functionally defined as self-sustaining, independent units for management and conservation purposes. At first sight, the classical tools of fishery science such as production and analytical models, stock-recruitment and mortality-at-size relationships described in Ricker 1975, Beverton and Holt 1957 (or more recently, Hilborn and Walters, 1992 and Sparre and Venema, 1992) might reasonably be applied to analysing the demography and population dynamics of invertebrate stocks. The main complication for sedentary or semi-sedentary invertebrates however, is that the growth and mortality rate and the carrying capacity of the environment may vary spatially, as will the magnitude of density-dependent effects (for example, interactions between recruits and adults are likely to be a function of density within nursery areas). These recruit-stock interactions may be important (and mortality can be caused by adult cohorts to new recruits settling on the same grounds). Such mechanisms are not usually considered in finfish stock assessment, and some examples for invertebrates of these interactions are described in the anthology of case studies edited by Caddy (1989a), and in ICES (e.g. Hancock, 1973, 1979). It is important in investigating shellfish populations through field observations, that observations be referred to a spatio-temporal context, and this also applies to the management strategies that need to be developed.

With a few exceptions (e.g. Ennis and Fogarty, 1997 for *Homarus americanus*), stock-recruitment relationships (SRRs) have not been derived for invertebrate resources. For spatially structured populations of sedentary species, SRRs may depend more on local densities than on absolute stock size (Hancock, 1973; Caddy, 1999a, Orensanz and Jamieson, 1998). In fact, until recently, the general consensus seems to be that adult stock size is not critical in determining spawning/recruitment processes for sedentary organisms, but some studies suggest that, even for broadcast spawners, many discrete aggregations of sessile and semi-sessile invertebrates forming mesoscale shellfish beds or fishing grounds are self-sustaining within the larger metapopulation. Evidence for this comes from studies of coastal molluscan shellfishes (Efford, 1970; Defeo, 1996a, b; Lima, Brazeiro and Defeo, 2000) and from open sea scallop stocks (Peterson and Summerson, 1992; McGarvey, Serchuk and McLaren, 1993). This population typography has definite advantages where enhancement programmes are concerned, because of the likely reduced importance of larval exchanges. There are some important exceptions, as, for example, populations of macrocrustaceans such as Palinurids, where long larval life histories may result in wide dispersion of offspring to distant habitats. Some dispersal undoubtedly also occurs for molluscan and other sessile invertebrates, and when it does, given their sessile habit, the dynamics of larval dispersal from source populations to peripheral sink populations (Lesica and Allendorf, 1995), opens some interesting management perspectives that are not available for managing motile organisms.

For sedentary species local stock-dependent factors occur; i.e. local recruitment success is often limited by the biomass of parental stock already established. For example, adults of the common cockle *Cerastoderma edule* may smother spat falling on grounds densely populated by adults (Hancock, 1973). In cases where strong overcompensation mechanisms operate within a SRR

(i.e. inhibition of recruitment at high adult densities), an extended closed season protecting high densities of adults from exploitation could inhibit recruitment and growth of the enhanced stock. Defeo (1996a) showed that a 3-year closed season resulted in a rapid recovery of the yellow clam population to levels above those recorded during exploitation, but this was accompanied by a dramatic reduction in *Mesodesma mactroides* recruitment due to stock-dependence. In such cases, passive or active enhancement programmes should be complemented by adequate levels of exploitation, in order to: (a) prevent monopoly of spatial resources by slow-growing adults; (b) decrease the probability of ingestion or passive filtration of larvae by established adults (overcompensation: see Defeo, 1996b); and (c) promote an increase in settlement/recruitment of the population. Ideally, the threshold spawning-stock biomass levels required to generate sustainable recruitment should be estimated from field observations.

Figure 2.6 illustrates a recruitment curve fitted by Hancock (1973) to a sedentary population of the cockle, *Cerastoderma edule*. The recruitment curve fitted by non-linear procedures shows extreme interannual variability and strong compensation for overexploitation, which comes largely from freeing of settlement areas from intergenerational competition during settlement at low adult density. The annual population surveys this study was based on, involved transects crossing the entire spatial distribution of the population, and thus measurement errors in estimating stock and recruitment densities were minimized compared with finfish SRRs, but the much more accurate census possible for an intertidal bivalve compared with finfish stocks, evidently did not eliminate the strong inter-annual variability (Hancock, 1973). The key year of 1965, when a high spawning stock density was present, might indicate that an asymptotic "Beverton and Holt curve" (shown by the dotted line), rather than the dome-shaped "Ricker" curve fitted by Hancock would be equally appropriate.

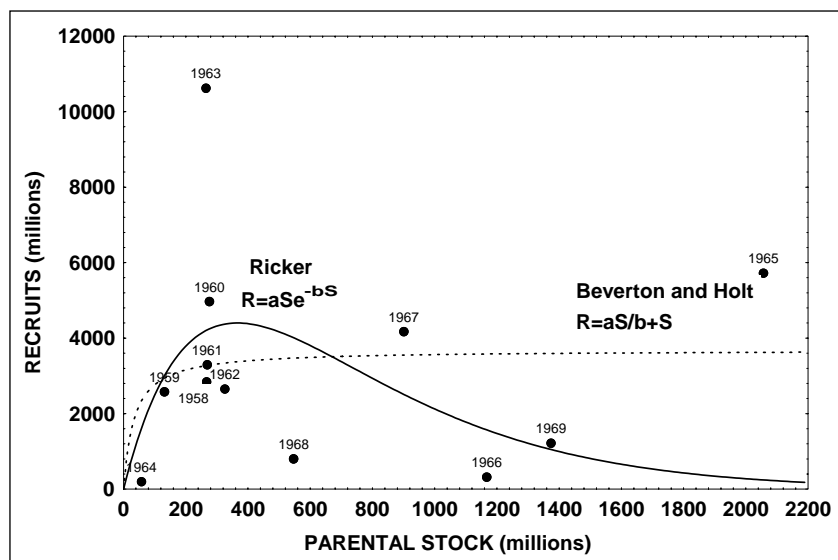


Figure 2.6 Stock-recruitment relationships for the cockle *Cerastoderma (Cardium) edule* of Burry Inlet (data from Hancock, 1973). Ricker and Beverton-Holt stock-recruitment relationships are presented for comparative purposes.

More convincing than the effect of total stock size on recruitment, seems to be the effect of environment in many invertebrates (see e.g. Addison, 1997; Botsford, 2001), and as mentioned above, of local adult biomass as a negative indicator of settlement success for bivalves (e.g. Hancock, 1973; Defeo, 1998). Age composition can also play a critical role: for example, McGarvey and Willison (1995) note that while an average female scallop in the exploited population of a mean age of roughly 3.1 year produces some 15 million eggs; in the protected closure zone mean ages may reach roughly eight years, and the individual fecundity

would have increased to some 153 million eggs: a 21-fold difference. As they note, although density-dependent factors might limit recruitment to the adult population due to crowding and competition for food, these are unlikely to be major factors for heavily fished populations.

Knowledge of the SRR that applies might still be useful where natural enhancement is the approach used, but a relatively weak SRR, and high and often unexplained variations in recruitment strength, are among the major sources of uncertainty in management of invertebrate resources (see papers edited in Caddy, 1989a). This high variability in recruitment makes it difficult to determine the level of parental stock that will maximize recruitment abundance over the long run. In fact, environmental variability is often seen as the main driving factor for invertebrate recruitment success. Environmental trends may in fact provide the main objective criterion for a rough forecast of the level of recruitment, although predicting the success of an enhancement programme is rarely straightforward. Overestimation of the level of recruitment (and equally serious, the assumption that recruitment will occur annually at more or less the same level from year to year), can lead to overexploitation and even collapse the stock. Although underestimating recruitment may result in lost income opportunities, it has less serious consequences for the continuity of future supply. Collapses of shellfisheries due to unexpected failures in recruitment produced by an adverse physical environment or strong density-dependence processes, makes prediction of the magnitude of benthic stocks problematic, and strong recruitment variability needs to be taken into account in management (Ulanowicz *et al.*, 1982).

There is some evidence however, of a change in perspective emerging in recent years with respect to the low importance formerly accorded to spawning stock size in broadcast spawners. Previously the paradigm was that only low abundances of the parental generation were needed for stock replacement of populations of highly fecund spawners, and it is true that better than average recruitment may be produced by small spawning stock sizes. More recently, evidence from Mutsu Bay suggests that good recruitment years are more frequent for Japanese scallop (*Patinopecten yessoensis*) since hanging culture has added a much greater spawning biomass (and higher spawning concentrations) than was previously present only on natural beds (Aoyama, 1989). This is of importance and useful, if the experimental hatchery stock is not severely inbred and if gene flow between the wild stock and the broodstock has been sufficient to prevent divergence (Boulding, Boom and Beckenbach, 1993).

A major problem with stock-recruitment (SR) analysis is that a relatively long time-series spanning a range of stock sizes is needed to produce a reliable relationship (Myers *et al.*, 1994). Even though longer data series for stock and recruitment of benthic resources are now becoming available, a common problem in fitting this non-linear relationship is clearly the key importance of outliers on the left and right-hand side of the SR curves. As a result, many analyses based on a cluster of points offer little or no information at all on model performance at extreme population levels. Such predictions have a high possibility of being misleading, thus precluding adequate definitions of management strategies to optimize yield (Sissenwine, Fogarty and Overholtz, 1988). In this context, the Ricker and Beverton-Holt SR curves predict quite different levels of recruitment at high adult densities. Whether the right-hand limb (RHL) of a SRR is a flat asymptote (Beverton and Holt relationship), or a descending one (Ricker relationship), may be a key issue for enhancement initiatives. The lack of contrast in spawning stock levels for stocks already reduced in abundance when observations began, often restricts the range of stock and recruitment sizes to the left of any inflection point in the SRR. Thus, the RHL it is unlikely to be estimated with great precision from field data (see e.g. Garcia, 1983; Cobb and Caddy, 1989). It is often the case in regulatory programmes, both for finfish and invertebrates, that

relatively stable population sizes and harvests generate many points at moderate exploitation rates and population levels, without providing information about the relationship at higher or lower spawning stock levels (Walters and Hilborn, 1978; Walters and Holling, 1990). In this context, one way to determine a SRR is by simultaneous estimation of recruit and adult densities in different management subunits subject to contrasting fishing effort level. This would result in a broad range of spawning stock densities and thus increase the range of the independent variable, stock density (Walters, 1986; Walters and Collie, 1988).

The experimental manipulation of fishing effort and population density through area closures is a promising approach to collecting data on density-dependent recruitment in addition to its practical importance as a fishery management tool. For example, experimental manipulation of fishing effort in the yellow clam of Uruguay was useful in elucidating the form of the SRR (a typical Ricker curve), derived from a nine-year data series (Defeo, 1996a). The yellow clam SRR showed overcompensation, with a strong inhibition of recruitment at high adult densities during the fishery closure (Figure 2.7). The human exclusion experiment was also perceived as a way to acquire knowledge as to population structure and dynamics. The closure of the fishery for 32 months was encouraged by the local community and the coastal marine authorities, who were involved in control operations. This example demonstrates that estimating the SRR for spatially differentiated populations would not necessarily require long-term databases, but the implementation of management experiments designed to test specific hypotheses as to the population dynamic processes prevailing (Defeo, 1998). The existence of dominant age classes and the observation of quasi-cyclic trends in infaunal assemblages may in part be due to interactions between adults and settling larvae. Among the three different mechanisms of succession, i.e. facilitation, tolerance and inhibition (Connell and Slatyer, 1977), the last-mentioned seems to better explain the process underlying yellow clam population fluctuations.

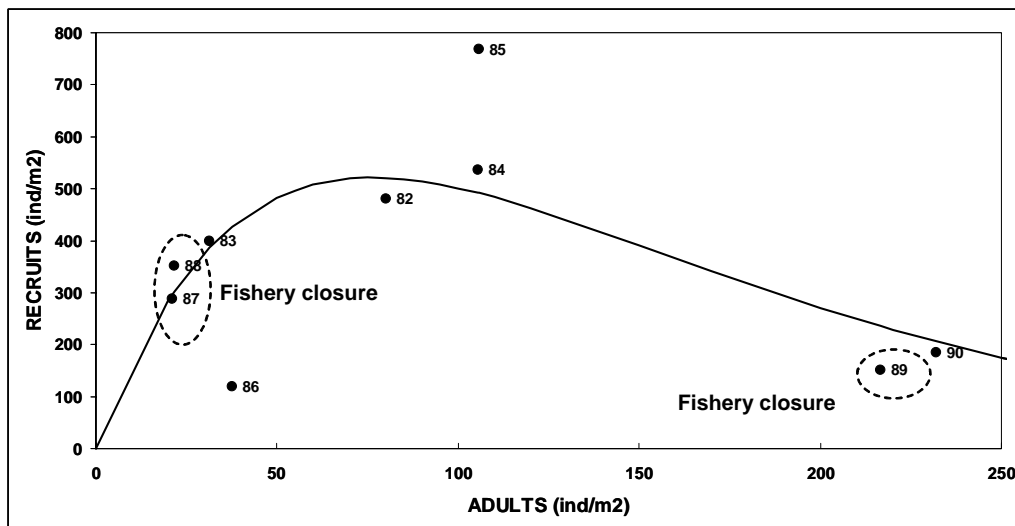


Figure 2.7 SRR for the yellow clam *Mesodesma mactroides* of Uruguayan beaches. The fishery was closed between 1987 and 1989 (highlighted in the figure). Detection of strong overcompensation was possible because of the rapid population build-up as a result of the experimental closure, and recurrently detected in 1989 and 1990 (after Defeo, 1998).

The concept of a “bottleneck” in the recruitment process, suggested by Caddy (1986a) and Caddy and Stamatopoulos (1990) for crevice-dwelling organisms, may be applied (with obvious modifications because sandy beaches do not constitute dissected surfaces) to the yellow clam

population. In this case, the "bottleneck" effect may occur during the spatfall period, in which a high density of adults (e.g. greater than adult density in 1984-1985: Figure 2.7) increases the probability that a resident adult population filters out settling larvae, and prevents colonization by new recruits. i.e. the "bottleneck" presumably occurs when the resident population density or biomass exceeded some limiting carrying capacity, which, according to the results obtained in the SRR and transect scale analyses, would be presumably close to 100 adults/m² (Defeo, 1998). Another important bottleneck has been noted for American lobster production resulting from the limiting availability of cobble-bottom which has proved the ideal habitat for juvenile cryptic stages in the life history.

In some cases, fitting of SR models may be misleading for invertebrates with complex life cycles or where spatially segregated populations belonging to a metapopulation occur. Thus, some of the basic assumptions of SRR theory, such as, that an individual spawning population exists, or that density-dependent effects are uniform across the population, are violated. Before using overall SR models for prediction, there should be a careful judgment to determine if the population under study actually acts as a closed population (assumptions on this point are spelled out in Hilborn and Walters, 1992).

2.2.3 *Compensation or depensation?*

More recent practice for finfish management has been to consider the degree of compensation shown by the curvature of the SRR, and for abalone, Shepherd, Rodda and Vargas (2001) found SRRs for this species to be flat. For finfish and other organisms fished down to relatively low densities, it is often assumed that compensation for low density occurs, whereby survival of gametes improves and juvenile mortality is reduced at low stock sizes (reviewed in Rose *et al.*, 2001). However, small-scale experiments and measurements in depleted habitats show no compensatory enhancement of hard clam *Mercenaria mercenaria* recruitment with local reduction in adult density in North Carolina (Peterson, 2002). Indeed, once density falls below a certain level, so called "Allee effects" may occur in some species, otherwise referred to as "depensation", whereby reproductive success drops below a certain parental population size. Various life history mechanisms could lead to this effect, notably a low density of spawners or excessive abundance of predators supported trophically by an abundance of another species that had replaced the former target species now decimated (which is therefore kept at low densities by predators, and/or fishers taking it now as an incidental catch). Other behavioural mechanisms such as reduced mortality during migration occur if adult numbers are high. The occurrence of Allee effects is generally discounted for high fecundity invertebrates, but Stoner and Culp (2000) describe its operation for queen conch, and Shepherd, Rodda and Vargas (2001), as mentioned, have suggested similar mechanisms may apply at low densities for abalone stocks. In the case of conch, mating rarely occurs when density falls below 48 conch/ha, but above this, reproductive activity rises to an asymptote near 200 conch/ha. This may explain why heavily exploited conch populations are slow to recover even with closures in place, and argues for a recovery programme that artificially maintains high densities of spawners in a "mother lode" or source area situated in a historically optimal spawning location, as evidenced by a wide size range of individuals in the local sub-population.

The possibility of depensation (see e.g. Liermann and Hilborn, 2001) is suggested by the failure of depleted abalone grounds to recover after 15-20 years of no or low fishing. Relatively high values of $F_{50\%}$ for small stocks and $F_{40\%}$ for large abalone stocks were suggested by Shepherd and Baker (1998); Shepherd, Rodda and Vargas (2001) from egg-per-

recruit analysis used to generate limit reference points (LRPs). In other words, for abalone it is unsafe to allow exploitation rates that drop egg production/recruit below these rather high percentages of the unexploited egg production. Thus, for invertebrates we have examples spanning a wide range of spawning stock sizes from which populations are recoverable, from abalones and king crabs which need a high threshold for recoverable depletion, to high fecundity spawners with apparently low thresholds such as many sessile molluscs; for example the Georges Bank scallop stock. Interestingly enough, management procedures for Falkland Island squid require a 40 percent of the stock to remain available for spawning (after which of course the whole cohort dies) - e.g. Basson *et al.* (1996) and Agnew *et al.* (1998).

Classically, it was assumed that high fecundity broadcast spawners such as most marine molluscs were capable of recovering from low densities. Whether a scallop population could recover from a stock size as low as two percent of the “spawning units per recruit” (%SPR, expressed in biomass or eggs: see Section 2.4.2) of the unexploited stock (Mace and Sissenwine, 1998). In fact, recovery success probably depends more on the local density and location and aggregation of the remaining spawners, and not on total stock size, as the key to successful replenishment. The role of source populations for Georges Bank scallops was in fact commented on by McGarvey, Serchuk and McLaren (1992) who found that 82 percent of egg production came from the Northern Edge and Northeast Peak of the Bank, and was produced at a high adult density. For sedentary species, the source and sink concept evidently needs to be taken into account. More recent results suggest that although recovery from very low stock sizes may occur at the extreme for some broadcast spawners, local density is critically important if rate of fertilization by a dispersing sperm cloud is to be significant. This is especially true where epidemic spawning seems to be necessary to ensure adequately high gamete density (e.g. *P. magellanicus*). Local spawner density may then be important for triggering successful spawning episodes, as well as assuring adequate fertilization rates. Clark (1974) suggested a theoretical framework for stocks that form schools, and a similar vulnerability for some macrocrustaceans that form large, compact aggregations such as some Alaska crab stocks, was suggested by Orensanz, Parma and Hall (1998). He proposes these may be subject to a “depensation catastrophe” in which a heavily exploited population cannot sustain itself by reproduction, and may collapse and not readily recover. MacCall’s (1990) “basin theory” suggests that species, whose geographical range contracts with exploitation such as king crabs, are especially vulnerable to overexploitation. Another example of depensation in invertebrate resources is provided by sea urchins. Two possible depensatory mechanisms were suggested for red sea urchins by Botsford *et al.* (1993): a juvenile refuge from predation under adult spines, and a minimum density for successful spawning by mature adults, estimated: at least two urchins (one female) per m².

2.3 Information requirements for monitoring stock condition and recovery

Perry, Walters and Boutillier (1999) proposed that typically, three phases occur in obtaining the necessary scientific information to support management of marine sedentary benthic species:

1. Collect and synthesize existing information on the target stock, and on similar stocks and species.
2. Collect new information by surveys or site depletion experiments, to supplement that found insufficient from the first phase that will allow alternative management strategies to be proposed and evaluated, and to propose regulatory approaches.

3. In the course of “fishing for commerce”, while implementing chosen management actions, seek to maintain and complete the informational data base from the previous phases. They note that strong interaction between science, management and stakeholders is essential during all three phases.

In conventional stock assessment of finfish resources, regular surveys of stock biomass, catch weight and its structure by size or age, form the main basis for estimates of population size and fishing mortality rates, using analytical methods and production modelling procedures (see references above). For most invertebrate resources similar data to finfish needs to be collected, but with more emphasis on the spatial breakdown of the population and a corresponding discrimination of catches and effort by geographical subarea. Some examples of special data requirements for different species categories are given in Table 2.1. Even from the limited data provided in Table 2.1, it is clear that any assessment approach for invertebrates needs to take into account the specifics of the life history of the species in question and its ecological situation.

Where several or many local populations exist within a metapopulation, the possibility of carrying out a full stock assessment annually for each sub-population probably does not exist, and the strategy suggested by Shepherd, Rodda and Vargas (2001) for local abalone stocks appears the most feasible, namely to implement a monitoring system for each sub-population, but devote priority attention to those areas where indicator values approach those pre-defined “red” or dangerous conditions that will be touched on later in this report.

Table 2.1 Some specific indicators useful for evaluating stock status of specific invertebrate resources.

Species group	Indicator	Significance	Reference
Whelks, conch	Proportion of animals with thickened shell lip	Thickening occurs at maturity, providing an index of % mature animals in population	Stoner and Sandt (1992)
Squid	Annulae on statoliths, and on the gladius used for age reading	Daily age rings may provide information on short-term growth and mortality	Arkhipkin (1988), Bizikov (1991)
Scallops	Breakage marks on shell or <i>shock marks</i>	Provide information on frequency of past fishing activities	Caddy (1972), Naidu (1988)
Pandalid shrimp	Sex ratio	As protandric hermaphrodites, ratio provides an index of fishing mortality, and varies with mean annual T°C	Hannah and Jones (1991); Fu, Quinn II and Shirley (2001)
Decapod crustaceans	Percentage of soft shelled animals	An index of a recent moulting, which generally decreases with age, hence indirectly tracks mean age in the population	Yamasaki (2000), Hébert <i>et al.</i> (2001)
Crabs, homarid lobsters	Proportion of egg-bearing females, and sex ratio	Index of population fecundity and perhaps exploitation rate	Bennett (1974)

2.4 Management advice and organizational requirements for managing invertebrates

A fishery management regime may go through a series of stages in the introduction of spatial components into the management framework, and some possible transitions are illustrated in Figure 2.8. Thus, a transition from open access to various modalities in which access to the shellfish grounds become specified in different ways may be observed.

Caddy and Gulland (1983), Perry, Walters and Boutillier (1999) and Castilla and Defeo (2001) draw attention to the phases that typically are passed through by fisheries before management becomes sustainable. Perry, Walters and Boutillier (1999) suggest three phases:

1. A “Developing” period.
2. A “Crisis” period, leading to a call for implementation of license limitation.
3. A “Sustainable” period, often leading to closures in time and space, and more frequently in recent years, to the granting of ITQs or other strict limits on access (e.g. Castilla and Fernández, 1998).

During at least the first two phases, the classical data-intensive approaches used for finfish stocks are unlikely to be available, and a focus should be on developing indicator series that measure key aspects of the resource and fishery.

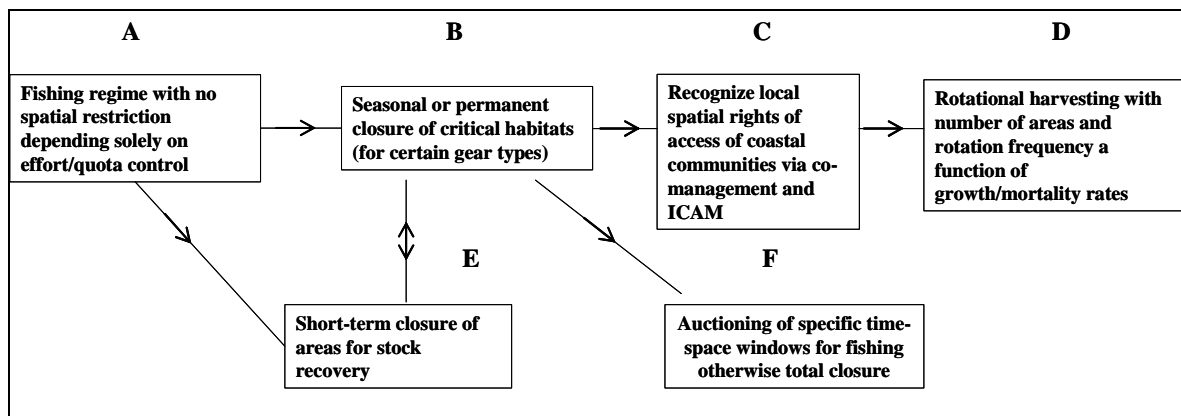


Figure 2.8 Illustrating progressive introduction of spatial components into a harvesting scheme for shellfish populations.

A method of restricting the fleet capacity exerted on the resource will be essential, and a degree of management redundancy, and hence safety, would be provided by using two or more of the following management measures:

1. Control of fleet capacity and of the individual fishing power of harvest units
2. License limitation
3. Total Allowable Catches
4. Daily bag limits
5. Allowable fishing days per week/month
6. ITQ allocations
7. Technical limitations of gear/vessels

8. Season duration
9. Closed areas
10. Apply rotating harvest schemes

With the exception of some offshore resources such as squids, and for resources where ITQ or similar management systems are in place (as in Chile: see Castilla and Defeo, 2001) the use of an overall Total Allowable Catch (TAC) is not a common modality, at least for inshore invertebrates. Castilla and Defeo (2001) showed that global quotas (i.e. TACs), if administrated through Individual Non-Transferable Quotas as in Chile, mean that fishers are forced to use their “quotas” more wisely, following a long-term perspective (Castilla and Fernández, 1998). Additionally, they showed that if a TAC is regulated through Individual Non-Transferable Quotas (INTQs), and shellfish extractions are authorized exclusively inside protected areas (e.g. Management and Exploitation Areas –MEAs- used in Chile for shellfish and other invertebrates), then a global quota may reinforce co-management procedures. All the above require legislation and enforcement of legal frameworks, and cooperation of fisher-communities, which need to be adapted to countries and idiosyncrasies.

In the absence of a fixed quota, strict attention to items 1 and 2 above provides a coarse control on fishing pressure, which can be refined and made more responsive to changes in abundance by also implementing at least one of items 3–10, which may be regarded as measures to “fine tune” the fishing pressure exerted. A more formal approach will require agreement on a “fisheries control law” by stakeholders such as was shown in Figure 2.8. If the goal is to restore a stock by reducing fishing effort for a specified period, then evidently short term sacrifices will have to be made in reducing fishing effort.

Spatially explicit operational management tools must be complemented by other management measures that take into account reductions in catch and effort, in the context of a framework of management redundancy (*sensu* Caddy, 1999a). It is a common practice that fishers illegally move pre-recruit shellfishes to areas in which their own gear is situated, in order to enhance recruitment on their grounds using juveniles from other fishing grounds. This fact is particularly noticeable when catch quotas are set under an open access system. In these cases, quotas are reached in a very short time due to the stockpiling of organisms during the days preceding the opening of the season (Geaghan and Castilla, 1986; Castilla and Defeo, 2001). This fact cannot be considered as a planned transplanting procedure and its control deserves special consideration when managing a coastal shellfish resource.

A responsive management approach will have to incorporate the regular monitoring of indicators of stock and fishery condition (see FAO, 1999). Apart from indicators of fishing pressure such as the number of days fished, close attention to changes in fishing power and ownership of fishing units or replacement of boats will be needed, in order to ensure overall fishing power does not increase as a result. Biological monitoring measures may follow changes in resource biomass or catch rate, fishing intensity, and the productivity of the system, and fleet indicators should monitor catch rate of key vessel and gear types. In addition to the just-mentioned biological indicators, there will be required a monitoring of annual recruitment success, and ideally seasonal growth rate and condition factor. Annual variations in those environmental conditions shown to be important to the species in question should also be followed. A regular control of the availability of suitable habitat for critical life history stages would also be advisable.

The brief summation provided above of course simplifies the management situation, and implementation within a co-management context will be most efficiently achieved through a fisheries management cycle, with annual and preferably semi-annual meetings of a management committee consisting of stakeholder representatives, resource managers and scientific advisors. Such a repeated cycle of events suggested by Figure 2.9 will be needed to consider and react to new developments in the fishery and its coastal environment, and to develop equitable rules for the fishery. The management committee would be strongly advised to set up a management plan to be rolled over on (say) a five-year time horizon, and this would ideally incorporate a medium term vision of the fishery, including the objectives of stock enhancement or restoration if this is needed. Since important issues for most inshore shellfish involve actors from outside the fisheries sector, a linkage of the committee to an Integrated Coastal Area Management body, if one exists, will be required. If it does not exist, a specific subcommittee of the shellfish management committee to look at environmental impacts on resource and habitat is advisable. Here, indicator values are compared with previously agreed decision rules, historical values, and after consideration of the data, recommendations for implementation should be agreed to by members. An alternative that is strongly recommended is that indicator series be incorporated within a “decision rule” requiring actions of a non-discretionary nature when dangerous conditions are evident.

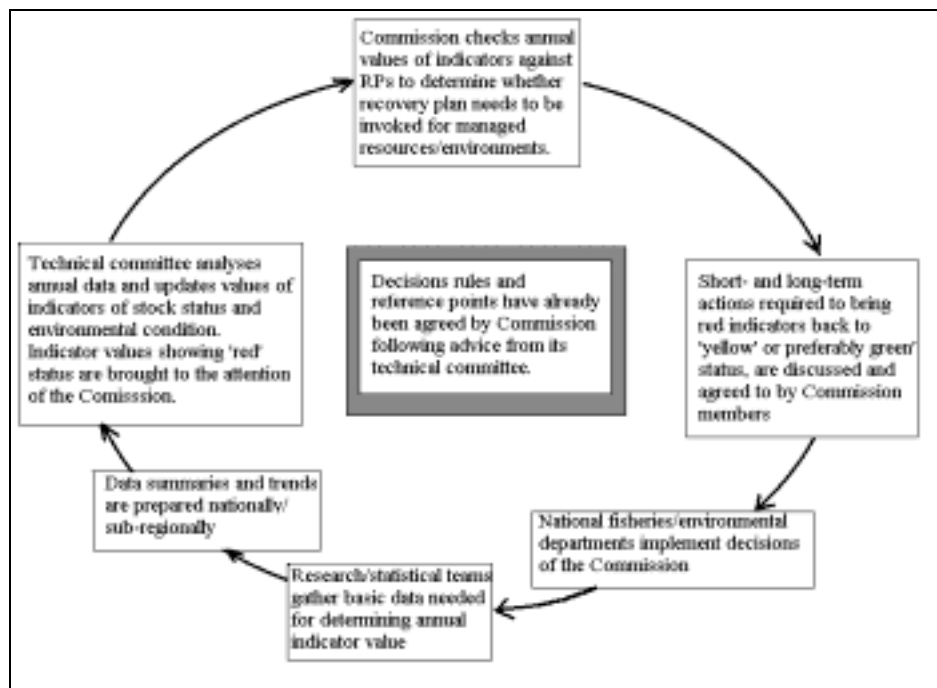


Figure 2.9 An idealized fisheries management cycle in which data on selected indicator values are collected and analysed annually by a technical working group, and values indicating dangerous conditions brought to the attention of managers and stakeholders in an overview management body referred to here as “the Commission”. Such a “cycle” will be needed both for routine resource management, but more so if a recovery plan is being implemented.

2.5 The use of indicators and reference points

2.5.1 *The management context for indicators and reference points*

The current approach to fisheries management since 1995, and the UN Fish Stock Agreement and FAO Code of Conduct, is to see reference points (RPs) as specific values of indicator series that represent a characteristic of the stock that is of concern to managers (see also FAO, 2001). When the Law of the Sea was being negotiated, Maximum Sustainable Yield was the Target Reference Point (TRP) of particular importance which was “aimed at” by fisheries management; often with effort overshoots and consequent stock declines. With UNCED, the 1995 UN Fish Stock Agreement and the FAO Code of Conduct for Responsible Fisheries, precautionary approaches were operationalized by Limit Reference Points (LRPs) that represent conditions of immediate concern to management; the occurrence of which should lead to calls for a cessation of fishing, or the curtailment of fishing effort to much lower levels (Caddy and Mahon, 1995). A list of some common RPs in use in invertebrate fisheries is given in Table 2.2. Several monitoring formats using indicators classify them functionally (e.g. Malkina-Pykh, 2000 and Muller, Hoffmann-Kroll and Wiggering, 2000 for the PSIR framework, and FAO, 1999 and Garcia and Staples, 2000 for the PSR framework) see indicators as divided into classes, each representing one aspect of the fishery and ecosystem. Thus, for the PSIR system, indicators of “Pressure” are those factors believed to influence the stock under consideration. Catch, either as an absolute variable, or expressed as a fraction of an “optimum” condition (e.g. C_t/MSY), or relative to some earlier base period believed to be optimal (C_t/C_U), or as a proportional change relative to the catch the previous year, are all indirect measures of pressure exerted by the fishery on the stock. Direct measures of pressure from the fishery are # licenses, fleet size or days fished, while the abundance of predators and (unfavourable) environmental conditions could be regarded as other forms of pressure from the ecosystem, (or alternatively could be included in the next category). This contains indicators of “State” or “status”, such as stock size or biomass - possibly expressed relative to some earlier favourable period, population fecundity, and the abundance of key prey for the species being considered. “Impacts” of fishing and other ecological or environmental factors can be measured in terms of the mean size and fecundity of the stock, or as the fraction of older spawners in the population compared with some previous reference period (U), or as an incidental effect of anthropogenic factors and/or natural environmental variation on the extent of critical habitat. Finally, “Responses” are indicators that measure the reactivity of the management system, such as the degree of precaution used in setting a TAC in relation to that predicted yield (Y) considered safe and generated by a population model; or the TAC set in relation to that in a previous productive period.

Management actions constitute the important “Responses” and other indicators could be envisaged here from activities of MCS (Monitoring, Control and Surveillance) that are measures of management reactivity to serious conditions. For example, the proportion of the grounds (or seasons) closed to fishing, or number of infringements of the control law prosecuted.

As noted, some systems of classification do not distinguish “Impacts” as such, and these are included under Pressure or State, in PSR systems (Garcia, Staples and Chesson, 2000). This slightly different classification of indicators is not critical to the function of the system; the key issue of importance is that the system does react to critical values of indicators! This issue will be discussed in the following section.

Table 2.2 Some variables for which indicators may be developed in invertebrate fisheries.

Pressure	State	Impact	Response
*Catch (C_t)	*Stock size	Mean size or age	*TAC/Y
* C_t/MSY	* B_t/B_{MSY}	Egg/recruit	*TAC/TAC _U
* C_t/C_U , § ΔC_t (+5%/year)	* B_t/B_U	Declining species diversity	§TAC reduced
(f/A) _t , F _t , (C/B) _t , u _t , Z _t	*CPUE _t /CPUE _U	loss of cover, habitat or rugosity	§ Limit access, protect areas
# licenses, fleet capacity, (Σ HP) _t , Σ (Fleet Tonnage) _t	*RV _t /RV _U	Value of state indicators (S _t)/ corresponding LRP value; S _t /S _U	§ Close seasons
# trips or #trap or dredge hauls/A	§ ΔB (declines at - 4%/year)	NA _t /NA _U , N ^{OLD} _t /N ^{OLD} _U	§ Δ (-) subsidies
Predator/stock abundance	Prey abundance or condition factor or growth rate K(von Bertalanffy)	Discards (directed and incidental fisheries) /catch, or discards/ biomass.	# infringements-prosecutions
Status of the environment	Popln. fecundity or % mature in catch or R _t /R _U	Incidental effects of trawling on epifauna?	Other regulatory responses

* Suggested by Gilbert, Annala and Johnston (2000); § suggested by Garcia and Staples (2000). Suffix U denotes a value calculated over an earlier base period when stock was sustainably exploited. RV = mean research vessel sampling, CPUE = commercial catch rate, Z = total mortality rate, A = stock area, ΔX = annual change in X, R = annual recruitment, f = (annual) fishing effort, F = fishing mortality rate, u = exploitation rate, TAC = Total Allowable Catch, Y = yield as predicted by a fitted model, NA = extent of nursery area/critical habitat, N^{OLD} = abundance of older mature age groups.

2.5.2 Fishing indicators, recruitment success and reference points

Classically, overfishing has been divided into “yield overfishing” in which too high a level of fishing intensity reduces the potential yield, and “recruitment overfishing” where the impact is on future recruitment through the SRR. Because of their high fecundity, marine invertebrate fisheries are rarely considered at risk to recruitment overfishing, even though this presumption can be criticized because of growing evidence of recruitment limitation in several marine invertebrate populations (Defeo, 1996a, 1998; Peterson, 2002). Peterson (2002), sampling in 11 years spanning a 24-year period from 1978 to 2001, showed that hard clam (*Mercenaria mercenaria*) recruitment declined significantly by 65-72 percent within the fishing grounds of central North Carolina. Fishery-independent surveys demonstrate declines of up to 95 percent in hard clam density and of up to 83 percent in spawning stock biomass during the years of 1980-1997. Consequently, the hard clam in North Carolina is a compelling example of unsustainable fishing mortality leading to recruitment overfishing in a bivalve mollusc stock. Caddy (1986a) noted that SRRs are very difficult to estimate for species where age reading is not possible, and Kruse (1992) records that of all the Alaskan crab stocks, only for the Bristol Bay red king crab stock has a SRR been estimated, suggesting that empirical approaches based on regular surveying of adults and juveniles may be the only practically feasible approach to detecting recruitment overfishing for many invertebrate stocks.

Spawner-per-recruit theory (Gabriel, Sissenwine and Overholtz, 1989) has been progressively used as a way of obtaining useful reproductively based reference points for stocks in the

absence of SRRs, and rests on the postulate that for continuity, successive generations (of females) need to produce sufficient “spawning units per recruit” (%SPR, expressed in biomass or eggs) over their lifespan to replace themselves. The observed ratio of R/S is the “survival ratio” \underline{s} and $SPR \geq 1/s^*$, where s^* is an average value. Obviously %SPR does not provide an absolute criterion for judging overfishing, since a regime shift may reduce productivity, or mean recruitment may decline. Hence some experts prefer to calculate the actual number of eggs produced by the population, but this is not always possible. An example of a precautionary management approach is to calculate numbers of eggs effectively hatched per recruit under current regulations, including fishing mortality and size limits. The number of eggs produced by American lobster stocks in eastern Canada has recently been mandated by the relevant Canadian management body to increase by one percent, and by US management authorities by five percent. In the first case, this result may be achieved at the discretion of the local management authority by any of the following measures: - increasing the minimum size limit, reducing fishing effort, introducing an upper allowable catch size to protect older spawners, or by tail clipping (“v- notching” berried (egg bearing) females and returning them to the water in areas where this is practiced (see www.mar.dfo-mpo.gc.ca/fisheries/res/imp/99offlob.htm for details). The retention of lobsters with a tail notch is prohibited whether the females are berried or not, thus the measure protects older spawning females. The application of %SPR reference points in management measures to ensure adequate spawning potential in the U.S. came with the requirement under the Magnuson-Stevens Act that the Fishery Management Councils establish in their fishery management plans (FMPs) measurable definitions of overfishing for all managed stocks. These regulations, published in 1989 require FMPs to “Specify to the maximum extent possible, an objective and measurable definition of overfishing for each stock or stock complex covered by the FMP...and how it relates to the reproductive potential” (see also Rosenberg *et al.*, 1994).

Mace and Sissenwine (1993) note that it is surprising that the SPR approach has been adopted so widely, since “few critical levels of SPR have been calculated from actual S-R data”. From a few empirical results, Goodyear (1980) suggested using the ratio of egg-per-recruit of the fished stock as a ratio of that before exploitation, and based on theoretical considerations Clark (1991) preferred a limiting management target of 35 percent SPR. Most overfishing thresholds used by FMCs have been in the range 20-35 percent. From theoretical and some practical experience, the %SPR is considered a measure of the resilience of the stock to the effects of exploitation, and Mace and Sissenwine (1993) give a range of values for %SPR that come from well-studied fisheries. For further comments on RPs derived from SRRs, the reader is referred to finfish studies (Hilden, 1993; Mace, 1994; Caddy and Mahon, 1995; Murawski, Rago and Trippel, 2001).

2.5.3 *Fecundity-based reference points*

In general, when defining the level of harvesting that is safe to apply, it is useful to calculate the number of eggs per recruit which a cohort of females will produce for a specified rate of harvest, if analytical parameters such as growth, mortality, and fecundity or egg production at age are known. These relationships may be modelled and used to develop fecundity-based RPs (see e.g. Fogarty and Idoine, 1988 for lobsters). A useful index may be obtained by expressing the calculated fecundity under current exploitation rates, as a percentage of the population fecundity when only natural mortality applied, and expressing this “relative fecundity” as a percentage. The fishing mortality that results in x% of the recruits produced by an unfished stock is then a criterion of the impact of fishing on the original reproductive

potential. Relatively high values of $F_{50\%}$ (the fishing mortality reducing population fecundity to 50 percent of unexploited conditions) were found for small abalone stocks, and $F_{40\%}$ for large stocks by Shepherd, Rodda and Vargas (2001) when using this relative egg-per-recruit analysis, suggesting that it is necessary to keep egg production above these rather high percentages of the unexploited egg production for this type of organism. The values for fishing mortality provided by this procedure constitute LRPs for the population. In fact, the derivation of model-based RPs for invertebrates looks like following the %SPR or fecundity/recruit approaches, but as noted, for sedentary species local density and the location of spawners within the metapopulation, rather than just population size, are probably the key variables.

2.5.4 Other empirical reference points

Where stock analysis does not lead to clear SRRs which can be used to formulate RPs, as in the case of many invertebrates, Annala (1993) suggests a variety of empirical RPs which he claims may steer a close to constant yield with less danger of overexploitation than aiming for MSY (Maximum Sustainable Yield). In place of MSY, he proposes TRPs based on “Maximum Constant Yield”, defined as the level of yield which is low enough that it should be sustainable from year to year even in unfavourable conditions of recruitment (see Table 2.3).

Table 2.3 Suggested empirical formulations for the Maximum Constant Yield (MCY) reference points suggested by Annala (1993). B_0 is the virgin biomass and B_{AV} is a long-term average of biomass.

Phase of fishery evolution	Expression suggested for MCY
New fisheries	$MCY = 0.25 * F_{0.1} * B_0$
Fisheries with historical estimates of biomass	$MCY = 0.5 * F_{0.1} * B_{AV}$
Developed fisheries with adequate data to fit a production model	$MCY = (2/3) * MSY$

Indicators and their critical values may in fact be incorporated into a so-called “Harvest Control Law”, which specifies non-discretionary actions that must be taken by management in response to certain indicator values. Figure 2.10 shows a hypothetical example for American lobster, *Homarus americanus*, which uses the numbers of eggs/recruit calculated as being produced by the population, as a fraction of that for the unexploited stock (in this case, ten percent of the virgin egg production is marking the fishery entering a dangerous state, and if the relative value falls between ten percent and one percent, the number of days fished in this hypothetical control law is reduced correspondingly), possibly by controlling the number of traps or trap hauls, or reducing the number of days per week on which fishing is allowed. Below one percent of the virgin egg production, the fishery is closed until recovery is evident to above the ten percent value. Of course, these “control points”, however measured, can be set at higher or more conservationist levels, depending on information on previous levels of egg production that were sustainable in this particular fishery.

A similar “Trouble Spot Protocol” for spotting early declines in individual greenlip abalone populations where critical states are recognized for a given fishing ground likely to constitute a “trouble spot” (Shepherd and Baker, 1998). The occurrence of a “trouble spot” (Table 2.4) should lead either to a demand for more detailed research, or a sterner management response, with closure as the last resort (Shepherd and Baker, 1998; Shepherd, Rodda and Vargas, 2001).

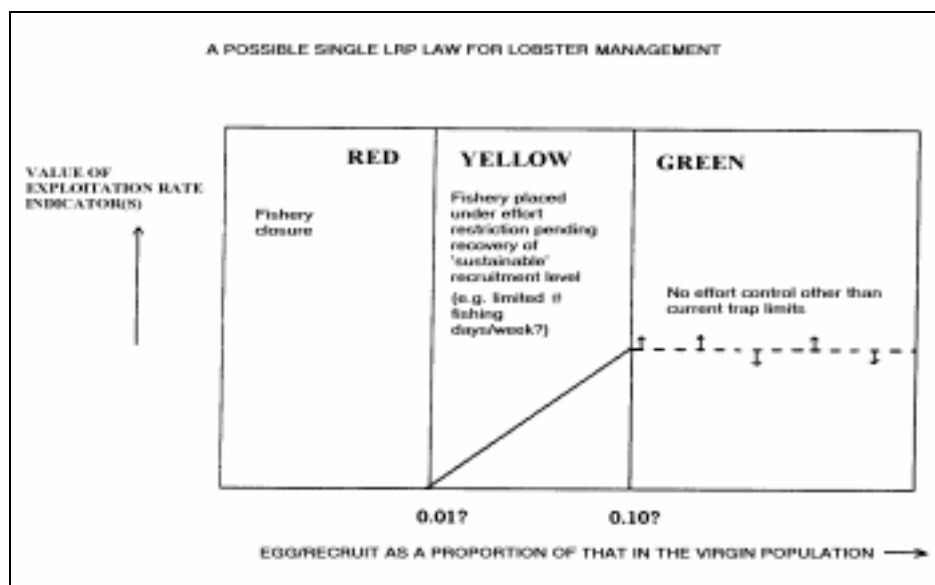


Figure 2.10 A hypothetical fishery control law for a lobster fishery, expressed in terms of its calculated egg production, as a fraction of that in the virgin population (horizontal axis). The fishery is placed under progressively more severe controls of exploitation rate (the descending ramp) until one percent of egg production by the virgin stock is reached, when the fishery is closed and not reopened until relative egg production exceeds ten percent once again (traffic light colours can be used to communicate the relative “safety” of the current fishery situation in each year).

Table 2.4 Trouble spot protocol for managing abalone populations (from Shepherd and Baker 1998).

Level of severity of indicator values	Metapopulation Fishery Indicator	Agreed management response
4	Total catch decline > 60% (since 1985) OR: Recruitment declined >20% over last 4 year	Close fishery. Establish recovery plan.
3	$F > F_{40\%}$ (initial productivity > 10 t/year); > $F_{60\%}$ (Initial productivity < 10 t/year) – according to site	Reduce F (reduced season, closure or increased size limit)
2	Estimated spatial decline > 50% OR: Mean survey density < 0.25/m ² OR: $Z > 0.4$	Do Egg/recruit analysis (?). Commence annual recruitment survey
1	Total catch decline > 30%	Survey spatial extent of population and compare with historical records. Do catch curve analysis.

2.6 Harvest control laws and indicators of productivity for managing and restoring invertebrate fisheries

The development of reference points based on indicator series of fishing mortality, biomass and recruitment inevitably led to a further development, mainly for finfish management so far, namely an agreement on “harvest control laws” which specify for specific indicator values what actions (hopefully non-discretionary) should be taken by management once there is a high probability of such a dangerous LRP being infringed (Figure 2.11). In order to provide a “safety margin” before an LRP was triggered, ICES proposed a further class of precautionary reference points, F_{PR} and B_{PR} , which mark points which have an acceptably low level of probability of infringing the corresponding LRP for the same indicator series. A simple harvest law using these two RPs is illustrated in Figure 2.10, in which a relative egg production of ten percent effectively is a precautionary level. This kind of approach has been used in managing invertebrate fisheries by Shepherd and Baker (1998).

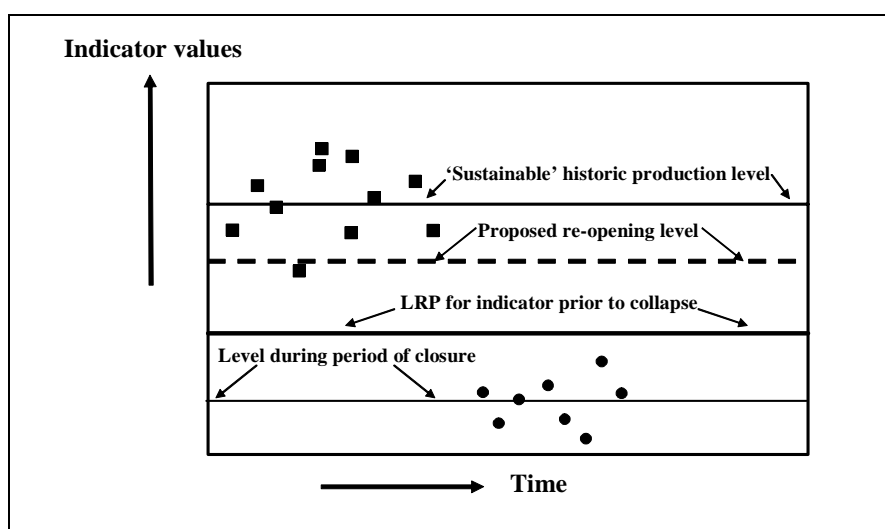


Figure 2.11 After a population collapses below a LRP set earlier, based on the mean value of the indicator during earlier sustainable production, the fishery is closed once the minimum value specified in some harvest control law is infringed. Reopening the fishery should not occur until the stock (and indicator value) has risen at least a significant way towards (or even has reached) the previously historic production levels.

The problem with the above two-indicator approach (usually spawning biomass or egg production, and some indicator of effective fishing mortality, being the two indicator series most used in fishery management procedures), is when environmental conditions change. This almost inevitably leads to a change in system productivity, and often a decline (or increase) in recruitment. This situation is especially likely to occur close to the base of the food web, and for species with a limited ability to move to more productive environments. This situation suggests the need for a third class of indicators and RPs to be introduced into the control law, namely “State” indicators measuring resource/habitat productivity, such as annual recruitment, annual growth rate, condition and meat content (which may also vary seasonally in shellfish, and affects their market value) (see also Anonymous, 2000). Possibly for some species such as oysters where disease outbreaks are common, the prevalence of

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.

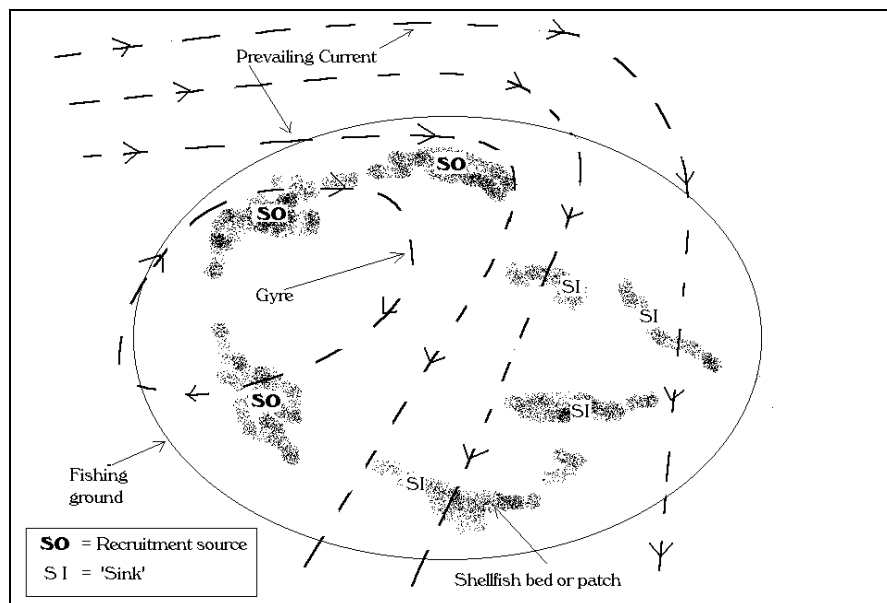


Figure 3.1 Illustrating the concept of source and sink populations in relation to the prevailing current system, which for source populations provides a measurable probability of larval return to spawning populations, which is not generally the case for sink populations.

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.

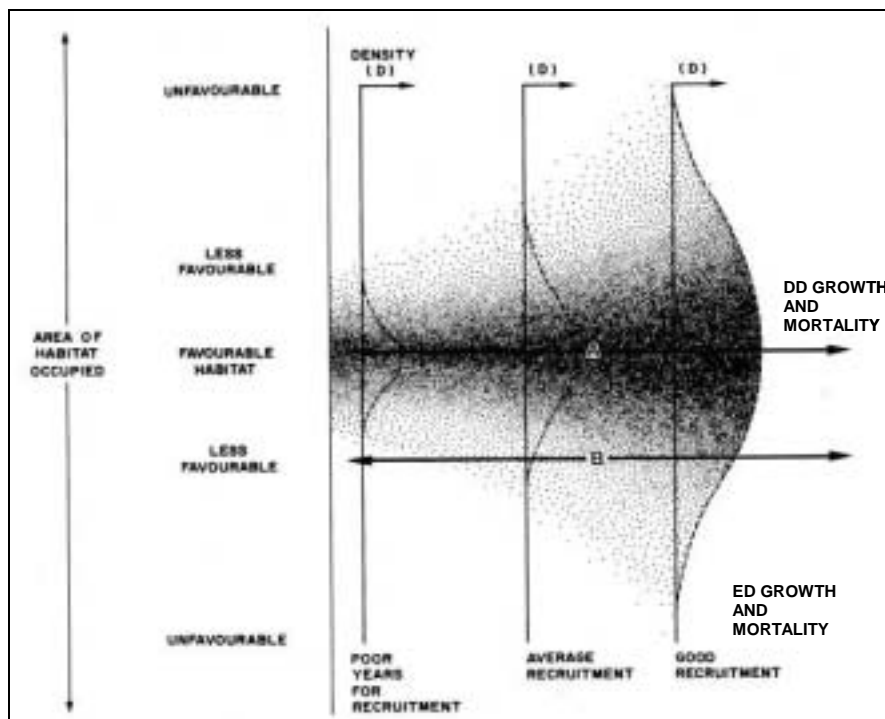


Figure 3.2 Variations in the spatio-temporal extent of recruitment and consequent stock contraction or expansion (from Caddy, 1989b). In "core" favourable habitats, density-dependent (DD) mechanisms prevail, lowering growth and mortality, whereas environmentally dependent (ED) mechanisms primarily regulate 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.

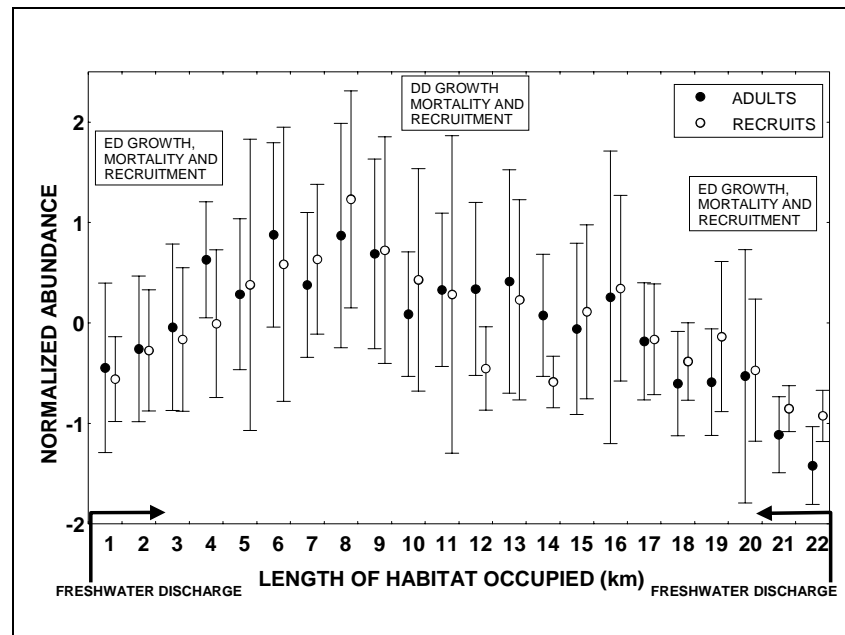


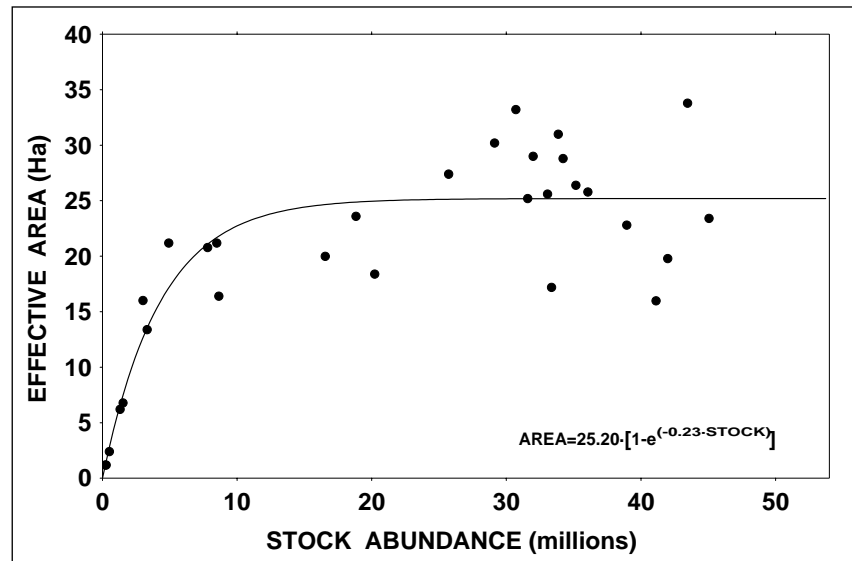
Figure 3.3 Diagrammatic representation of variations in the alongshore variability of the yellow clam *Mesodesma mactroides* over favourable and unfavourable loci, following Caddy's hypothesis of habitat suitability. Recruits occupied unfavourable habitats only during periods of good recruitment.

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.

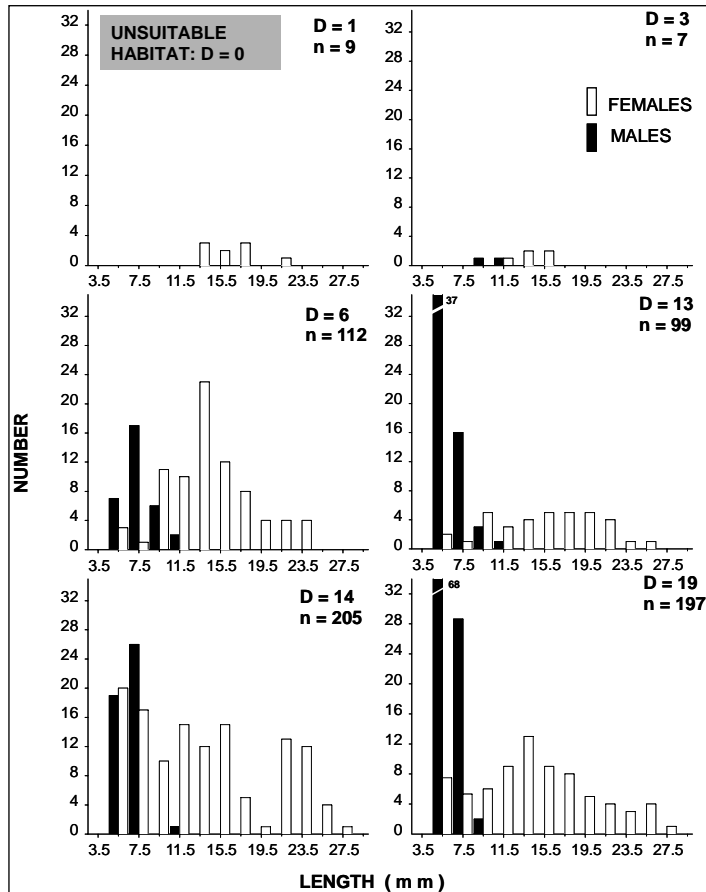


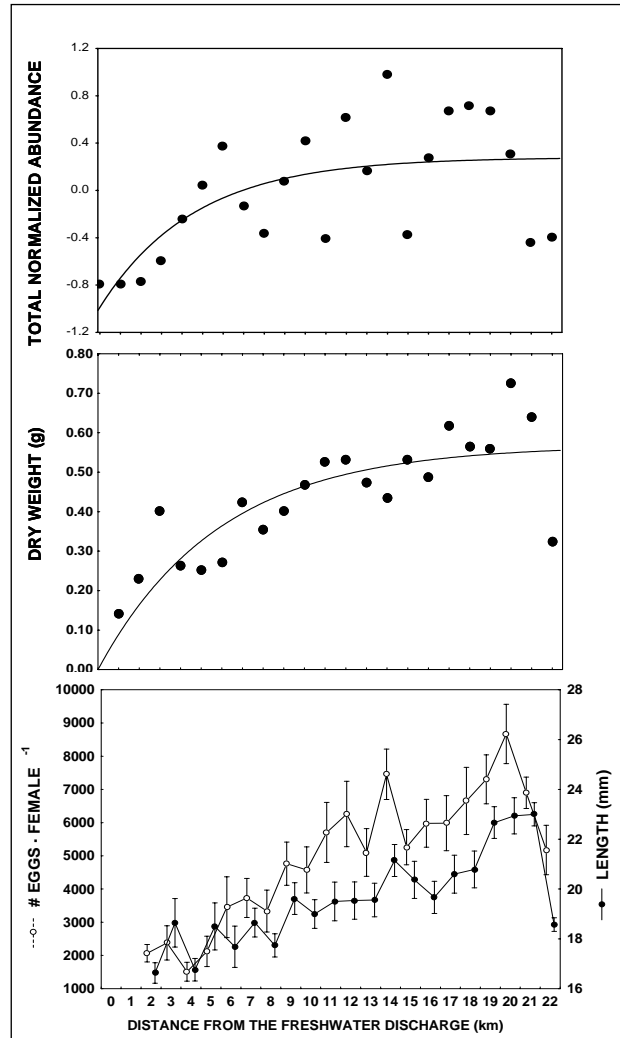
Figure 3.5 Length frequency distributions of the mole crab (Uruguay) discriminated by sex at different distances (D , in km) from the unsuitable habitat, defined by the presence of a human-made freshwater canal. Note the absence of smallest and largest sizes close to the freshwater discharge (see Lercari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

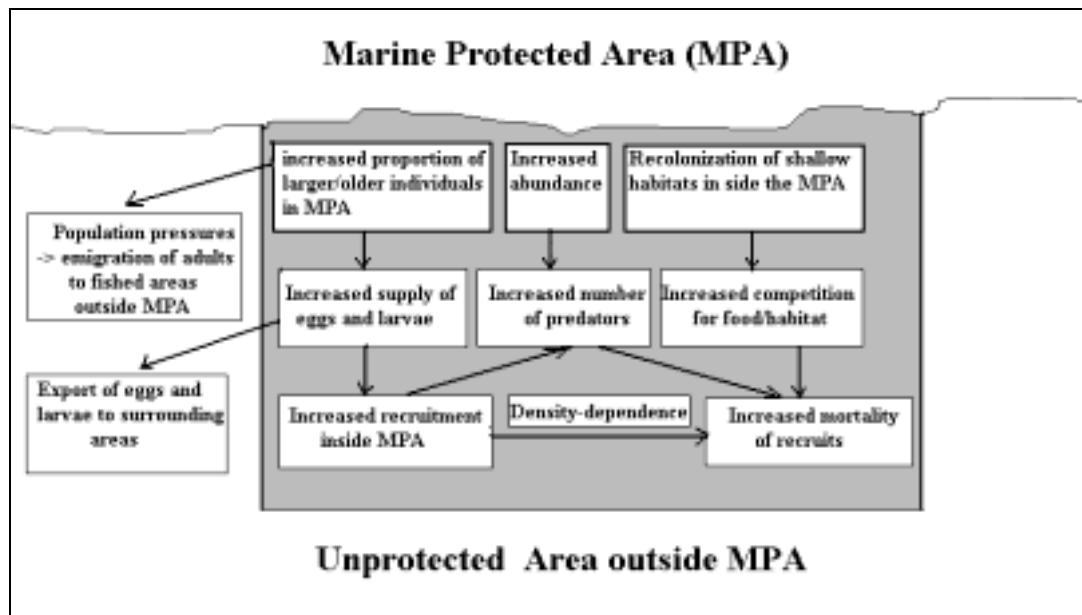


Figure 3.7 Some characteristics of MPAs, particularly with respect to recruitment and density dependence, and their potential contributions to fisheries in surrounding areas. Modified from Planes *et al.* (2000).

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.

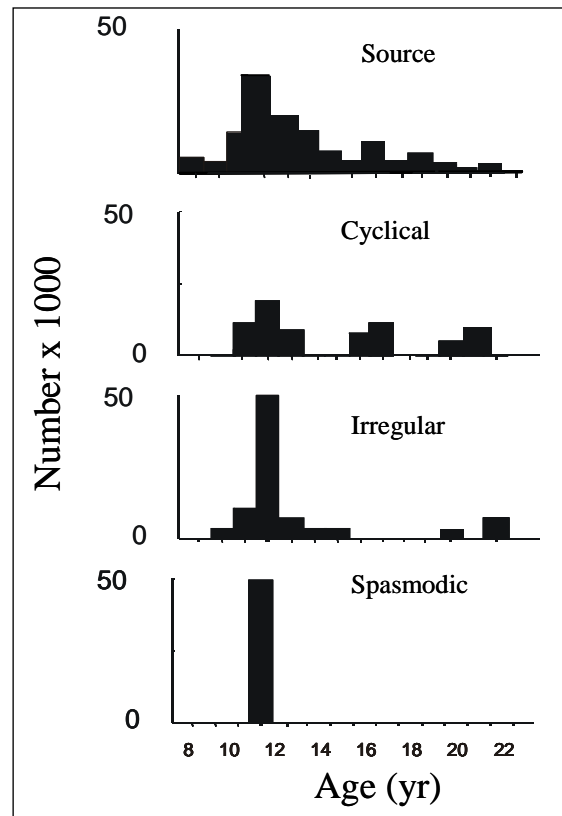
Figure 3.8 The “source-sink hypothesis” and population structure. Sources (upper panel) and Sinks (three last panels) in sedentary invertebrate populations, and the expected age structure as a result of larval dispersal and retention to the parental spawning area and differential post-settlement mortality 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 *N_{ages}* defines the number of year classes in a sample and *M_{age}* 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.

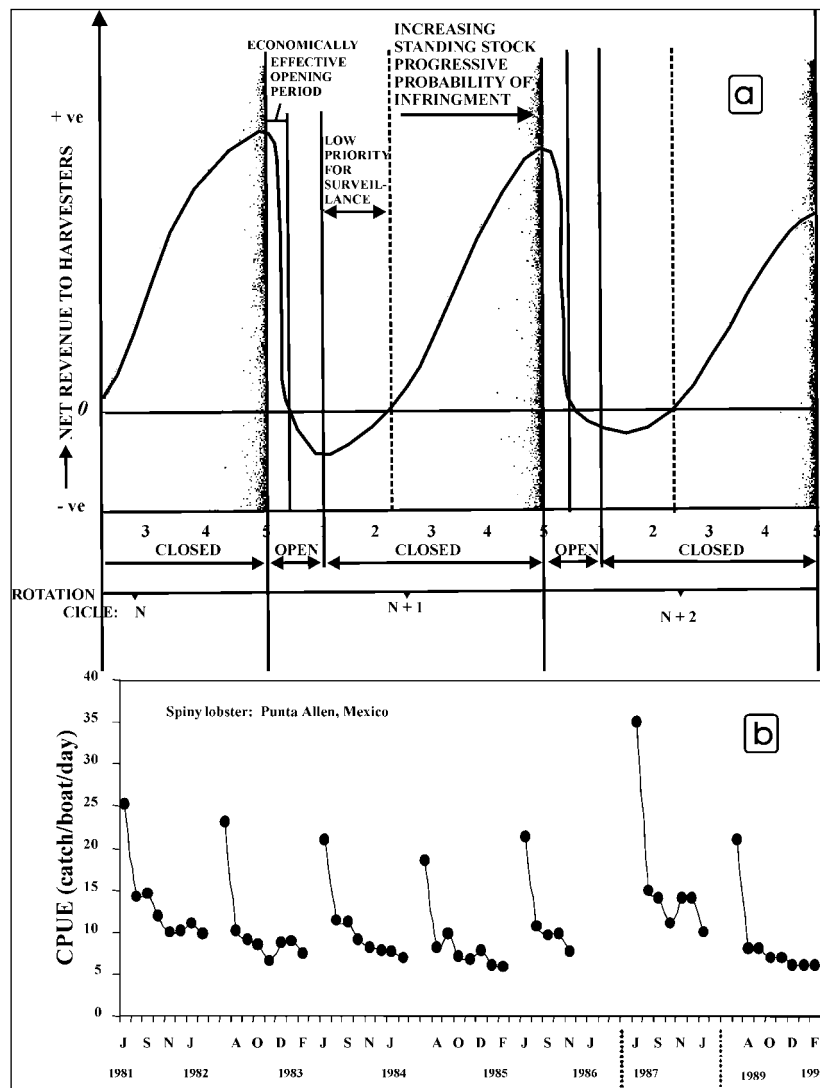


Figure 3.9 (a) Some features of a rotating harvesting framework, include a perspective on control and surveillance of fishers' adherence to the rotating closure under the assumption of constant unit stock prices (after Caddy, 1993b). (b) Monthly mean CPUE values for the spiny lobster (*Panulirus argus*) 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.

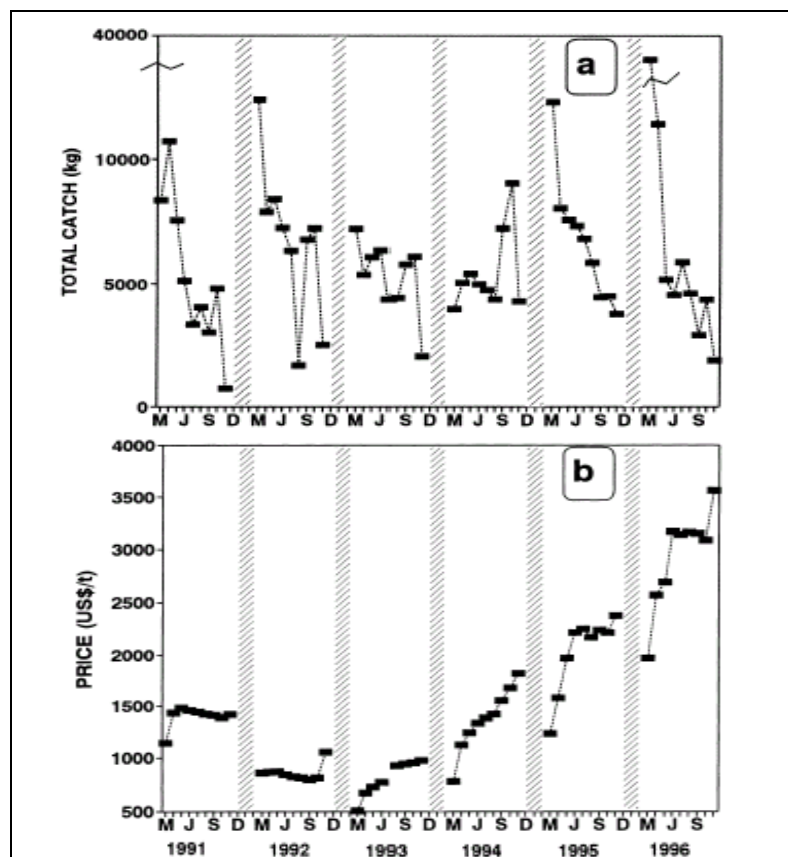


Figure 3.10 Monthly values of (a) catch and (b) mean prices paid to the fishers for the *Octopus mimus* fishery of Caleta Coloso (Antofagasta, Chile) between 1991 and 1996. See the marked inverse relationship between catches and unit prices within seasons (after Defeo and Castilla, 1998).

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 reseeding of 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 mum 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.

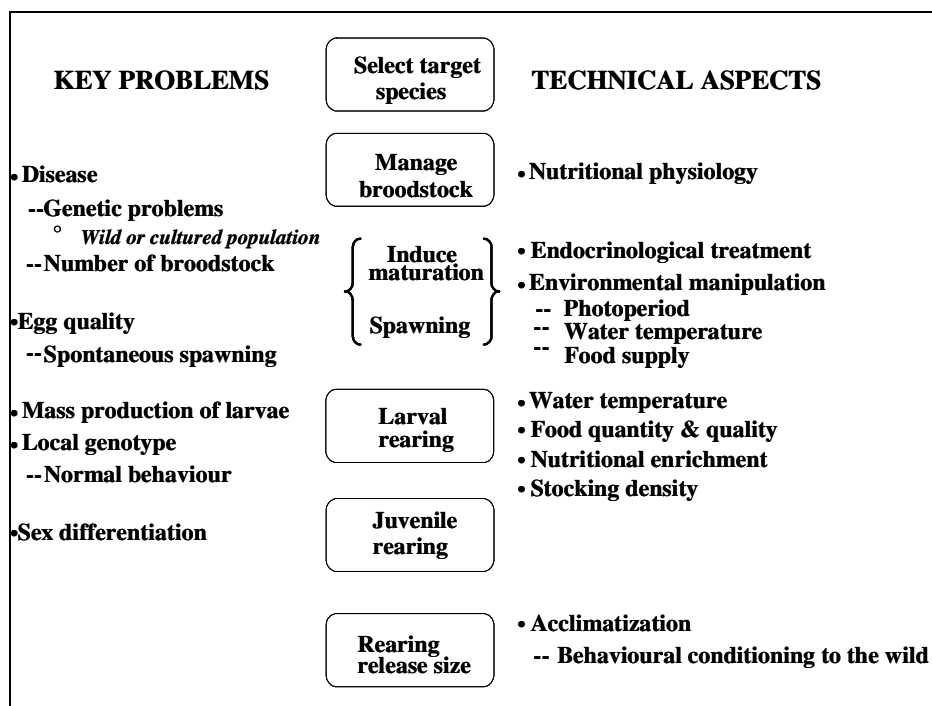


Figure 4.1 A listing of some of the key problems to be faced in a shellfish enhancement programme (after Tanaka, Seikai and Furuta, 1998).

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.

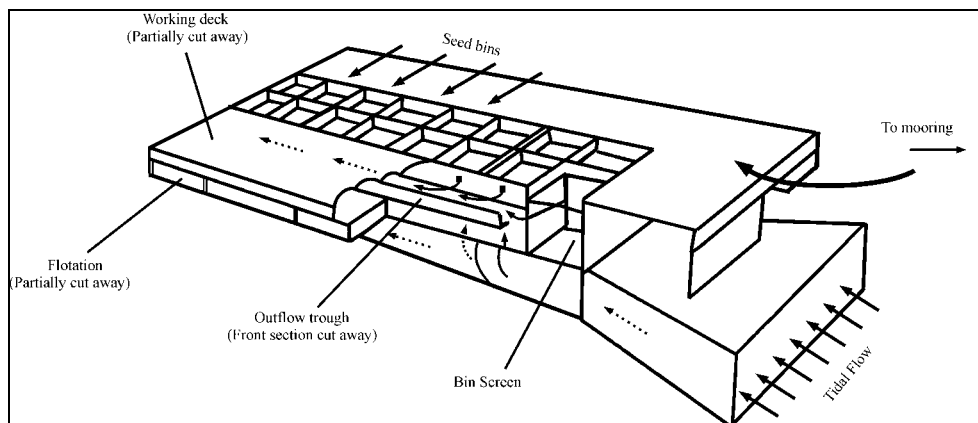


Figure 4.2 Representation of a tidal-powered upwelling system for spat rearing (redrawn from Hadley *et al.*, 1999).

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 reseeding 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).

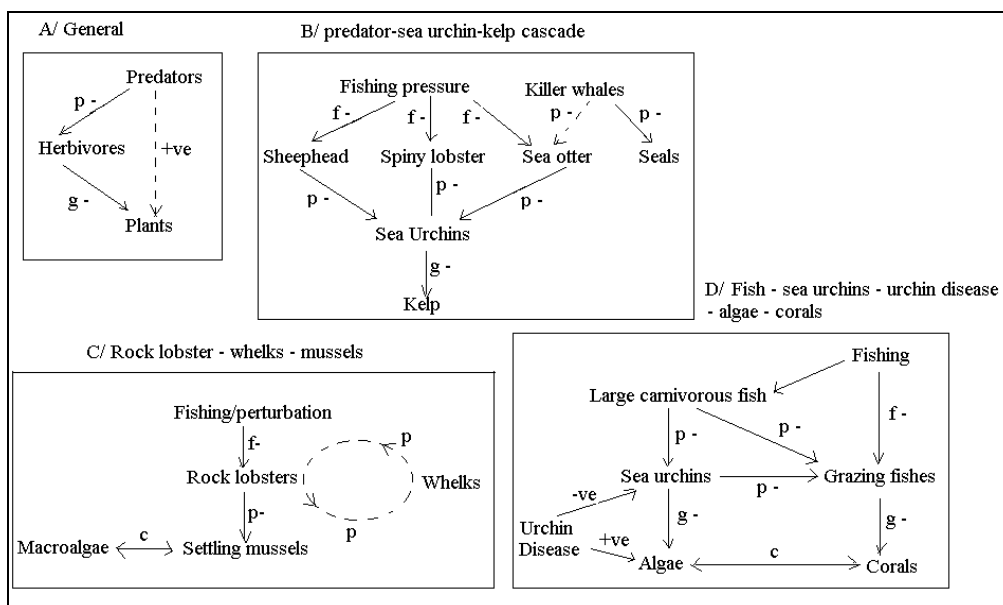
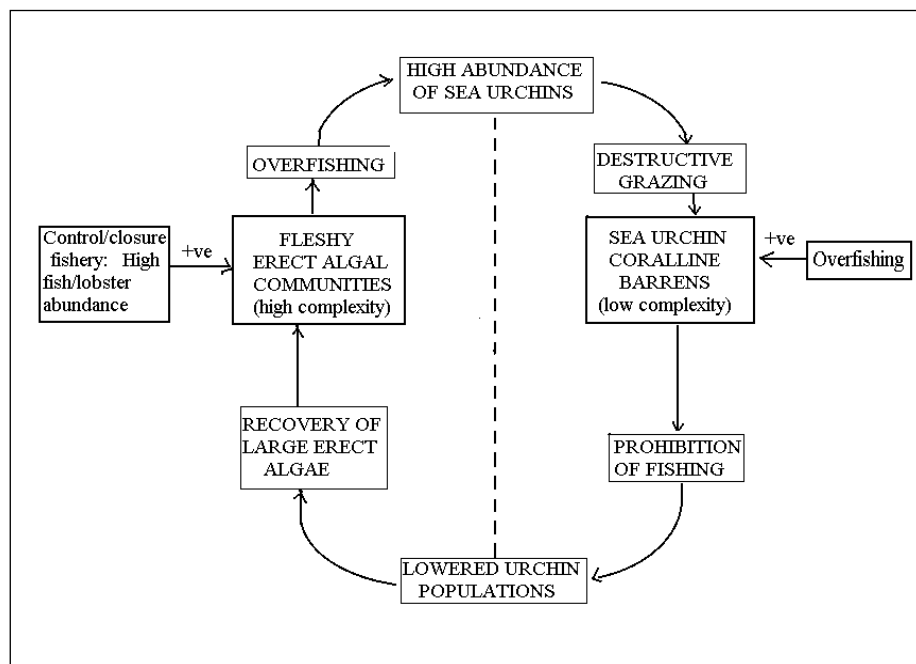


Figure 5.2 Examples of trophic cascades involving invertebrate resources (modified from Pinnegar *et al.*, 2000). [Key: f – negative effect of fishing on population size pointed to; p- similar effect due to predation; g – similar effect due to grazing; +ve and –ve: positive and negative effects of the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

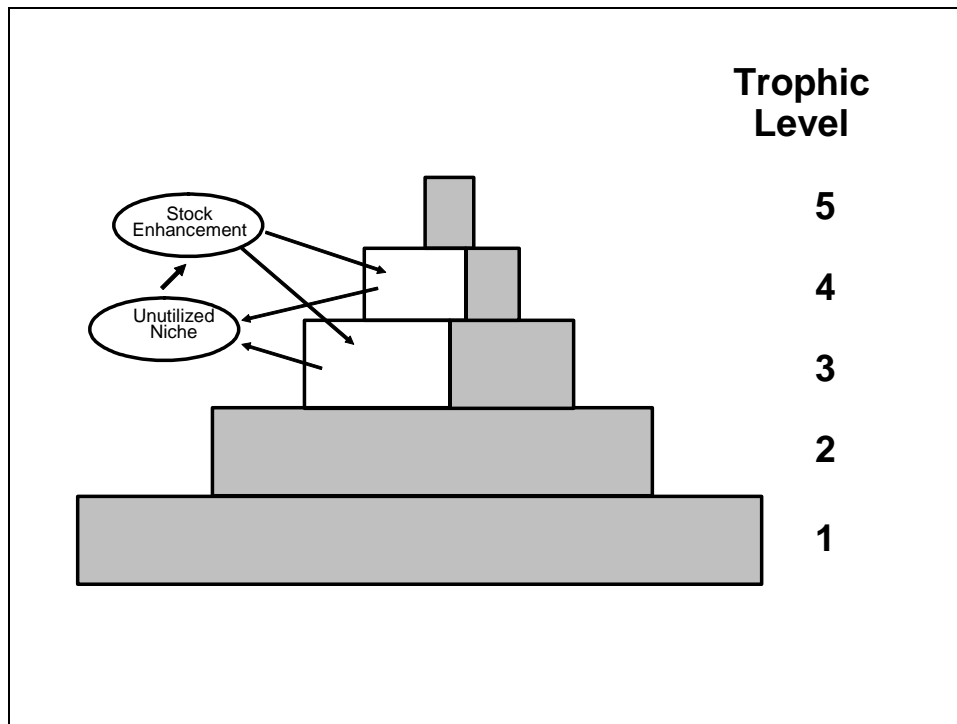


Figure 5.3 One of the suggested justifications for enhancement programmes is that an unutilized niche in the food web or pyramid may exist, that can be filled by enhancement experiments. This diagram (modified from Masuda and Tsukamoto, 1998) illustrates the concept, and may be valid where overexploitation 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).

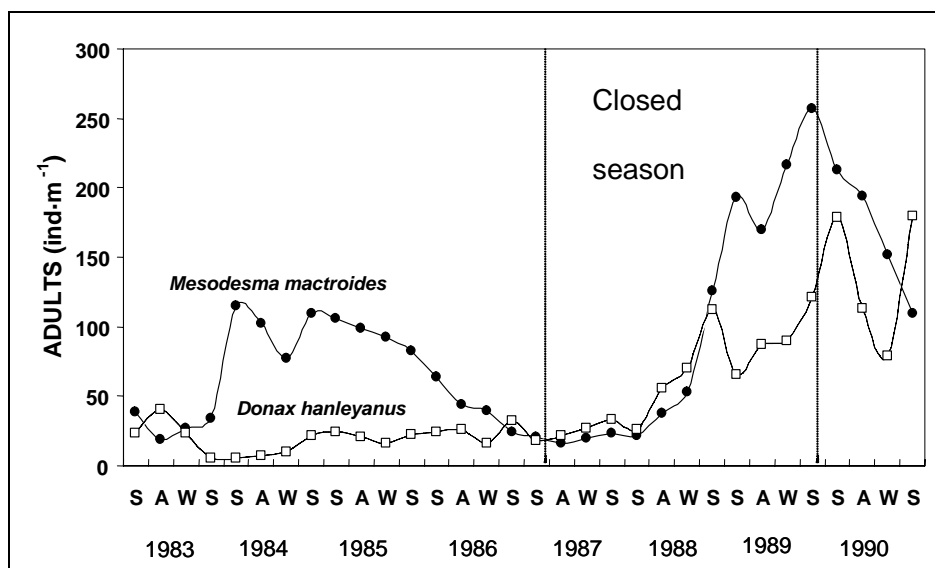


Figure 5.4 Long-term fluctuations in abundance (ind per stripe transect: ind·m⁻¹) of adults of *M. mactroides* (—●—) and *D. hanleyanus* (—□—) in Uruguay.

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

Defeo, 2001). This issue has also been addressed in a text on fisheries bioeconomics published by FAO (Seijo, Defeo and Salas, 1998).

6. THE ROLE OF HABITAT IN STOCK ENHANCEMENT AND RESTORATION

Successful stock restoration or enhancement requires harvest controls but also demands and attention to human impacts on the habitat. Reducing exploitation alone on the stock being restored will not be effective if critical habitat has disappeared. Figure 6.1 points to the role of habitat as an important sequential constraint. The use of habitat restoration to improve yields of marine coastal species does occur locally, but often has to be searched for in the literature on marine ecology, the role of marine parks, etc. Habitat restoration has on occasions been considered more feasible than stock enhancement *per se*. Hilborn (1998) for example, points to the low success rate in economic terms of most stock enhancement exercises, although most cases he refers to relate to finfish. Nonetheless, we agree with his suggestion that stock enhancement should be compared with alternatives such as habitat protection, fishery regulation and stricter enforcement before embarking on potentially costly and uneconomic large scale operations without prior experimentation. In this section we consider the first of these options. Performing a formal cost-benefit analysis on habitat restoration is feasible where artificial structures are added to the water to improve holding capacity, but basic pilot stage applications that allow us to establish feasibility, would seem required first.

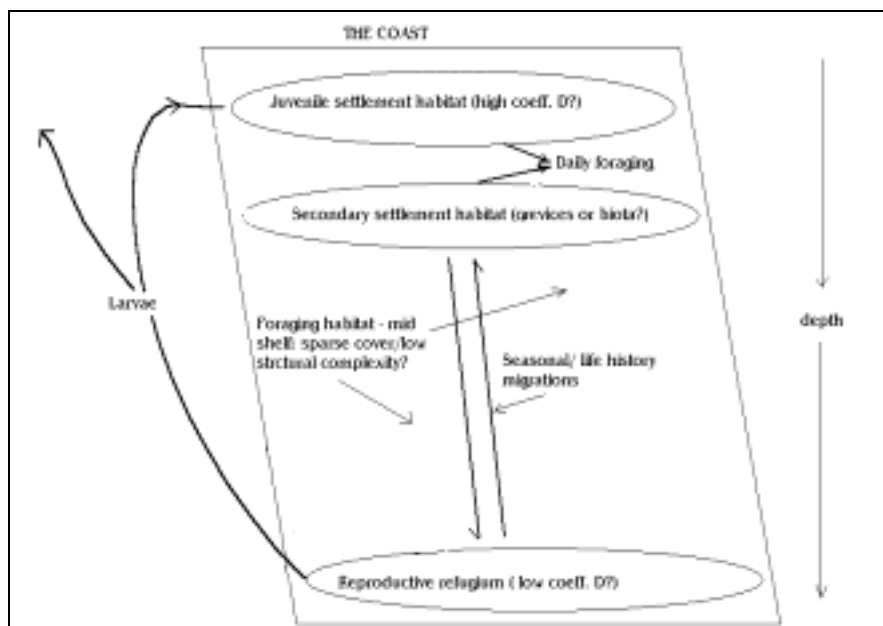


Figure 6.1 Showing how different stages of the life history (in this case of a crustacean such as a lobster) may be carried out within different habitats and depths.

Perhaps the Multispecies Virtual Population Analysis (MSVPA) experiment carried out for North Sea fish species (Sparholt, Larsen and Nielsen, 2002) provides the most eloquent argument against automatically assuming that juvenile enhancement programmes, sea ranching or restocking programmes will necessarily be effective. This extensive programme of stomach content analysis revealed that juvenile fish (as for juvenile shellfish) have a

generally high vulnerability to predation, and extremely high juvenile mortalities apply in the first 1-3 years of life. While this experiment suggests that any reduction in juvenile mortality of commercially important species could pay major dividends, evidence will be presented that there may be a need to mitigate the impacts of habitat-mediated bottlenecks.

6.1 Habitat requirements

In the United States, the Magnuson-Stevens Act requires fisheries managers to describe essential fish habitat, and to minimize the impacts on this by fishing. “Essential Fish Habitat” (EFH) is defined as “those waters and substrate necessary for spawning, breeding, feeding or growth to maturity”, and requires to be defined for all species under management. Mapping such areas using GIS techniques is now an essential component for deciding on closed areas, leases, enhancement areas, and in assigning priority use within an Integrated Coastal Area Management (ICAM) activity. This may involve remote sensing (see Rubec *et al.*, 1998). Figure 6.2 illustrates the complexity of decision-making in the coastal zone, and the fact that many other activities impinge on shellfish production, and will need to be reconciled in a multi-disciplinary way, involving all “players” or stakeholders in the coastal zone.

Figure 6.2 attempts to map some of the activities, causes and effects of human activities, starting with those associated with runoff from the adjacent freshwater catchment basin (upper left). This has effects listed on the right (e.g. increased red tides, shellfish toxicity etc) which impact the human activities on the right (e.g. aquaculture, fish processing etc), The fishery and fish culture activities in the box with dotted lines is thus seen as small “downstream” components vulnerable to these non-fishing anthropogenic effects.

6.2 Bottlenecks in production

Limitations of habitat may be important bottlenecks for some invertebrate populations, thus Scheduling *et al.* (2001) found that the presence of sandy bottom used by ovigerous females to bury themselves in aggregations during egg incubation, may be a limiting factor for adult Dungeness crab abundance in Alaska. Experience suggests that benthic and demersal organisms of a wide range of taxonomic groups and species often pass through primary and secondary habitats in the course of their life histories, thus, American lobsters may first occupy crevices in cobble bottom areas in a completely cryptic life stage until 5-10 cm in length (Wahle and Steneck 1991), when they migrate to burrows under stones or construct burrows on more sedimentary bottom. Similarly, Palinurid lobsters settle first in finely branching substrates such as red algae or mangrove roots, before migrating to sea grass beds and later to caves under coral patches further offshore. In both cases, the extent of these critical juvenile habitats may be the bottleneck limiting overall production, given that habitat and food supplies available to older stages may not be limiting.

The giant scallop *Placopecten magellanicus* and various species of *Chlamys* have been described as settling on bryozoa before attaching with a byssus to shell gravel, even inside the umbones of dead adult scallops. Similar primary and secondary settlement episodes, and the characteristic type of bottom conditions that identify them, have also been described for *Mytilus edulis* (see e.g. Bayne, 1964, 1976). Such primary and secondary “nursery” habitats have been described for a wide range of invertebrate species, and their often restricted occurrence makes one wonder if this poses a limit to recruitment, or in other words forms a “bottleneck” in the production process. Various kinds of bottlenecks have been proposed, from the more general term “demographic bottleneck” which covers all forms of restriction

on survival of a year class, to more specific “shelter-limited bottlenecks” which imply a structural limit, or “trophic bottlenecks” where food is the limiting variable. In fact Walters and Juanes (1993) show that it is the limitation of food adjacent to cover that requires organisms to be “risk-takers” and feed outside of cover.

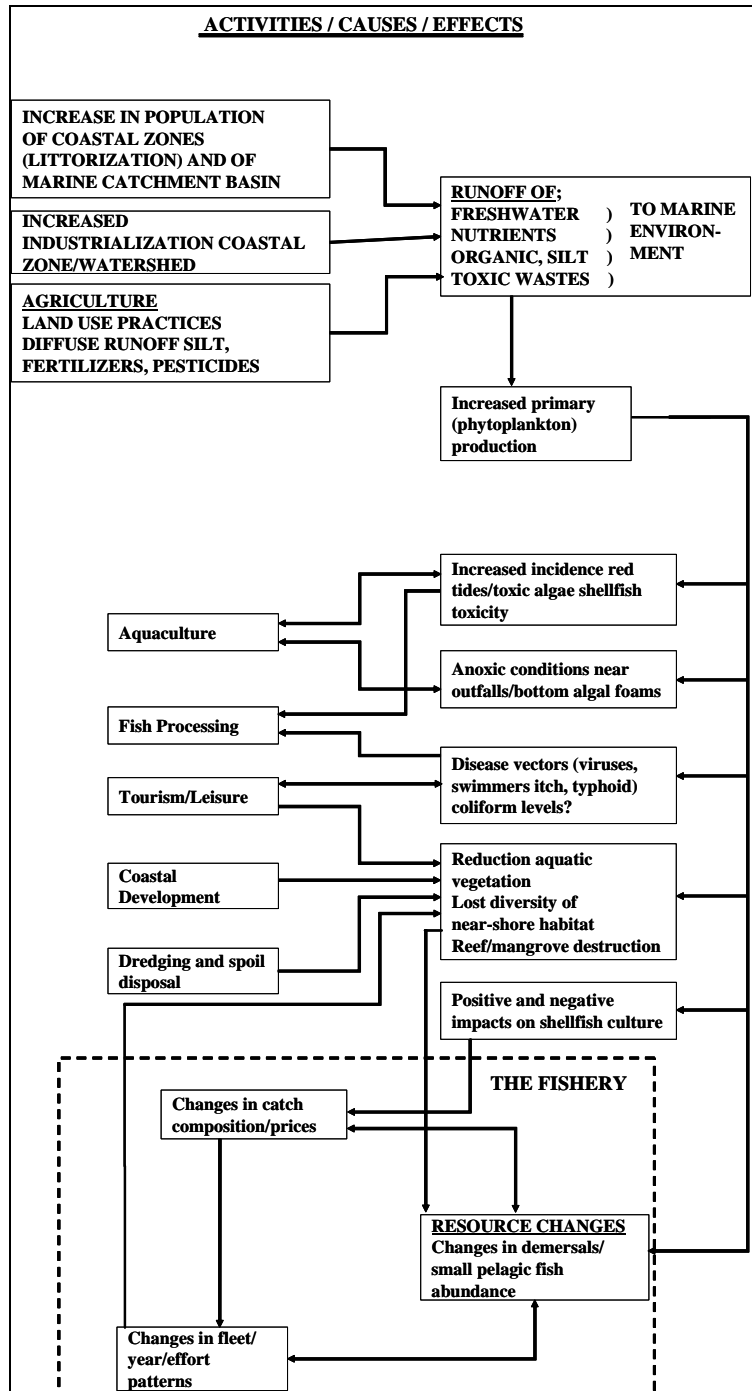


Figure 6.2 Showing a framework for policy development in the coastal zone, the socio-economic context for integrated policy formulation, and interactions of a variety of environmental factors. The interactions between different social users of the coastal environment, including shellfish production are shown. (after Caddy and Bakun, 1995).

A feature first observed by Morse *et al.* (1985) as a consequence of the fractal structure of most complex surfaces in nature, is that on a complex surface such as that of aquatic vegetation, there are “more surfaces available for small (arthropods) than large ones”. Caddy and Stamatopoulos (1990) generalized this observation to show that the fractal nature of habitat structure results in small crevice sizes being much more common than large ones, hence migration or mortality by predation are the two options that await those juveniles displaced from crevices of the appropriate size while searching for much less abundant larger crevices.

Mya arenaria was introduced to Grays Harbor (Washington) during the 1880s. Palacios, Orensanz and Armstrong (1994, 2000) showed that the maximum size of members of the current population is much smaller than of clams found dead in situ from preceding decades, and which nowadays form extensive “death assemblages”. Palacios, Orensanz and Armstrong (1994) concluded that extinct clams grew faster and lived longer because they occupied the best habitats available. After an extensive mass-mortality episode between 1895 and 1897 that resulted in the formation of the deposits, the population has never rebounded into its prime habitat, in spite of potential seeds being regularly available. They also showed that Dungeness crab larvae settle preferentially in these shell deposits, where the abundance of 0 + age juveniles is orders of magnitude higher than on the adjacent flats. They hypothesize that predation by juvenile crabs is the main factor that limits clam recruitment (see also Iribarne *et al.*, 1992).

The point which can only be touched on here is that where such critical habitats occur, their holding capacity will to a significant extent determine the size of the new recruiting age class to the population. Thus there will be no point attempting stock enhancement if the existing population size will subsequently be restricted by some form of bottleneck. As noted, another implication of this type of phenomenon is that even if there may be adequate food for many more adult animals than are actually present, these population levels are unlikely to be realized if there is a bottleneck at or following recruitment. This emphasizes the importance of ensuring that primary and secondary habitat types and cover characteristics are not degraded by environmental influences, and that suitable habitat is provided in extensive culture or where enhancement of depleted wild populations is underway, especially in the presence of predators for the species in question.

6.3 Stock replacement, habitat rehabilitation or mitigation?

There have been many criticisms of hatchery rearing and release programmes aimed at stock enhancement, and as we have noted, the record of success is rather spotty, especially for finfish, but should not prevent careful consideration of this mechanism in certain well-studied situations. Despite the five conferences held on the issue in recent years (Grimes, 1998), there has been a relatively minor focus on related marine habitat issues, and in particular, cover and habitat complexity. A more general consideration is the widespread occurrence of density-dependent mortality in natural systems, which ensures that increases of population size above some carrying capacity will be rapidly reduced. In this sense, Heppell and Crowder (1998) suggest that before considering stock enhancement, the existence of habitat constraints should be checked for. Does the environment contain sufficient critical habitat needed for the life history stages introduced for example? They also stress the need for harvest controls to be in place. An example for a finfish in Florida nearshore waters, the gag grouper (*Mycteroperca microlepis*), showed that the existence of adequate sea grass beds is a precondition for restoration (Koenig

and Coleman, 1998). For another finfish species important to anglers, the red drum, Grimes (1998) notes there is little point in attempting stock enhancement if density-dependent processes in the early life history result in high loss rates of juveniles. At the same time (and this defines one particular focus for any enhancement programme), in this case, recovery of as few as one percent of stocked fish need to be recaptured by high value sports fisheries for enhancement to be considered successful. Achieving an increase in recruitment in the range of five and ten percent by either stock or habitat enhancement would then seem to be a worthwhile and possibly achievable target. Whether this would be cost-effective as questioned by Hilborn (1998) still remains an important question, but in the case of restoration of a stock that has disappeared from its former range, such considerations must take second place to first establishing feasibility, and second, deciding what the restoration of a train of utility values into the indefinite future is worth? If the issue is to restore a train of benefits that has been lost, or otherwise would not continue into the future, and if the population would then be self-sustaining, restoration may be a feasible objective.

Habitat replacement or rehabilitation are less ambitious interventions than aiming for complete ecosystem restoration or rehabilitation, which are goals that are likely to be difficult or in some cases, impossible to achieve, and certainly more costly, and would involve whole system manipulation. Replacement or reclamation of damaged or degraded ecosystems constitutes interventions aimed at restoring economic productivity to a habitat that, due to human intervention, is currently unproductive. In this sense, a stock enhancement or replacement exercise may be a component of a more general environmental intervention aimed at improving habitat “quality”, where quality is defined in the sense that it contributes to human welfare. Finally mitigation, the least ambitious type of intervention, aims to reduce the losses incurred due to ecosystem damage, and here again, shellfish enhancement schemes may play a part in a broader context, and is likely to be more feasible than, for example, restoring fish populations. Some definitions for these terms are provided in Table 6.1.

Table 6.1 Some human interventions on depleted or degraded ecosystems
(after Bradshaw, 1996 and Cairns, 1994).

<i>Societal action:</i>	Defined as:
<i>Rehabilitation or restoration</i>	The action of restoring a thing to a previous condition or status
<i>Reclamation</i>	To bring back to a proper state (which may not be the original one)
<i>Replacement</i>	To procure a satisfactory substitute in place of the original
<i>Remediation</i>	To rectify or make good, places the emphasis on the process rather than the end point reached
<i>Mitigation</i>	To reduce the negative effects of change (especially habitat destruction) where these cannot be eliminated (or to soften the loss of a particular ecosystem)

The importance of habitat for management of wild resources is made evident in Figure 6.3, based on Marshall (1996). This emphasizes the importance of characterizing the biological suitability of the habitat and the biological community within which the species in question is being enhanced. If the habitat has deteriorated, for example through anthropological stresses, and is biologically complex, there has to be less expectation of a successful result. Probably it will be necessary first to restore the ecosystem, to the extent possible, to a productive situation before beginning an enhancement procedure. Better still is to choose another area where these stresses or impacts are less pronounced.

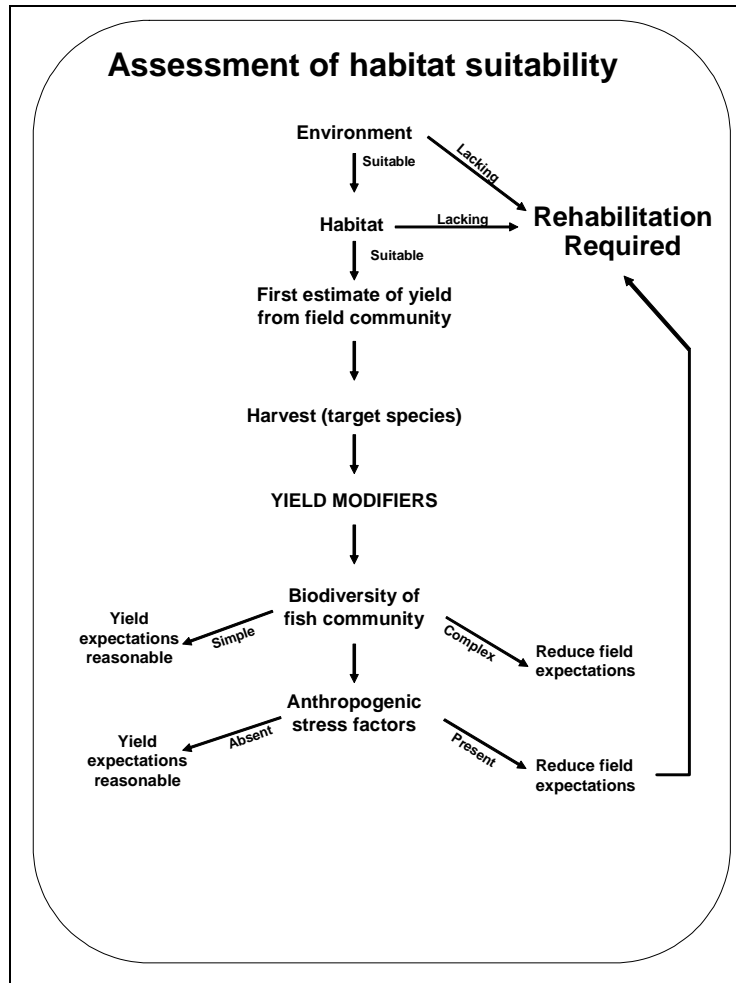


Figure 6.3 An approach to assessing habitat suitability (after Marshall, 1996).

As an example of a rehabilitation or mitigation exercise, we note that included in the goals of the US National Research Council (1992) for national aquatic ecosystems between now and 2010, is to restore ten million acres of wetlands out of the 117 million impaired or destroyed since 1800. Such wetland areas are frequently very productive, and shellfish form key components of these ecosystems and should be harvested in moderation. It is worth noting here that wholesale raking of oyster beds in the Chesapeake Bay system removed these higher relief shell or cutch banks which formerly were “islands” of hard bottom above the Bay floor, and were of ecological importance to a range of species.

Cairns (1994) notes that: “although precise replication of predisturbance conditions will rarely be possible, achieving a naturalistic assemblage of plants and animals” (at the landscape level) “of similar structure and function should be possible in most cases”, and comments that: “It is a sine qua non that ecological repair is preferable to neglect of damaged ecosystems”. He remarks that it is not excluded that this restoration could be (in the case of wetlands) in areas which did not have them in the first place, as a way of building “ecological capital”. He goes on to say: “Necessarily, local societies must have accepted the goal of restoration and cooperate, which in turn requires greater ecological literacy”. If self-maintenance is to be achieved, the scale of restoration increases considerably, and ecological restoration is seen as “buying more time for human society to develop less threatening life styles”.

Langton *et al.* (1996) suggested a prioritization of research questions as shown in Figure 6.4, which can equally be used when contemplating an enhancement programme. If the questions in the list of “prioritized research questions” cannot be answered in advance, it is important that priority work be done on resolving them before full scale enhancement begins.

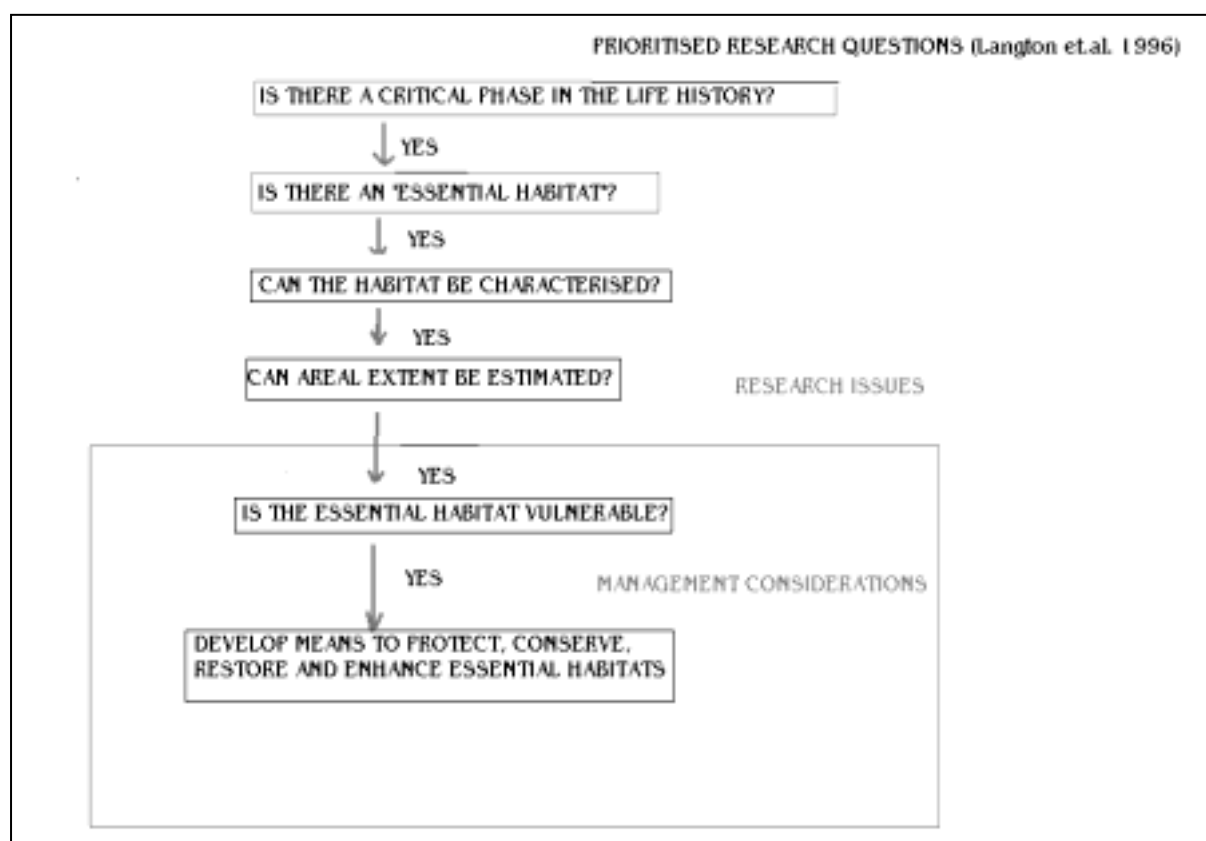


Figure 6.4 A list of research questions proposed by Langton *et al.* (1996) prior to beginning any intervention involving natural systems.

The experience with shellfish enhancement procedures as implied earlier, has not been uniformly positive, and it is instructive to consider why. Figure 6.5 places enhancement at the summit of a sequence of human ecosystem interventions, which are perhaps more realizable from the bottom of the triangle than the top, and this especially applies to marine finfish stocks.

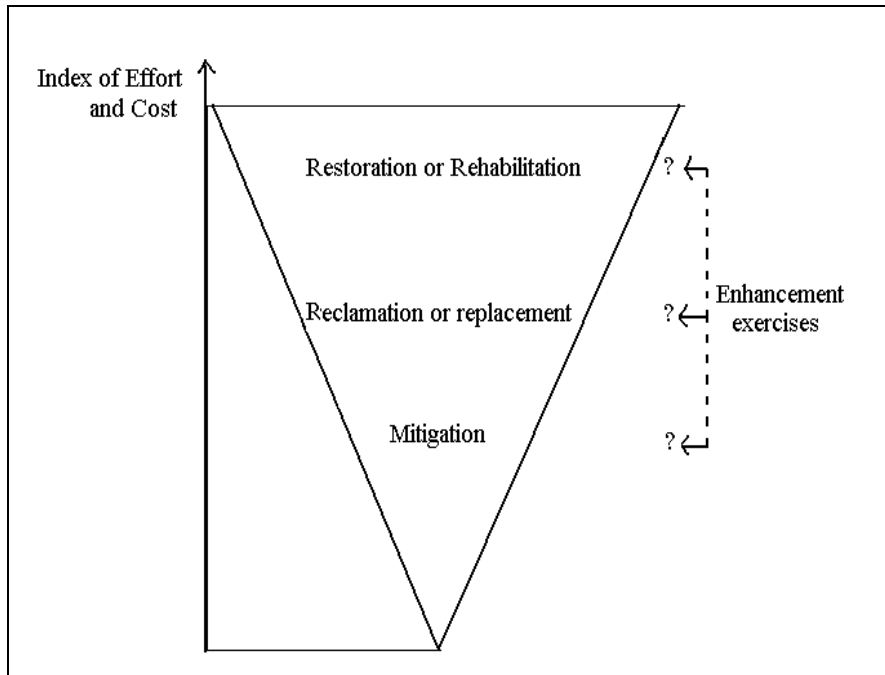


Figure 6.5 Illustrating a sequence of human ecosystem interventions, arranged from the bottom of the inverted triangle to the top according to their likely feasibility and cost. Shellfish enhancement may play a role in all of these activities, but the implication is that this is likely to be more feasible and relevant for uncontaminated ecosystems that have been otherwise impacted by human activities.

Figure 6.6 needs to be kept in mind when restoring a stock through stock enhancement, which is unlikely to be successful if the critical habitat that limits life history stages is not present, and if effort control does not allow parental stocks to build up so that natural population replenishment can occur. Trophic conditions are also important in providing overall basic requirements for food, but this alone is unlikely to be adequate in ensuring population build-up if the other two factors are not given priority. Mitigation of negative impacts is less demanding than reclamation or replacement, which in turn are less problematic than full restoration of the original ecosystem.

Enhancement, which in the strictest sense implies “improving on nature” would imply even more costs since an “enhanced” system is implied to be an improbable state differing from the equilibrium situation often characterized by the term “virgin conditions”. In fact however, enhancement becomes more feasible when it is considered in the context of restoring an ecosystem after serious stock depletion, and is also appropriate for systems which are recovering from disturbance, where for example an unfilled ecological niche may be temporarily present. It is mainly in this sense that the term is used in this paper, so the apical position of enhancement in Figure 6.6 is probably anomalous.

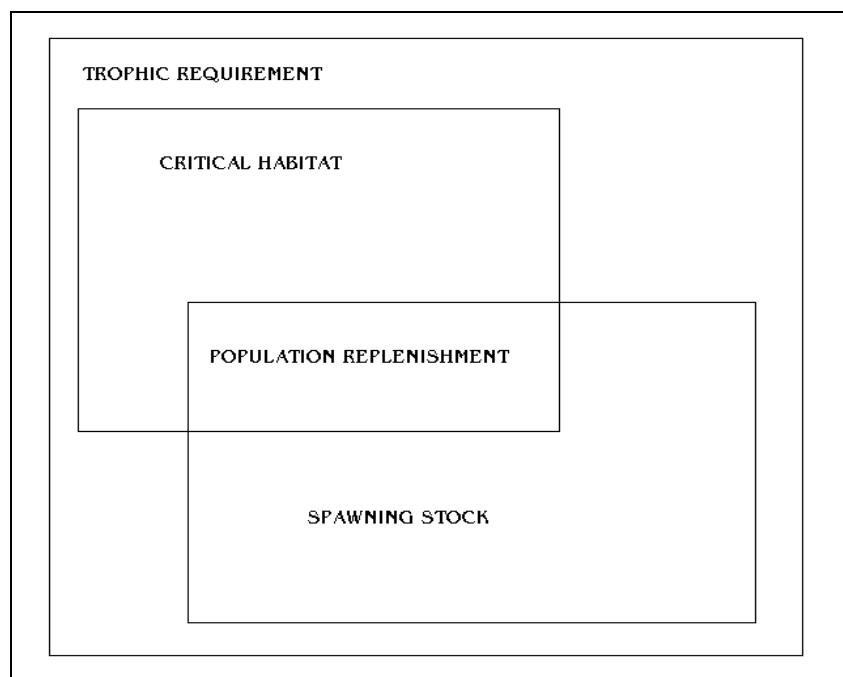
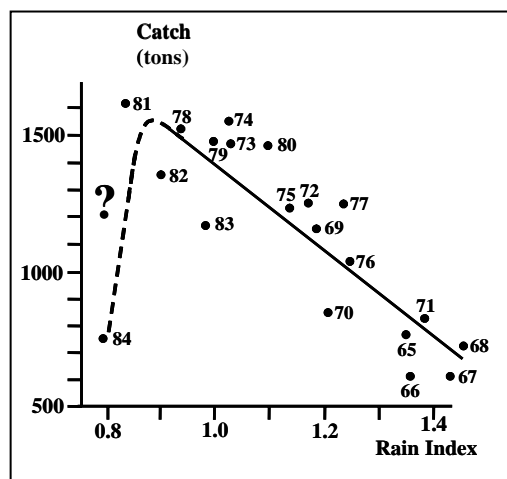


Figure 6.6 Factors that need to be considered when restoring shellfish populations through stock enhancement include basic trophic requirements and special habitat requirements, the latter more difficult to satisfy, while full restoration will require an adequate spawning stock.

In some cases (e.g. for penaeid shrimp stocks, Figure 6.7), river outflow patterns have a major role in determining shrimp production, and drainage of wet lands, cutting of mangrove forests and the use of herbicides in coastal areas can negatively affect shrimp production.

Figure 6.7 Catches of the shrimp *Penaeus notialis* in Casamance river estuary as a function of rainfall index (after Le Reste, 1992).



Determining the effects of land usage on intertidal and estuarine resources is an important precondition to producing safe shellfish products. White *et al.* (2000) mention a multi-agency project that was carried out in an Integrated Coastal Area Management (ICAM) context, to determine the effects land use in the adjacent watershed had on shellfish closures. Bacterial data were monitored and indicated increasing loadings in runoff water, with especially high levels during storm events. Dye studies confirmed that bacteria would move through the watershed over a brief time period with negligible mortality. Low levels of bacteria were found during dry weather. Most contamination came from a nearby residential area with

some malfunctioning septic tanks, but also from pets and wildlife. A mitigation programme was designed using GIS, and included education, and restoration of wetlands, automated storm water monitoring, and DNA tracking of faecal sources.

A general discussion of shellfish restoration activities in the context of ecological functions is provided by Coen and Luckenbach (2000), who mention some of the “ecosystem services” provided by shellfish beds, whose value is usually underestimated. These include contributions to the filtering capacity of the water column, benthic-pelagic coupling, a role in nutrient dynamics, increased suspended sediment deposition, and stabilization of bottom sediments. Very dense shellfish beds may have negative impacts due to fouling by pseudofaeces, and Kaiser *et al.* (1998) review some of the impacts caused by dense shellfish culture. Castel *et al.* (1989) find that densely stocked oyster beds elevated organic carbon levels in adjacent sediments, sometimes producing hypoxic conditions. Site selection preferably in areas of current flow is therefore important. However, considering that shellfish beds were certainly denser before human harvesting, such negative impacts of shellfish populations are in themselves, local effects; and under natural conditions would be less evident. One reason being that through accumulation of shell material, native shellfish beds were often raised above the sedimentary level of the estuary floor and hence cleaned by stronger local currents. Sparsis, Lin and Hagood (2001) even evaluated the feasibility of using juvenile giant clams to remove dissolved inorganic phosphate and nitrate from holding tanks of ornamental or food fish. The nutrients were removed by zooxanthellae in the mantle of giant clams in lighted periods, and all species tested except *Tridacna gigas* survived, and some grew faster in effluent than elsewhere, suggesting the possibility of using giant clams in polyculture.

Restoring whole ecosystems where the environment has changed due to human intervention or climate change is a much less certain prospect, and in this case, actions to mitigate the damage may be in order. An example from other than shellfish enhancement comes from the North American Great Lakes (Regier *et al.*, 1988), where eutrophication and overfishing had destroyed the valuable deep water lake trout fishery, but subsequently established an abundant but low value resource of small forage fish. The introduction of a west coast salmon species which could prey on these forage fish completed the transformation of the system into an “exotic” pelagic ecosystem (where effectively no economic resources of surface waters existed before) and this now has high economic value for sports anglers. This example is not an apologia for habitat degradation, just that restoring the Great Lakes to their pristine condition was probably infeasible, and would anyway have meant radical changes to the life of several million inhabitants within the catchment basin of the Great Lakes, hence restoring a productive, if alternative, system appears the most feasible option available. For this reason, fully restoring the native lake trout population is a costly option compared with the current sports fishery for introduced coho salmon. This example of a successful mitigation of human impacts shows that the more general objectives of restoring habitat quality for a range of purposes (recreation, quality of life issues etc), will usually have to precede the restoration of a population of organisms of value to humans, and these may be different from those originally present.

Another example can be cited in the case of the Black Sea. At the start of the twentieth century this was a mesotrophic body of water with oxygenated waters on shelf areas, and a rich fauna of indigenous species (see Caddy and Griffiths, 1995). The eutrophication of the basin led to a cascade of ecological effects described in Zaitsev (1993). Seasonal anoxia of shelf areas and the littoral in summer led rapidly to the elimination of many indigenous species. Eutrophication coincided with the likely accidental introduction of two exotic

species, the clam *Mya arenaria*, and a gastropod *Rapana* sp. both adapted to eutrophic conditions. This latter species, a predatory snail introduced from Japan with oyster imports, has acclimatized, and now supports a fishery of some 40 000 t/year. So far *Mya* is unexploited but is believed to support a very large biomass. The fate of a large subtidal population of the mussel, *Mytilus galloprovincialis* in the Northwest of the Black Sea is also instructive. This was the target of a Russian fishery, but subsequent events suggest it may have played a major role in controlling turbidity of shelf waters (Sorokin, 1993). With seasonal hypoxia, this deeper water mussel population has largely collapsed, and coincidentally, a subtidal population of a red alga, *Phyllophora* sp. in the same area disappeared, presumably due to poor light penetration caused by algal blooms. Again Sorokin (1993) deduced that both of these declines played a significant role in oxygenation of shallow shelf waters and reduction of suspended material, thus improving light penetration. This example illustrates that the services provided by bottom fauna and flora, including populations of filter feeders, have a significant role, in this case in controlling suspended sediments and phytoplankton and coastal eutrophication, apart from their importance for human food.

Hypoxic conditions can of course be detrimental to shellfish enhancement operations, depending on species tolerances. Diaz and Rosenberg (1995) found that commercial species varied considerably in their resistance to hypoxia; thus, bivalves *Arctica islandica* and *Mytilus edulis* were most resistant, the clams *Mercenaria mercenaria* and *Spisula solidissima* were intermediate, while benthic crustaceans, *Nephrops norvegicus*, *Crangon crangon*, *Carcinus maenas*, and *Spisula solida*, a clam typical of clean sand, were the most sensitive.

The effects of bottom-water hypoxia on the population density of the clam *Macoma balthica* was estimated using a survival-based approach by Borsuk, Powers and Peterson (2002). They used a Bayesian parameter estimation to fit a survival model to times-to-death corresponding to multiple dissolved oxygen (DO) concentrations assessed by scientific experts, and combined the survival model with a model describing the time dependence of DO. Under current conditions, the mean summer survival rate was predicted to be only 11 percent. However, if sediment oxygen demand (SOD) is reduced as a result of nutrient management, survival rates increased, reaching 23 percent with a 25 percent reduction in SOD and 46 percent with a 50 percent SOD reduction (Borsuk, Powers and Peterson, 2002).

Lenihan *et al.* (2001) tested the hypothesis that mobile consumers have the potential to cause a cascading of habitat degradation beyond the region that is directly stressed, by concentrating in refuges where they intensify biological interactions and can deplete prey resources. They worked on structurally complex, species-rich biogenic reefs created by the eastern oyster, *Crassostrea virginica*, in the Neuse River estuary, North Carolina. Bottom-water hypoxia and fishery-caused degradation of reef habitat induced mass emigration of fish, thus modifying community composition in refuges across an estuarine seascape. Moreover, oyster dredging reduced reef height and exposed the reefs located in deep water to hypoxia/anoxia for more than two weeks, killing reef-associated invertebrate prey and forcing mobile fishes into refuge habitats. High-density accumulations of refugee fishes on reefs in oxygenated shallow water depleted epibenthic crustacean prey populations. Thus, the interaction of reef habitat degradation through fishery disturbance and extended bottom-water hypoxia/anoxia caused oyster mortality and influenced the abundance and distribution of fish and invertebrates that use this reef habitat (see also Lenihan and Peterson, 1998). The authors concluded that physical disturbances can impact remote, undisturbed refuge habitats through the movement and abnormal concentration of refugee organisms that have subsequent strong trophic impacts. In this context, they highlight the implications of MPAs as critical refuges.

The upper Adriatic Sea, an area of predominantly fine bottom sediments acts as an “outer estuary” by receiving some thousand tonnes a year of nutrients from the very eutrophic Po river. Italian workers (e.g. Bombaci, Fabi and Fiorentini, 2000) have focussed on use of artificial reefs colonized densely by *Mytilus* as a way of making use of these high productivities and precipitating suspended material from the water in the pseudofaeces of mussels. The potential role of mytiliculture here is not only to provide considerable economic add-on food value, but also to act as a depurator of estuarine discharges and the precipitation of sediments and algae from the water column: a function of importance to bathing resorts in the Adriatic. These kinds of ecosystem functions that may be achieved through a shellfish enhancement programme deserve further economic analysis. The dramatic increase in shellfish production in the Mediterranean shown from FAO statistics (Figure 6.8), especially in the upper Adriatic and Gulf of Lions under the influence of the Po and Rhone river outflows, needs attention. As noted by Caddy (1993a) and de Leiva Moreno *et al.* (2000), European inland seas such as the Baltic, Adriatic, Mediterranean and southern North Sea, depending on their degree of enclosure and the extent of the catchment areas feeding them, have, become eutrophic to different degrees, under anthropogenic influences from adjacent catchment basins. Molluscan shellfish production to a significant extent has benefited from this situation, although issues of depuration and the control of transmission of disease vectors through untreated shellfish have also become important. Thus, macroenvironmental trends in an area provide an important context for the shellfish enhancement activities we have been discussing here. It may be noted that in terms of the production of animal protein, shellfish cultivation does not depend on resources of fish meal or agricultural products as for most (carnivorous) species used in marine finfish culture, and as we have noted, if used strategically, mollusc shellfish stocks can play an important role in locally enhancing water transparency and hence in restoring aquatic vegetation.

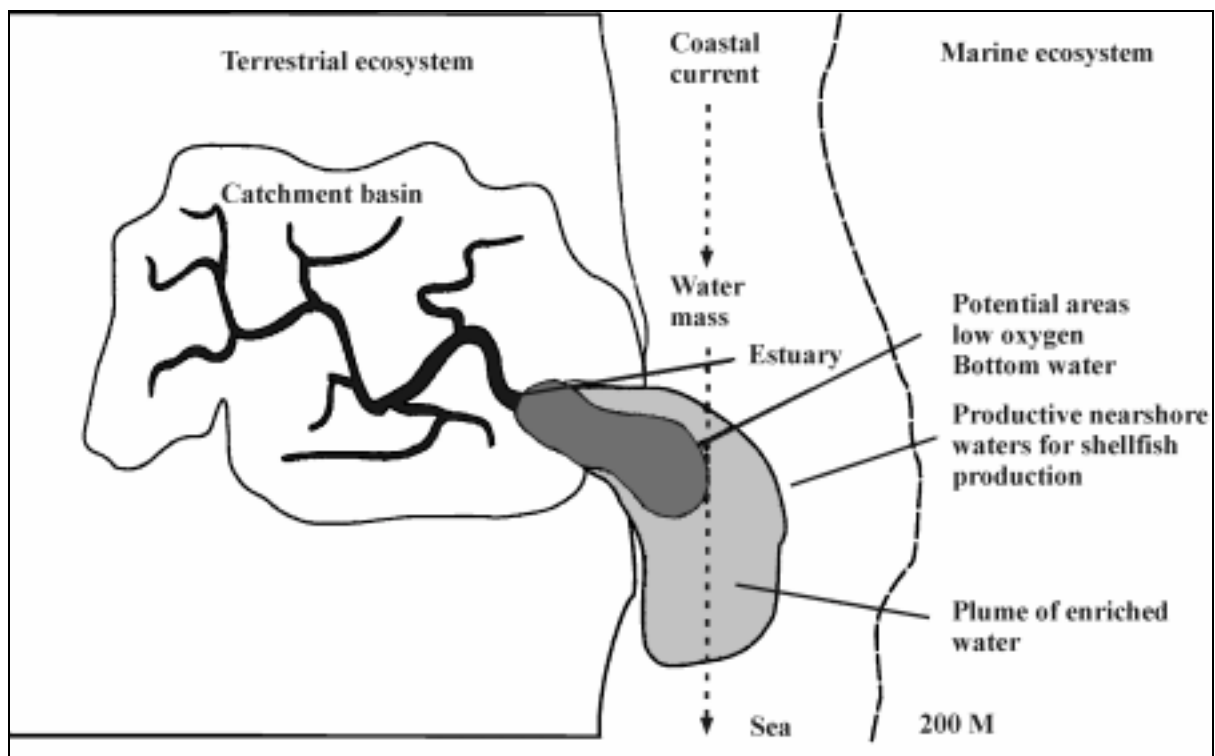


Figure 6.8 Illustrating the role of nutrients from river catchment areas and river plumes in enriching nearshore shellfish fisheries (after Caddy, 2000b).

6.4 Choosing a site for enhancement activities

The selection of adequate habitats is crucial for the development of enhancement programmes. Recognition of gradients in habitat quality is important in defining the extent of the area available for seeding. A range of habitat sites must be analysed to evaluate likely differences in seeding success according to habitat suitability. Consider for example that a seeding programme for an intertidal soft-bottom bivalve is started with the intention to colonize new areas and develop a new fishery. In this case, some critical variables detailed below will give useful insights as to which sites would be optimal.

6.4.1 Sediment properties

Exposure (exposed-sheltered). The choice of an adequate habitat for seeding should be a trade-off between different factors acting simultaneously. For example, when considering intertidal oysters, the level of the intertidal chosen to seed is critical, because lower tidal levels are more susceptible to predation. Alternatively, higher tidal levels commonly have a higher degree of silting which increases mortality and lower growth rates. Quantity and quality of food might depend on exposure and the degree of turbidity. Some exposed sandy coasts could constitute semi-closed ecosystems in which high concentrations of surf phytoplankton occur in waters rich in nutrients and oxygen. These sites could be useful for enhancement operations of intertidal suspension feeders (including passive restocking, see Defeo, 1993b, 1996a). However, wave action and speed of currents could act as negative forces that could preclude spat settlement. Once again, a trade-off between these different factors must be evaluated. If a sandy beach mollusc is selected, the definition of beach morphodynamics will be critical, i.e. if it is reflective or dissipative (McLachlan *et al.*, 1996).

Grain size preferences (fine - coarse). Settlement rates could be accelerated in the presence of a suitable substrate. For example, Tong, Moss and Illingworth (1987) reported that juveniles of the abalone *Haliotis iris* tend to settle in almost all cases associated with the encrusting algae *Lithothamnium*. A careful selection of sites for seeding can help reduce mortality rates. In some cases (e.g. oysters), ground selection according to consistency of the bottom can also reduce silting mortality. Shifts in habitats, especially burial by sand, in the abalone *Haliotis iris* (Schiel, 1993), led to high mortality rates and negative rates of return in the enhancement operation.

Other sediment features, such as face slope, substratum penetrability, sediment water content, texture and roughness, are also important agents defining settlement variation among sites. Space availability in proportion to the amount of spats to be seeded should also be assessed.

Knowledge of sediment preferences at different life stages helps the shellfish farmer use adaptive behaviour of shellfish in protecting them from abiotic (e.g. hydrodynamic factors, exposure) and biotic (e.g. predation) factors. By carefully choosing sites, within-site sources and levels of natural mortality due to abiotic and biotic factors can be minimized. Historically productive fishing grounds, which have high probability of recolonization and generally low mortality levels, could serve as potential sources for seed replenishment (Caddy, 1989b). The quality and quantity of food present, or added as supplements, can be critical if economic losses are to be avoided due to density-dependent processes. Food availability often depends on habitat quality, and mortalities will occur due to starvation if seeding is conducted in the wrong place (see e.g. Tegner, 1989; Kristensen and Hoffmann, 1991).

Substrate preferences for many crustacean and molluscan larvae are often rather specific: thus Stevens (2003) found that late larval king crab demonstrated preferences for structurally complex substrates and a low preference for sand where mortalities were higher. This illustrates the importance of leaving “biological oases” where bottom contact fishing gear such as dredges and trawls are prohibited. Tegner *et al.* (2001) tied declines in abalone production in Southern California not only to overfishing but to the cessation of growth of the alga *Macrocystis pyrifera* which provides food through drift of debris under the canopy, as well as providing habitat for abalones; such cessation coinciding with the warm, nutrient-poor waters associated with El Niño events.

6.4.2 *Hydrodynamic factors*

Hydrodynamic factors act to generate spatio-temporal settlement patterns in shellfish populations. As population patterns and processes in shellfishes are scale-dependent, depending on the stage of the life history involved (Orensanz, 1986; Thrush, 1991; Defeo, 1996a, b), analysis of the physical-biological coupling at different scales is useful in the context of enhancement programmes. Peterson, Summerson and Luettich Jr. (1996) showed for the scallop *Argopecten irradians* that larvae larval settlement drops off sharply as a result of physical transport of their short-lived pelagic larvae. This has important implications in regulating population size in the system, as well as in developing adequate strategies for enhancement.

Oceanographic factors lead to site-specific variations in the local abundance of larvae and subsequent successful settlement, and thus determine the optimum times and sites for seed collection. For example, lack of suitable hydrographic conditions for supplying and retaining large numbers of larvae in the vicinity of collectors could lead to the failure of seed collection. Often, large settlements occur in semi-enclosed bodies of water or enclosed bays, which can also be good sites for early survival. These places are recurrent sites for successful settlement since they avoid mortalities due to flushing of water masses in the area. This is an important consideration when considering metapopulations, in which the capacity of larval dispersal over the fishing grounds is often dependent on the intensity and direction of wind-driven currents. In this context, self-recruiting, “source” areas (Carr and Reed, 1993) should be differentiated from “sink habitats” (see Chapter 3). As each ground has its distinct regime of primary production, nutrients, food availability, predation and disturbance, in theory, between-ground differences in these features could be quantified.

Enhancement operations will be increasingly affected by pollution on the coastal zone. Nearshore environments are more and more vulnerable to harmful algal blooms, sewage discharges, oil spills and so on. The quality of the site for seeding must be assessed from these points of view also, because their occurrence implies increasing variable costs and investment.

6.4.3 *Carrying capacity and habitat suitability*

For shellfish resources, it is common to find some portions of the habitat more densely populated than others as a response to gradients in habitat quality. Such spatial variations might be assessed to determine distributional patterns common to adults and recruits, in order to select a site for restocking. The following mechanisms could explain patchy distribution patterns and should ideally be evaluated: (1) active larval choice, and ability to colonize areas of habitat with greater environmental stability where population growth is maximized; (2) occurrence of higher mortalities operating before and after settlement due to adverse environmental effects (e.g. low

salinity); and (3) a major incidence of hydrodynamic forces, which determines passive transport of larvae to a given receiver site.

Population regulation may be habitat-dependent, as demonstrated for shellfish populations by the positive covariance between density, resources and environmental harshness (e.g. salinity, seston, food availability). Density-dependent habitat limitation within the seeding area could greatly reduce the potential benefit of any restocking programme. Shelter/space availability may control the size of many shellfish populations (see e.g. Caddy and Stamatopoulos, 1990; Beck, 1995). An attempt to investigate experimentally whether hatchery-reared animals displace natural stocks should aim at testing the hypothesis of habitat limitation.

The above facts clearly suggest that the optimum individual size for restocking and the carrying capacity of the system will depend on site quality and extent: suitable hydrographic conditions, absence or rarity of predators, food availability and available shelter could be some of the factors affecting habitat quality and thus carrying capacity. Carrying capacity will also differ at different stages of the life cycle (Orensanz, 1986; Fréchette, 1991) and restocking operations must take this into account. For example, if a natural stock is already present, the total biomass of wild plus enhanced stock should not lead to compensatory mortality and depressed growth rates as a result of stocking. Dijkema, Bol and Vrooland (1987) found that high population densities of the cockle *Cerastoderma edule* in Netherlands determined density-dependent growth rates and that at very high densities, some individuals are pushed out of the sediment and subsequently die. The re-seeding of cockles on an experimental scale demonstrated the major advantages to thinning very dense natural cockle beds in order to improve growth rates. All of these factors affect production and thus the economic viability of the operation (see Schiel, 1993 and Brand *et al.*, 1991 for examples).

Maller (1990) and Blackburn, Lawton and Perry (1992) developed a simple and effective method to determine the slopes of the upper boundary (maximum densities) of the relationship between density and body size. Even though the original procedure was conceived for scaling body size to density, an issue also relevant for stock enhancement initiatives as an indicator of available energy in the ecosystem, the methodology equally applies to any combination of variables in which a Constraint Envelope Pattern (CEP: *sensu* Marquet, Navarrete and Castilla, 1995) has a real biological meaning. The procedure involves dividing the X-axis into intervals of equal length and recording the maximum value of the response variable on the Y-axis for each X interval (see also Marquet, Navarrete and Castilla, 1995 and Blackburn and Gaston, 2001 for additional theory). Because the value of the slope depends on interval size used in the X-axis, it is suggested to consider a range of interval sizes from, say, 0.1 units of the X variable up to a value that renders at least three values of Y (Marquet, Navarrete and Castilla, 1995). Then, the nature of the relationship defined by the points of the upper boundary is visualized through a simple scatterplot and then the appropriate (linear or non-linear) model is fitted. The upper limit corresponds to optimal combinations of the X and Y variables, whereas values within this "envelope", well below the upper ceiling, represent a wide range of suboptimal conditions. Typically, the CEP has a well-defined upper boundary with a negative slope indicating an inverse relationship between X and Y.

The above methodological approach has been suggested as a simple way of estimating carrying capacity through the use of a scatter diagram of adult and/or recruits density in each sampling unit or quadrat. At this small-scale of spatial resolution, a boundary of carrying capacity for both population components (adults and recruits combined) could be estimated (Orensanz, 1986). This must be done for different degrees of fishing pressure, and by site. Defeo (1996a) estimated

carrying capacity with and without fishing activities. However, in the context of stock rebuilding initiatives, this approach is useful for evaluating optimal levels of abundance of the different population components at a given site, and thus is a help to planning the intensity of seeding operations through the estimation of optimal stocking densities (OSD). At a “quadrat scale”, Defeo (1996a) showed that highest densities of recruits were never coincident with highest densities of older clams. Maximum densities of recruits per sample core were observed during 1984 and 1985, when they reached between 4 000 and 5 000 ind·m⁻²; during the same period, maximum adult densities were between 400 and 600 ind·m⁻² but not in the same samples where the maximum recruit densities were recorded. These values of adult density, which correspond to the period of active fishery, were far below the maxima recorded after the fishery had been closed; in 1989 they reached 800-900 ind·m⁻². It is notable that when adult densities were at least 300 ind·m⁻², recruitment was almost absent in the same sample. The negative relation between recruit and adult densities for all years combined is shown in Figure 6.9. The line which defines the upper limits of the relationship represents maximum adult densities for varying levels of maximum recruitment; below the line, the lower values represent a wide range of suboptimal environmental conditions (Maller, 1990). The upper boundary mainly reflected higher densities of recruits during the years 1984-1985, and those of adults inhibiting recruitment during the experiment, i.e. in 1989 (Figure 6.9a). This “envelope” is linear in this case, but could take different forms (e.g. a monotonically decreasing exponential model). The form of this upper boundary should be taken into account when defining the appropriate combination of adult and recruitment densities in a stock-rebuilding experiment.

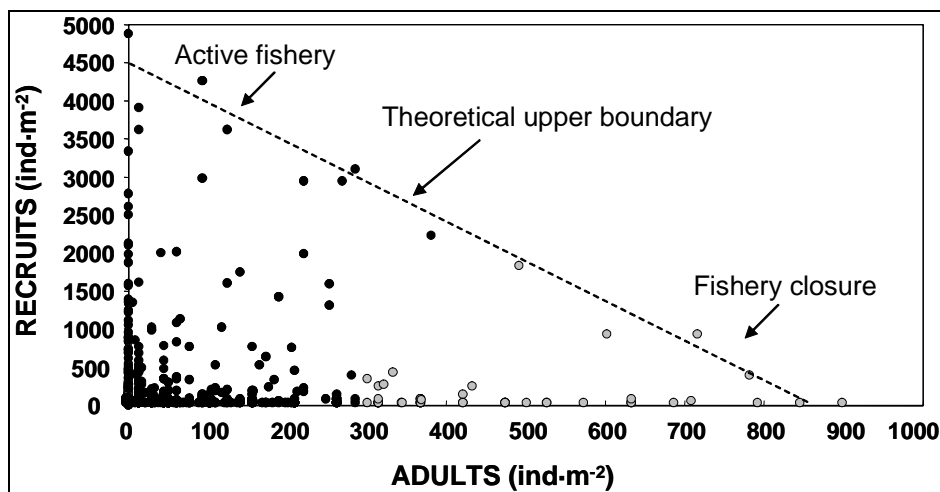


Figure 6.9 Scatter diagram of yellow clam recruit density plotted against adult density in each quadrat, for the months when recruitment peaked: see the difference between recruitment densities observed between 1983 and 1988 (●) under low adult densities and high extracting levels (1983-1987), and in 1989-1990 (○), as a result of the closure of the fishery. The dotted line defines the upper limit of the “envelope” between stock and recruitment, representing maximum recruitment densities for varying levels of maximum adult densities determined following Blackburn, Lawton and Perry (1992: see text for details).

Parsons and Dadswell (1992) found an inverse relationship between growth (shell height, meat weight, and whole weight) and stocking density in juvenile giant scallops, *Placopecten magellanicus*. This could affect OSD estimates, which was also dependent on the overall cultivation strategy type of grow-out technique, and the optimal timing of transfer from the pearl nets. Fréchette, Bergeron and Gagnon (1996) presented a method for estimating OSD via

the analysis of the relationship between yield (biomass, B) and population density (N) at harvest, using a B-N diagram (BND). The analysis provided by the authors differs from the usual approach in aquaculture, in which yield is expressed as a function of initial population density, and B and N are analysed separately. Both methods allow estimation of OSD. The BND potentially allows (Fréchette, Bergeron and Gagnon, 1996): (1) assessment of the relative importance of competition-dependent and competition-independent mortality factors; (2) estimation of approximate OSD and maximum yield by extrapolation of results from short-term experiments; and (3) identification of the nature of the factor regulating competition-dependent mortality. They also compared the classical and BND methods using data from mussels grown in suspension cultures, and found that mortality patterns were the same for all stocking densities, and that competition-dependent mortality occurred only at high density. In an experiment designed to test the effect of spat origin (stock effect) on commercial yield, the classical approach suggested that there were no differences in yield and survival, despite differences in growth rate. The biomass-density approach (BN), however, showed that yield was constrained by self-thinning, not by intrinsic properties of the stocks. The BN approach, unlike the classical approach, yielded results consistent with state-of-the-art commercial practice and general knowledge about the stocks tested (Fréchette, Bergeron and Gagnon, 1996). Rheault and Rice (1996) showed that doubling the stocking density from 2.5 to 5.0 kg of oysters *Crassostrea virginica* per bag resulted in a 20 percent decrease in both the condition index and the growth rate (percent increase in weight). These observations may assist commercial growers determine optimal stocking density for their aquaculture grow-out systems. The variation in food concentration superimposed on the tidal current oscillation leads to massive changes in food flux and the degree of local resource competition.

Fréchette and Bacher (1998) noted that estimating physiological rates of the blue mussel *Mytilus edulis* in the field as a central part of carrying capacity studies. They also presented a strategy for estimating site-specific physiological rates based on the modelling of a reference growth experiment at a standard site. Growth of mussels was modelled as a function of population density to obtain estimates of biomass-density and production-density curves for the reference experiment. The authors stressed that these curves provide much of the information usually required for managing cultured populations. They concluded that combining the modelling of reference experiments in this way with particle transport models, may prove useful for assessing optimal stocking density in situations where intensive field work programs are not possible.

Intertidal mussels usually form complex multilayered matrices with density-dependent effects on survival and growth, and self-thinning scaling between biomass (B) and density (D) is expected. Guíñez and Castilla (1999) develop a tridimensional model of space-driven self-thinning that in addition to BN, explicitly includes the degree of packing of the mussels, measured as the number of layers (L). The model BNL could be considered as a generalized one in the sense that it encompasses previous bidimensional models (BN) of self-thinning (e.g. Fréchette and Lefaivre, 1990, 1995; Fréchette and Bacher, 1998) as special cases, and enables comparisons between mono- and multilayered populations. Guíñez and Castilla (1999) contrasted the predictions of the bi- and tridimensional models using data obtained from *Perumytilus purpuratus* mussel beds on the rocky shores of central Chile monitored during a 28-mo period. The B-N-L model suggested that density dependence is much more frequent than hitherto indicated by bidimensional models. The authors also applied their space-driven tridimensional model to other species where spatial overlapping configurations occur, such as the case of tunicate population of *Pyura praeputialis* in the Antofagasta Bay, northern Chile (Guíñez and Castilla, 2001).

7. GUIDELINES FOR CONDUCTING AND EVALUATING STOCK ENHANCEMENT PROGRAMMES

From what has been said up to now, it must be clear that an enhancement programme needs rigorous design, and requires not only in-depth knowledge about the life history of the species, but also an economic evaluation of the activity through the intertemporal flow of benefits and costs. While planning a restocking programme, the following topics should be considered:

7.1 Experimental design

Enhancement programmes need careful experimental design. Whatever the seeding technique selected, the appropriate scale of the experiment must be clearly defined according to the desired objectives (Sainsbury *et al.*, 1997).

7.1.1 Local scale

The wide variety of physical, environmental, biological, economic and social circumstances encountered in shellfish production requires that enhancement programmes should be site-specific. A good strategy is to design such experiments on relatively small spatial scales at first in order to allow a "hypothesis-falsifying" procedure to be followed (see McAllister and Peterman, 1992; Walters, 1997; Castilla and Defeo, 2001 and Section 3.5), incorporating control sites/replicates of e.g. selected spat densities.

In order to conduct enhancement experiments, each experimental unit must be adequately replicated in order that monitoring of growth, survival and production according to specific environmental and habitat characteristics, in such a way that estimates can be established within limits of statistical confidence. In this way, estimates of variability could also be used to evaluate the success of the experiment under uncertainty. Small-scale, replicated plots can be used to evaluate alternative scenarios (e.g. different stocking densities of the enhanced population) and effects of habitat quality (substratum, hydrodynamics). Basic ecological considerations, such as predator-prey interactions and the effects on the benthic community of massive transplantation/seeding of organisms, should be analysed before extrapolating results to a larger scale.

If adequately replicated, enhanced pilot scale sub-populations in experimental plots can be used to evaluate the success of mixed management strategies within an adaptive framework. For example, small areas could be closed to fishing or even subjected to different intensities of fishing in order to assess the potential benefits both of a rotational management scheme and restocking with seeded juveniles (Brand *et al.*, 1991). If areas of similar productivity are considered, the experiment might be successful even on a short-term basis.

7.1.2 Large scale

The increasing demand for seafood places emphasis on large-scale, commercially oriented, technology and intensive enhancement programmes. Thus, results obtained on an experimental, local or pilot scale, must then be evaluated at larger scales (see May, 1994 for useful concepts relating ecological questions and spatial scales). For example, a large-scale transplantation of spat must consider the ecological implications of such a perturbation on conspecific organisms (e.g. the effects of "genetic contamination" by interbreeding of hatchery stock, which might be less adapted to the environment, with local stocks), and on the benthic community as a whole (see Castilla, 1988; Bailly, 1991; Brand *et al.*, 1991). Schiel (1993) gives one of the most useful

examples of the experimental evaluation of commercial-scale enhancement of a shellfish population. He described a large-scale experiment in which growth/survival of seeded abalone *Haliotis iris* was assessed at a range of sites.

As in any ecological experiment, it is difficult to trace a rigorous sampling design in large-scale enhancement operations for the following reasons:

- The varying nature of each site (habitat quality) precludes the definition of adequate control areas and replicates. In many cases areas are so large that replication is almost impossible.
- Difficulties occur in filtering out the effects of a restocking programme from natural fluctuations of the stock or alternative management initiatives. Concomitant changes in fishing effort could also confound the results of the seeding process.
- Stock enhancement is a long-term goal and must be evaluated accordingly. However, it is difficult to wait for a commercially harvestable size to evaluate success. Some projections, based on knowledge obtained from short-term experiments, might help overcome this obstacle.

The experimental design of enhancement exercises therefore requires careful attention to metapopulation dynamics and recruitment processes. In this vein, the existence of a metapopulation offers an opportunity to perform large-scale enhancement experiments in order to evaluate the capacity of the species to restock population subunits previously depleted by fishing or other disturbance (such as red tide outbreaks). Transplanting could be particularly useful where metapopulations have clearly defined "source" or "sink" characteristics (Shepherd and Brown, 1993). In order to conduct active enhancement of a shellfish metapopulation, and define harvest refuges serving as sources of individuals for replenishment or transplanting, information on the early stages of the life cycle is critical. Information on habitat quality or adult density alone is not enough to assure a higher probability of success, and Lipcius, Stockhausen and Eggleston (2001) discounted determining the site of the reserve by chance without information on transport processes of larvae.

Shepherd and Brown (1993) provided a preliminary example on how to apply metapopulation theory to South Australian abalone stocks; the first requirement being to define the complex of substock units. They integrated within this the concept of a "minimum viable population" in order to develop a cost-effective management framework for such a complex of stock units. This and other studies on metapopulations are used here to define a tentative guideline on how to apply metapopulation theory for the purposes of experimental enhancement of shellfish productivity. The main steps could be summarized as follows:

1. Define subareas by extension and number, according to the intrinsic characteristics of the resource and the fishery (i.e. by scale of aggregation of the resource and behaviour and subregional access rights of the fishers). Mapping the fishing grounds and stock abundance should precede the design of a system for acquiring information on the spatial dynamics of settlement over the long-term (see Caddy and Garcia, 1986). Subareas should be easy to identify for fishers and researchers, and should facilitate the collection of spatially accurate information (Cabrera and Defeo, 2001).
2. Estimate the times of settlement and recruitment. Identify potential sources of larvae and discern between source and sink areas. Care should be taken to evaluate larval connectivity

between the discrete areas already defined. Monitor local recruitment of postlarvae and the degree of replenishment of different grounds. It is important to consider here the duration of the larval dispersal stage: those with a shorter larval development period may be more suitable candidates for hatchery rearing and subsequent seeding.

3. Identify key environmental variables, notably intensity and direction of currents that could explain prevailing larval dispersal and settlement. As each ground may be exposed to a distinct regime of primary production, nutrients, food availability, predation and disturbance, these between-ground differences should, if possible, be quantified.
4. Quantify spatial and temporal variations in density of recruits and adults (defined as sexually mature individuals), over a reasonable time frame and by site (e.g. source and sink areas). In each naturally seeded area, acquire information on resource users, local stock dynamics (growth and mortality). Accurate definition of spawning and recruitment timing is critical to providing fine-tuning of the appropriate timing for conducting stock enhancement programmes. Indeed, timing and durations of settlement of many species were often specific and quite short; especially in temperate latitudes (see e.g. Robinson and Tully, 2000). Thus, choosing the specific habitat and time of year for enhancement of a benthic species may be the key to success, and for most species, information on specific environmental requirements is generally lacking. Seasonal lows in abundance of previously established cohorts may represent the most suitable time for releasing juveniles in order to minimize inter- and intraspecific competition and predation, thus highlighting the value of careful ecological study of the potential release sites.
5. Compare growth and mortality information from fished and unfished grounds, in order to isolate effects of density and fishing intensity from those induced by environmental gradients in habitat quality. Growth and mortality patterns should be quantified through time (e.g. under different densities) and in space (e.g. by fishing grounds or LPs) in order to evaluate variations in density-dependent processes and habitat quality. Growth rates of transplanted/seeded individuals must be compared to those of the natural stock under different densities. Estimates of age-specific natural mortality (see Chapter 2) are particularly useful for detecting these critical periods when natural mortality from predation or other causes drops sharply from high values for spat to older animals. In order to have some idea of growth rates and development times from egg to mature adult, some information on environmental factors is critical, and it will be useful to keep time series of relevant water temperatures and wind conditions (e.g. Caddy, 1979c, Botsford, 2001). If development is protracted, and there are high rates of density-dependent mortality (e.g. cannibalism), then culture will be labour-intensive and economically prohibitive. Biometric relationships such as length vs. total weight/muscle weight should be determined to predict the expected meat yield from a mean individual size or age, thus allowing some economic projections for cultivation times.
6. If fishing rights are assigned geographically, quantify spatial variations in fishing intensity using e.g. a composite production modelling approach that includes simultaneous levels of production and fishing intensity from areas with variable intensities of harvesting but a similar basic ecosystem.
7. Estimate appropriate target and limit reference points (*sensu* Caddy and Mahon, 1995) for each LP. Complementary management strategies, such as catch quotas, number of fishers allowed to fish/area of ground, and minimum individual harvestable sizes, should also be

agreed upon. A minimum viable population and optimal fishing mortality or harvest rate should be based on simple yield simulations from known growth and mortality rates, or empirically using the composite production modelling approach.

8. Depending on the inherent spatial characteristics of the metapopulation (see Shepherd and Brown, 1993) and prevailing fishing intensity, an effort should be made to identify existing spawning refugia and nursery areas (for motile species: Herrenkind *et al.*, 1997). In essence, the refugia should be large enough to diminish the risk of stock collapse despite prolonged recruitment failure in LPs due to adverse environmental conditions. Spatio-temporal variability in abundance of stock, larvae and subsequent recruitment, as well as in the prevailing hydrographic regimes, should be considered when evaluating number and/or size of refugia or other spatially explicit management tool (e.g. MPAs). The dimensions of the area protected should be large enough for stock rebuilding purposes within and outside its boundaries.
9. Genetic factors must be taken into account. Classically, it has often been assumed that past enhancement programmes have been successful if populations appear to have been restored in their area of introduction. Testing allele frequency and mtDNA in hatchery stock, and comparing it with that from supposedly successful transplants may however paint a different picture. Thus, Burton and Tegner (2000) found that a red abalone population in California planted in 1979 which supposedly supported the fishery there during the 1980s, resembled other robust natural populations in the region in its genotypic frequencies, and showed no genetic signature of the broodstock used in the transplants. Although the test was not considered conclusive, it does not suggest discarding the previous generalization that hatchery outplants of abalone attempted to date appear to have been unsuccessful. One of the problems of cultivating shellfish for transplanting was illustrated by a genotyping of individual abalone larvae produced in a hatchery (Selvamani, Degnan and Degnan, 2001). Despite attempts to normalize the share of sperm from a number of males used to fertilize eggs in culture, DNA markers revealed that a single father fertilized almost all eggs reaching larval stage. This suggests the need for highly controlled breeding practices to ensure that the genetic diversity of the broodstock for out-planting to the field is maintained. Evidence from finfish culture has already warned of the dangers that repeated enhancement using a narrow genotype will adversely affect species resilience over the long term, and the same message evidently applies to abalone and other invertebrates produced in culture.

7.2 Technical feasibility

While it is easy to import a technology from elsewhere, in many cases enhancement programmes fail when technical problems substantially increase processing costs and lead to serious economic losses. As already mentioned, high costs of production of spat, and high predation on them when released onto the grounds, are critical factors. Other technical problems mentioned are environmental impacts due to seasonally extreme conditions (e.g. ice cover in high latitude waters, summer hypoxia in shallow tropical waters and lagoons, or heavy wave action) and processing constraints (the byssus of *Mytilus edulis* clogs the sorting and cleaning machinery). These kinds of technical problems may lead to a drop in production or compromise enhancement programmes (Kristensen and Hoffmann, 1991). Technical feasibility in rearing larvae, juveniles or adults may also constitute major bottlenecks in enhancement activities. Progress therefore requires a combination of technical applications in the methodology, and

ecological acumen (see Peterson, Summerson and Luettich Jr., 1996 for a test of alternative transplantation techniques in scallops).

Facilitation of collection of sufficient numbers of larvae and juveniles from the wild for on-growing is of utmost importance: the timing of collector placement, and collector design, are essential to maximize seed collection during peak settlement periods. A key problem in enhancement programmes is the precise timing of release of juveniles or spat into the wild, in order to minimise mortality rates and costs. Release time should ideally be set after the critical stage in the life history has passed, where this is characterized for example by specialized diet or susceptibility to predation. In general, the longer the rearing time before release, the higher probability of survival. However, this increases production costs, so a trade-off between ecological and economic factors will need to be made in determining the optimum individual size for restocking (Tegner, 1989; Larkin, 1991).

The capacity to rear larval stages through to commercial size before releasing, and thus the appropriate duration of rearing for ranching is critical, i.e. whether the specimens are to be released in a recent post-settlement stage, or as adults, must be evaluated. Economic considerations are critical here, as well as ecological issues (competition, predation). For example, if some early stage is especially vulnerable to predation, it would be better to collect and release juveniles after this critical stage, particularly if natural mortality declines above a given size.

Another constraint may arise when shipping organisms to the transplanted sites. Schiel (1993) found that the greatest stress to transplanted abalone *Haliotis iris* occurred in packing and transport, and here the density per shipping tube needs to be carefully evaluated. The same author reported mortality rates of up to 47 percent in tubes where juveniles of *Haliotis iris* were packed at densities of 1000/tube. Many fragile organisms must be transported in aerated seawater and released at sea at well-defined experimental sites to assure the success of the operation. Peterson, Summerson and Luettich Jr. (1996) evaluated the success of alternative transplant methods for adult bay scallops *Argopecten irradians*, using five different sets of environmental conditions for a 6-h time of transfer from the source to the destination site. They found negligible mortality rates during travel times of up to four h with high flow speed and therefore high oxygen concentration, and this minimized the risks of stress and mortality from handling and transport.

Once in the wild, estimations of survival through recapture rates provide a way of monitoring success. Controlled release onto shellfish habitat, microtagging, and the development of a monitoring plan, represent three important methodological aspects directed at evaluating the technical feasibility of an enhancement programme. If microtagged, the precise location of recaptured animals is needed to evaluate the extent of local movement and the capacity of the seeded animals to restock target or adjacent areas (Addison and Bannister, 1994).

7.3 Economic feasibility

The economic significance of enhancement programmes has still not been fully evaluated, perhaps due to the difficulties in estimating total profits and costs derived from the seeding activity. One economic bottleneck derives from high hatchery costs: these programmes can be prohibitively expensive even for high unit-value resources (Addison and Bannister, 1994). One way to reduce total costs is by releasing juveniles at an early stage. However, this in turn could increase mortality rates after release, because of higher predation rates and

susceptibility to environmental variations. This clearly constitutes a bioeconomic trade-off, and must be evaluated accordingly. The maximum cost that could be justified for evaluating new enhancement practices, should be in proportion to the expected benefits and impacts.

Hilborn (1998) reviewed the economic performance of nine marine stock enhancement projects for fish, turtle and lobsters involving restocking. He noted that no project evaluated showed clear evidence of a resulting increase in abundance as a result, but then few were planned in such a way that success criteria or economic performance could be evaluated. His suggestions were that systematic marking of released individuals would help establish survival and population enhancement, with explicit control areas incorporated in a proper statistical design, and subject to prior peer review by experts. The economics of stocking should be compared with other approaches such as habitat protection or improved management of the wild stock, and in this connection, evaluating the various benefits to the stock and ecosystem of protected areas requires close consideration (see e.g. Dixon and Sherman, 1991).

Bioeconomic analysis must be defined at the planning stage of the enhancement programme and must be specific to a local (among grounds) and regional (among countries) basis. Especially the former is crucial for benthic species with marked spatial variations in carrying capacity, recruitment, and growth and mortality rates, which constitute input variables affecting the economic analysis of stock enhancement. Moreover, some economic inputs might differ on a regional scale (e.g. opportunity costs of labour and capital) and thus economic analyses must not be overgeneralized. An analysis of marketing is also needed, because the choice of the species to be enhanced will be guided by demand/supply market laws. Different product types (whole weight, muscle weight), and the corresponding unit prices must be also included in the economic analysis, according to variations in the local/international demand.

In enhancement operations, relatively short sampling periods are used to estimate abundance, growth and survival rates through time (Schiel, 1993). Thus, economic projections should be employed to estimate the net present value (*NPV*) of the enhancement activity: abundance, growth and survival estimates derived from the short-term project must be extrapolated to the period at which organisms will be available to harvesting. An enhancement programme will be economically efficient if it maximizes the *NPV* of the yield obtained, which could be estimated as:

$$NPV = \sum_{t=1}^T \frac{TR_t - TC_t}{(1 + d)^t}$$

where *TR* and *TC* are respectively the total revenues and costs in time *t*, and *d* is the discount rate. Total revenues are obtained by multiplying the unit price of the products (e.g. whole weight, muscle weight, shells) by the estimated catch according to specific growth and survival rates. Total costs in each year are mainly based on costs of rearing individuals through a selected “seeding stage”. The discount rate *d* considers the future value of the money invested.

An increasing discount rate diminishes the value of any future yield. Even though traditional values should approach an interest rate of *ca.* five percent, discount rates could generally takes higher values (up to ten percent), mainly as a result of uncertainty about future yields derived from the enhancement activity. As in fisheries, there are high uncertainty levels about changes in costs and prices, stock magnitude, growth and survival rates, and the prevailing economic and market regional situation. Therefore, *d* will tend to increase still further due to a probable

expectation about falling prices or rapid depletion of the enhanced stock, implying that high exploitation rates in the short-term will be preferred over a long-term sustainable goal. This is particularly important in open-access regimes, in which free-rider behaviour and externalities commonly occur (Seijo, Defeo and Salas, 1998).

The high variability and difficulties in the estimation of some inputs (supply of spats, recapture, survival and growth rates and economic variables), together with a costly and low intensity of sampling through time, add uncertainty to the estimation of the *NPV*. Thus, different sources of uncertainty should be included when estimating the economic feasibility of the enhancement operation, e.g. different scenarios of growth and survival rates, and prices and costs could be used as inputs to estimate benefit and costs and the corresponding *NPV* of the enhancement plan. Moreover, different d values should be used to reflect dissimilar intertemporal preferences in resource use (e.g. different minimum harvestable sizes according to market demand).

After estimating uncertainty in the input variables, a criterion for choice among estimates is needed to provide options to a decision-making body. This could be done through decision theory. Decision analysis applied in fisheries (Hilborn, Pickitch and Francis, 1993; Hilborn and Peterman, 1996) considers alternative bioeconomic states of the fishery with the corresponding probabilities of occurrence, as a function of some possible policy actions. In this context, Bayesian inference allows the simultaneous consideration of multiple hypotheses and the integration of different types of information from many sources, reflecting scientific judgement as well as existing empirical data. Decision analysis could also be used to incorporate the above estimates of uncertainty into choices of enhancement actions. Data gathered in surveys conducted over experimental grounds on which enhancement programmes are taking place, as well as life history parameters derived from these data, could be used to provide a formal assessment of the enhanced stock, and in such cases the Bayesian approach is robust for estimating parameters, despite concerns over possible data outliers and mis-specification of priors (Millar, 2002; Myers *et al.*, 2002).

In the above context, a decision table could be built on the basis of alternative enhancement actions and alternative hypotheses erected about parameter values and their corresponding probabilities of occurrence (Table 7.1). For example, high, medium and low levels of stocking densities ("alternative enhancement decisions") could be evaluated as a function of different hypotheses about resource performance (alternative scenarios of growth/survival rates; time needed to reach the minimum legal size, etc).

In some cases "experience may be insufficient for decision makers to be willing to attach numerical (cardinal) probabilities to the possible outcomes (states of nature)" (Schmid, 1989). Thus, decision tables could be created to account for different alternative system states (columns) and the possible decisions (rows), left with probabilities missing. The likelihood of outcomes could then be ranked only ordinally, and thus decision-makers could make a choice under uncertainty by expressing their subjective judgement about likelihoods in directional and qualitative terms. Schmid (1989) proposed three criteria for dealing with uncertainty and to guide decisions, without the need for explicit statements as to the probabilities of alternative parameter values: Maximin, Minimax and Maximax. These criteria vary according to degree of precaution. The Maximin criterion is a risk-averse approach that leads to selecting the maximum of all minimum outcomes. The Minimax Regret criterion is a less cautious approach that selects the minimum of the maximum regret, defined as the difference between the real benefit and the one that could have been obtained if the correct decision had been taken. Finally, the Maximax criterion is the most optimistic, in that it selects the highest outcome within the decision table.

Once the table is built, the *NPV* of the activity is estimated for each combination of the enhancement actions and parameter values. These criteria were successfully applied in fisheries management (FAO, 1995; Pérez and Defeo, 1996; Seijo, Defeo and Salas, 1998; Defeo and Seijo, 1999) and could be easily adapted to enhancement problems. The reader must refer to the papers above-mentioned for a detailed application of these criteria.

Table 7.1 Key elements of a hypothetical decision table directed at evaluating alternative enhancement options. S1 is a hypothesis that implies a lower level of individual growth rate or a higher survival than S2 and S3. D1 to D3 represent alternative decisions concerning stocking densities. *p* values represent the probabilities of alternative hypotheses being true, and O_{ij} represent the relative value of the outcome of a given stocking density *i* as applied to a given growth/survival rate *j*. O_{ij} values could be regarded as representing net revenues obtained by each enhancement option. Finally, V1 to V3 represent the expected values of each action across all alternative hypotheses. A variance term might be added to each expected *V* value (after FAO, 1995; Hilborn and Peterman, 1996; Defeo and Seijo, 1999).

Alternative stocking densities	Alternative hypotheses about parameter values (e.g. growth)			Expected values
	H1	H2	H3	
	P1	p2	p3	
D1 (50 ind·m ⁻²)	O_{11}	O_{21}	O_{31}	V1
D2 (100 ind·m ⁻²)	O_{12}	O_{22}	O_{32}	V2
D3 (150 ind·m ⁻²)	O_{13}	O_{23}	O_{33}	V3

Given the high uncertainty usually found in the majority of the parameters of an enhancement model, a precautionary approach must be considered suitable for evaluating the economic feasibility of the operation. Thus, not only the lower levels of the confidence intervals of the parameters should be used as inputs to estimates of the *NPV*, but also the criterion that gives a cautious approach (e.g. Maxim/In Defeo and Seijo, 1999).

7.4 Evaluating the success of enhancement exercises

Enhancement practices have been applied to protect, maintain or improve shellfish populations. Because of the increasing number of enhancement programmes around the world, a scientific approach to evaluate their effectiveness in stock rebuilding is essential. However, the extent to which stock enhancement programmes contributed to natural populations of shellfishes has not been adequately assessed. Indeed, even though intuitively attractive, restocking programmes have been pursued with little evaluation of their success or failure (Addison and Bannister, 1994). Some reasons arise from: (a) the absence of biological knowledge of the species; (b) the lack of definition of clear objectives from the beginning of the planning stage; (c) experimental inadequacies resulting from an undefined methodological framework; and (d) technical problems associated with the supply, maintenance and rearing of spat (Cowx, 1994).

The following steps summarize the information provided earlier in this document and could be considered when assessing success of any enhancement plan:

- (1) ***Determine the initial number and size structure of seeded organisms, together with the sites of placement. If possible, mark or differentiate them from wild animals. Use control, unseeded sites for comparative purposes. Characterize each site as precisely as possible.***

In order to evaluate the success of any seeding experiment, seeded animals should be microtagged (Wickins, Beard and Jones, 1986), thus permitting the identification of hatchery-reared animals during subsequent field sampling and monitoring of commercial landings. It is commonly difficult to discern whether hatchery-reared animals have survived in addition to, or at the expense of, natural stock. However, Schiel (1993) suggested an effective and cheap means of tagging abalone indelibly by allowing abalones to feed sequentially on different algae before releasing. A continuous switching between algae generates alternating bands of different colours on the apex of the shell that can be seen for several years. At least this is applicable to abalone stocks.

A target density should ideally be estimated for seeding. It will be based on previously acquired knowledge about the SRR and carrying capacity of the system. A range of sites and, if possible, densities at each site, should be used to test hypotheses related to habitat quality and variations in the carrying capacity in each habitat. Data must be interpreted quantitatively in order to assess among-site variations in growth and survival rates and the success of active restocking. Unseeded sites should be useful controls for comparative purposes. Some measures of the effectiveness of the restocking process should also be quantified. Site-specific survival and individual growth rates of released animals, from the beginning of the seeding process to the time at which the individuals become available to harvesting, could be used for this purpose.

(2) *Estimate abundance variations through successive and periodic sampling. Estimate survival and individual growth rates and compare them with those of the wild stock.*

Length-frequency analysis should be clearly the best way to provide estimates of growth and survival rates. Overall growth and mortality patterns must be compared to those of unseeded sites and also among seeded sites. ANOVA procedures should be useful for this purpose.

As mentioned above, an enhancement plan is essentially long-term. However, it will be difficult to carry on sampling for years in order to estimate population dynamics features (growth, survival) until the harvestable size is reached. This is almost impossible for long-lived shellfish. Thus, projections of growth and mortality rates must be done from the seeding stage to the length at which organisms reach the minimum legal size.

(3) *Estimate the number of microtagged organisms that survived to the harvestable size (biological samplings) and the relative contribution of the enhancement operation to the global landings from the whole area (by sampling landings and markets).*

The success of stock enhancement programmes should be evaluated by field sampling (target fishing close to the release sites) and by monitoring fishery landings. Stock enhancement, if effective, can be detected from the concomitant increase of fishing yields reported by fishers' logbooks. Concerning this important issue, Kitada, Taga and Kishino (1992, and references therein) reviewed four groups of methods for estimating of the effectiveness of enhancement programmes on the basis of tag recoveries, which can be summarized as follows:

(a) Estimation of total recoveries from fishers' reports. Tag recoveries are intuitively attractive because of low costs of acquiring information (Crowe, Dobson and Lee, 2001). However, the proportion of recaptured animals tends to underestimate the survival rate of seeds and the consequent measure of effectiveness of the enhancement programme, for several reasons (Addison and Bannister, 1994):

- A substantial part of the catch escapes monitoring.
- Landings away from the release site, and thus with low probability of recapture, tend not to be monitored.
- Estimates of abundance from tagging are based on some marked to unmarked ratio. However, dissimilar behaviour between marked and unmarked animals (survival rates of the former group tend to be lower), together with a generally low chance of recapture because of low percentages of marked animals, usually lead to underestimates of abundance (Hilborn and Walters, 1992).

These limitations could be mitigated by intensive sampling in the field and of landings (Kitada, Taga and Kishino, 1992). Bannister and Pawson (1991) showed that microtagged *Homarus americanus* in field samples at releasing sites constituted up to 50 percent of the catch on specific days and ten percent over a season, including egg-bearing females. This fact unambiguously shows that hatchery-reared animals survived to maturity and contributed to the breeding stock. However, scientific results concerning this point for most examples are usually either nonexistent or inconclusive.

(b) Correlation between annual number of fingerlings and the corresponding landing weight.

This method could be an option for shellfish with short life spans and relatively stable recruitment rates. However, recruitment tends to be highly variable and not related to the amount of the parental stock but to show environmentally driven fluctuations in early life stages. Even should the above assumption be valid, it is difficult to discern between increasing landings as the response to the enhancement programme, or as a result of natural recruitment. The situation is complicated when several age-classes are contributing to spawning.

(c) Prediction of recoveries by calculating yield per release based on the catch equation and simulation models. This method is a complement to the others mentioned, because the recovery rate of shellfish released is not taken into account. Once this measure is quantified, simulation models could be performed to evaluate the effectiveness of restocking.

(d) Sampling surveys of commercial landings and fish markets. Kitada, Taga and Kishino (1992) suggested that a proper estimate of recovery could not always be obtained by these three groups of methods. They proposed a two-stage sampling survey of markets of cooperative associations of fishers (primary sample unit) and landing days (secondary sample unit) to estimate the success of enhancement programmes. Measures of effectiveness included the ratio of marked animals in the landings and recovery rates. These estimates were then used to evaluate the economic feasibility of the programme.

(4) ***Perform an economic analysis of the activity through the estimation of the net present value of the intertemporal flow of benefits and costs. Use different discount rates to reflect dissimilar intertemporal preferences of society in resource use. Identify some possible bottlenecks that might have to be mitigated in order to reduce costs.***

As detailed earlier in this Chapter, the economic success of any restocking programme must be assessed to evaluate its commercial viability. To this end, costs (variable and fixed) and economic revenues must be carefully estimated in order to have indicators as to the feasibility of the operation. Simple spreadsheet methods incorporating life history parameters have commonly

been used for calculating mortality and growth of fish populations (see e.g. Sparre and Venema, 1992) using for example the Thompson and Bell procedure (Ricker, 1975). This approach has been employed for modelling abalone populations (see Sanders and Beinssen, 1998 and De Waal and Cook, 2001), who have extended it to incorporate a cost-benefit analysis. The economic effectiveness of a seeding operation under different conditions of survival, growth, labour costs and product sale prices can be investigated. De Waal and Cook (2001) show that ranching shellfish is only likely to be economically viable where mortality is not excessive and survival rate increases with age, which of course is generally the case (Caddy, 1991, 1996).

- (5) ***Estimate uncertainty in the main inputs of the enhancement model, i.e. from growth and survival rates to unit prices and costs. Employ for this purpose alternative hypotheses for parameter values to predict outcomes from alternative enhancement (e.g. stocking densities) strategies in a decision analysis.***

Uncertainty and risk analyses must be conducted to evaluate the bioeconomic feasibility of a stock enhancement programme. For example, the profit from a stock enhancement programme for a flatfish (the example is valid also for shellfish), as estimated by Kitada, Taga and Kishino (1992) was US\$ 63 000, but the 95 percent confidence interval ranged between unprofitable and profitable [- US\$ 4 000 to US\$ 151 000].

Given the high variability in outcomes, a precautionary approach should be used to minimize risks. Some specific Reference Points (Caddy and Mahon, 1995; FAO, 1995, 1996) should be used as targets. In this specific case, Reference Points are not necessarily those derived from classic surplus production and yield per recruit models, and conventionally used to manage fisheries (e.g. MSY , F_{MAX} , etc). Such models assume that recruitment is constant and rarely include input for recruitment variability, which can be one of the main sources of variability in invertebrate populations (Conan, 1986; Caddy, 1989b). In this specific case, variable stocking densities should be included as an option.

- (6) ***Try to reduce uncertainty in input variables by achieving as accurate biological and economic data as possible as a result of a rigorous experimental design. Focus research on improving the performance of different enhancement strategies. Develop methods for optimizing the monitoring system.***

Post-stocking evaluation has been largely neglected in enhancement programmes (Cowx, 1994). An enhancement programme requires explicit specification of the information needed to achieve enhancement objectives, taking into account all the processes (e.g. growth, mortality, prices, and market demand) required to ensure that these needs are met. Periodic evaluation and revision of the data collection and the results achieved is necessary. This should aid in reducing uncertainty in key variables, which in turn will affect the NPV from the activity. The evaluation should assess the long-term benefits of alternative stocking practices and regimes, and attempt to identify those factors precluding enhancement success.

8. MANAGEMENT OF ENHANCEMENT AND USER RIGHTS

8.1 The social context of stock enhancement

The implementation of stock enhancement as a management strategy requires a review of who has access to the resource, and if this has not yet been done, an allocation of rights. Indeed, stock enhancement initiatives are a waste of time if not complemented by additional management strategies directed to sustaining the activity over time. If the fishery is under an open access system, it is not clear how the biological and economic benefits of enhancement can be properly realized.

The social context is the key to success for local fishery restoration, if inshore fishery management programmes are to succeed. Local municipal control of shellfisheries is a common phenomenon in the USA, and has given rise to a diversity of shellfish cultivation techniques, some of which have been described in this report. The history of a shellfish management programme as described by MacFarlane (1998) on Cape Cod, Massachusetts, is of interest. This evolved from relaying native oysters, to the use of hatchery-raised seed and several approaches to nursery culture: bottom culture, raft culture, a municipal hatchery, a land-based upweller system, tidal upweller, and floating trays. The programme always operated under ongoing financial restrictions and changing political and social factors. The management priority was primarily on the high survival of spat rather than fast growth, and the most successful approach was found to be a land-based upweller system which provided 1 million seed/year with 95 percent survival. Subsequent survival in the field after relaying was determined mainly by the environmental conditions at the time of planting.

A further example is provided by MacFarlane (1996) of a local socially driven programme which arose from concern about declining stocks of municipally managed shellfish species. In this case, deterioration of water quality and habitat forced the local town council to address the causes of environmental degradation through instituting a water-quality task force, with terms of reference to recommend changes in land-use practices. This led to a drainage remediation programme, and resulted in the reopening of a shellfish ground after a 12 year closure for reasons of public health. The issues mentioned that adversely affected shellfish quality and hence enhancement, were nutrient runoff, groundwater, flushing rate of bays, and contamination associated with proliferation of private docks in the public tidelands, as well as the effects of beach dynamics and the erosion control mechanisms installed.

One conclusion that leads to a more specific and appropriate use of coastal areas with minimal negative interaction, is to ensure that user rights are specified for specific subareas of the coastal area within a realistic map, preferably specified within a GIS (Geographical Information System) (Taconet and Bensch, 2000; Manson and Die, 2001). This can become an essential basis for consideration by the local and regional authorities of suitable areas where exclusive user rights can permit cost-effective stock restoration. In many developing countries the question of creation of sources of employment is politically important, and often fisheries have been the “employment of last resort” for impoverished peoples. Removing this option, following the logic of restricted entry beloved of economists of developed countries, can have serious consequences on the quality of life and diet for the rural poor. It is this aspect that often leads to reluctance to allow exclusive user rights to coastal populations, but the best alternative seems to be to ensure that these rights are delegated to the community for reallocation to community members of specific areas/resources for stock enhancement.

8.2 Legislation and ownership

The elucidation of ownership is a critical issue in enhancement programmes. Free-rider behaviour under unrestricted access is a common feature in coastal shellfisheries (Seijo, 1993; Shepherd and Rodda, 2001). Enhancement of high-value shellfish stocks under a specified ownership regime will discourage unproductive investment (in time or money) by groups of fishers which will tend to absorb an important share of the enhancement benefits. Thus, methods of restricting access to the enhanced stock must be introduced, together with some legislation to protect rights of fishing of those persons or organizations that invested in the enhancement programme (Castilla, 1994; Addison and Bannister, 1994; Castilla and Defeo, 2001). This issue of limiting access to the fishery is still controversial: Mahon *et al.* (2003) stressed that, whereas some fishers recognize that the most efficient way to control sea urchin harvesting in Barbados is by limiting the number of fishers, the majority are of the view that no one should be prevented from harvesting, and that overfishing should be controlled by adjusting the length of the fishing season.

Institutional changes are needed in support of enhancement schemes, based on an adequate legislation that must recognize the concept of ownership and adequate use rights to protect investments (Bailly, 1991; Troadec, 1991; Bannister and Pawson, 1991; Castilla, 1994). This topic has been considered as a necessary condition for any enhancement programme to succeed (Larkin, 1991). It becomes critical to identify those who pay the hatchery costs in order to assign them the corresponding benefits. Thus, some legislation directed to protect the rights of authorized fishers will be required to ensure that only those who invested or who were responsible for the enhancement programme can benefit from the increased stocks. If a private company or fishery cooperative releases spat, there must be some confidence as to the benefits that will be obtained. This consideration increases in importance with the increasing scarcity and cost of catching wild shellfish, which in turn makes stock enhancement procedures economically attractive. If the resource is under open access, there is no basis for any private investment in stock enhancement, and little or no return to government from doing so.

The scale and objectives of stock enhancement are related to the entry or person who receives the allocation of rights. If it is intended to enhance the stock "for the public good", the scale of operation should probably be larger than in a strict private context. In the former case, some efforts must be made to legislate criteria for allocation of rights so as to favour those who wish to participate in enhancement of the fishery, and we may suggest that evidence of adequate funding set aside for the purpose would be one criterion for participation. Conflicts of interest might occur between different groups of resource users, as well as between fishers and other marine activities (see Bannister and Pawson, 1991). In cases of private hatcheries, the scale of enhancement should be smaller and restricted to those areas with specific rights of access. Commercial fishing licenses might be required for this purpose. Despite the above considerations, problems related to the allocation of space or catch between investing and non-investing groups are likely to remain.

Castilla (1994) illustrated a successful example of institutionalization of management practices in the Chilean small-scale benthic shellfisheries, notably those based on a mixed scheme. This included enhancement, together with allocation of rights through fishery preserves or concessions. The Chilean artisanal fishery activity is developed along more than 4 000 km of coastline, including 200 small coastal villages, coves or "caletas". After an increasing period of landings, which peaked in 1991 with *ca.* 150 000 t, many Chilean shellfishes were overexploited. In 1991 a new Chilean law was approved, and incorporated the concept of

"Maritime Destination", a management area for benthic resources accessed only by duly organized artisanal communities pertaining to each cove. Access to these areas by community members is free of cost, and based on an agreement on management and exploitation plans between fishers and the fishery authority. The management plan is periodically reviewed according to specific rules established in the legislation. The marine concessions were used to evaluate the recovering capacity of some shellfishes in the absence of fishing *i.e.* passive or natural restocking. Alternatively, the local community can subject these grounds to specific enhancement activities, including the granting of permits to use seed collectors. Thus, efficient management practices were accompanied by some sort of ownership, by which the artisanal community defended their grounds and promoted stock enhancement as in agriculture. Although there are several "similar" examples in other benthic shellfisheries, cultural perceptions, legal, political and economic factors, degree of knowledge about the resource and even the geography of each coastline are different in each case, and thus there is not a magic rule to apply to provide successful enhancement results (Castilla and Defeo, 2001).

The sessile or sedentary nature of shellfishes favours the allocation of TURFs to individuals or groups on specific grounds. However, shellfish have marked spatial variations in abundance, so that some rationale must be found to allocate ownership or access rights as a function of the relative productivity of each area. Priority might be given to those fishers with longer activity in the fishery. Grounds might be transferable according to the performance of each fisher, which could be evaluated on a communal basis. An example of this is given by Seijo (1993) for the collectively managed spiny lobster fishery of Punta Allen, Mexico. This isolated coastal community in the Yucatan Peninsula is a collective voluntary organization that performs informal privatization of fishing grounds to sustain resource rent over time. The temporary (renting) or permanent (selling) transfer of individual rights to fishing grounds involves simple artisanal transactions: a specific payment is made according to ground size and its perceived relative productivity in previous years. Permanent transfer of fishing grounds between cooperative members may include monetary payments and/or barter transactions. A variety of penalties imposed by strong community rules and self-policing strategies assure a relatively stable development of the community. Stock enhancement in this context is promoted through the use of artificial habitats or "sombras", so that each fishing ground can be subjected to a variety of enhancement initiatives as a result of a community-based management scheme (see also Miller, 1994 and references therein). Similar concepts were proposed by Brand *et al.* (1991) for the pectinid fisheries of the Isle of Man: the success of large-scale transplantations of spat depends on the voluntary cooperation of the local community (see example below). However, enforcement becomes more difficult as the number of fishers, landing sites, and regulated species, increases. The success of the earlier examples basically relies on the relative isolation of the local communities and the restricted scale of the territorial permit, which in turn favours the implementation of self-policing strategies and voluntary cooperative action to avoid the infringement of rules and free-rider behaviour (Seijo, 1993).

Jamieson (1986) explained the rationale behind fishery regulations on invertebrates in British Columbia, Canada, classifying them by management concern (Table 8.1), which illustrates the many and varied practical, theoretical, and administrative issues that require attention from fisheries scientists in a varied invertebrate fishery:

8.3 Co-management

High enforcement and policing costs attenuate efficient resource allocation over time. In this context, the legitimization of the participation of fishers in the management process is seen as

the only way to promote compliance with regulations (Castilla *et al.*, 1998). In contrast, minimum management controls need to be evaluated periodically to ensure that the privileged group is making socially acceptable use of the resource. In this context, effective control could be achieved through the joint management by fishers and government, *i.e.* co-management. Here, resource users must ideally be incorporated at various levels into management decision-making through active consultation within those bodies responsible for management. Moreover, the local community should be authorized to enforce and assure (through internal rules and self-policing strategies) that management tools (gear regulations, quotas, closed seasons/areas, harvest limits) are being respected, and free rider behaviour minimized or avoided. Hanna (1994) briefly documented the case of the Maine soft-shell clam *Mya arenaria* as a typical example of co-management, in which the State and the coastal towns share the control of management. “The local communities with approved shellfish conservation programmes are authorized to design and implement management plans which set harvest limits, establish open and closed areas, establish the rules of access and enforce regulations” (Hanna, 1994: p. 234). This is critical when an active enhancement of productivity is projected.

Table 8.1 Rationales behind invertebrate fisheries regulations: the British Columbia example (from Jamieson, 1986).

	Management concern	Management measures	Species
1	Conservation	- Area quotas and seasonal closures - Gear restrictions	- Abalone, geoduck, shrimp (trawl), sea-urchin - All species
2	Allocation	- Vessel quotas	- Abalone
3	Stability of return	- Minimum size limit - Limited entry - Area quota - Seasonal closure	- Abalone, intertidal clams, crabs, sea urchin - Abalone, geoducks, horse clams, shrimp (trawl) - Geoduck - Prawn, shrimp (trap)
4	Conflict over grounds/ resources	- Area closures - Quotas - Seasonal closures	- Shrimp (trawl and trap), euphausids - Euphausids - Euphausids
5	Processing economics	- Seasonal closures	- Crab, sea urchin
6	Social factors	- Closed areas - Human health closures	- Abalone, clams octopus, crabs - Horse clams, intertidal clams, goose barnacles
7	Administration	- Closed areas - Fishing log completion - Research study areas - License requirements	- Abalone - Abalone, geoduck, shrimp (trawl and trap), octopus, goose barnacles, euphausids, sea cucumber, sea urchin - Geoduck, shrimp trawl, sea cucumber - (Almost) all species

While it is generally accepted that “co-management is an effective means of minimizing conflict in fisheries management and recirculating the benefits of effective management back into the local communities” (Noble, 2000), the development of this strategic institutional structure (*sensu* Orensanz and Jamieson, 1998) has been slowed by institutional constraints. Institutions are important prerequisites to effective co-management, and form the substrate from which decisions are made and collective action is taken. In a context of uncertainty, it is imperative to develop and establish a legal framework formalizing community responsibility in the management process. This should preserve traditional rights of use and access to the resources, but also add modern elements of fisheries management. Thus, once this strategic institutional arrangement is in place, additional, risk-averse, precautionary management schemes could be gradually introduced (Castilla and Defeo, 2001).

Much attention has focused around co-management as a process for realizing effective fisheries management. In the light of the current dangerous state of many shellfish resources, a reasonable attitude to conduct enhancement initiatives is to “close the fisheries management cycle” (see Chapter 2) by involving the fishers communities in designing stock-rebuilding programmes. Adopting the traffic light approach (*sensu* Caddy, 2002) to management potentially restores to the local communities the necessary range of data for informed decision-making, and more control over their traditional fishing grounds (Castilla, 1994; Hanna, 1994). The absence of co-management practices supported by appropriate legislation, and guided by reliable data is a critical factor that has led to the collapse of coastal small-scale benthic fisheries around the world. Scientists and policy-makers must learn from the various forms of community-based management followed for centuries by traditional fisher communities, and not assume that traditional approaches must be discarded, as opposed to updated. Frequently this is the opposite approach to that followed by fishery management bodies over the past 30-40 years. Local communities need to agree on appropriate responses when an increasing number of indices move beyond their LRPs into a “red” category (Annex I), which justifies closure of fisheries for stock-rebuilding purposes. Once this agreement is achieved, local fishers must participate actively in the implementation and control and surveillance activities, and the management measures needed to restore stocks to health. They should know what indices, what values of indices, and why, should lead to prompt action by stakeholders. Thus, co-management of fisheries is likely to provide the context for applying traffic light control systems, since top-down management approaches arguably have not worked (Castilla and Defeo, 2001). The fruitful interaction among fishers, policy makers, scientists, extension workers and politicians should provide a comprehensive course of action in scope, including cooperation in setting up easily understandable and reactive mechanisms to respond to overfishing indicators (Caddy, 2002).

Castilla and Defeo (2001) concluded that co-management constitutes an effective institutional arrangement by which fishers and managers could interact to improve the quality of the regulatory process and to sustain Latin American shellfish over time. The authors also highlighted the advantages of institutionalizing co-management procedures for stock-rebuilding purposes. The most important factors supporting this statement concern the development of enhancement programmes, and were summarized by the authors as follows:

1. A comparatively reduced scale of fishing operations and well-defined boundaries for each management sub-unit is required. Whenever possible, the scale of the management unit should ideally be that corresponding to the range of activities of the local fishing community,

thus facilitating the application of co-management, as demonstrated by the successful Chilean examples documented in this text.

2. Allocation of institutionalized co-ownership authority and responsibility to fishers in shellfish management decisions and actions concerning stock enhancement programmes needs to be explicit (Pinkerton, 1994; Gimbel, 1994; Pomeroy and Williams, 1994; Mahon *et al.*, 2003). Shellfish co-management needs to be institutionalized within a legal framework including well-defined fishers' rights, responsibilities and a clear identification of the community role in the management process. Participation of fishers will improve shellfish management: and the perception of ownership by fishers is the most important focal point determining co-management success (Castilla, 1994). Informal government recognition is not enough for allocation of TURFs or other fishing rights and ad hoc implementation of co-management systems. Several examples which included the voluntary participation of the fishers in enforcing regulations became unsuccessful years later, due to changing management policies (Defeo, 2003). Fishers felt themselves unprotected under an uncertain management environment, and changed their long-term, "sustainable" perspective on the fishery to a short-term, profit-maximizing behavior. The legitimacy of co-management and the perception of ownership by fishers should override or constrain expectations of the benefits to be derived from shellfish extraction. The assignment of fishing grounds to well-defined groups of fishers represents the recognition of the role of local communities in conservation and management.

3. Communal ownership encourages cooperation among fishers and improves surveillance of regulations, and reduces information and enforcement costs. Well organized fisher communities take good care of their assigned fishing grounds by preventing illegal extractions. This has had major repercussions on yields, product quality (individual sizes far above the minimum legal size permitted) and economic returns (Castilla, 1997). In some cases, the relative isolation of the community and the restricted scale of the territorial permit, favor the implementation of self-policing strategies and a voluntary cooperative action to avoid infringement of rules (Seijo, 1993). Together, these may significantly increase yields from enhanced stocks. Thus, fishers play an outstanding role in the implementation and surveillance of regulations, and the reduction of enforcement costs. This is of utmost importance, because it has been widely documented that, at least in developing countries, operational and quota-based management measures are extremely difficult to enforce and are beyond the finances of most management agencies. Moreover, reliable information flowing from fishers to scientists implies lower monitoring and enforcement costs, and provides fine-grained signals about resource status, which allows spatially explicit management measures (e.g. ground closures) to be established. Implementation of regulatory measures in a co-management context provides an incentive to fishers to adhere to and get involved with enforcing regulations, thus reducing the probability of occurrence of free-riders and illegal fishing (Defeo, 1989; Castilla, 1994).

4. Improvement of the quality and quantity of fishery information results from cooperation and improved information flow. Cooperation among scientists, fishers and managers exponentially increases the quality and quantity of fishery information, with clear management connotations (McCay, 1989), reducing the misreporting and uncertainties inherent to stock assessment. Information on the spatial dynamics of fishing effort and economic indicators (fixed and variable operating costs, ex-vessel species prices) has also been improved (Defeo and Castilla, 1998). Cross-fertilization between large-scale and long-term field experiments and co-management has a synergistic effect on the acquisition of

knowledge on the dynamics of the stock and the fishery (Pinkerton, 1994, 1999; Jentoft, McCay and Wilson, 1998).

5. Existence of community fishery traditions needs to be conserved. Fisher communities that have taken the responsibility for managing coastal shellfish resources, often build upon old or traditional roots (Castilla, 1994; Johannes, 1998). Ancient collective organizations often found in coastal shellfisheries include strong community rules and voluntary self-policing tools. Small groups with clearly defined members and leadership encourage cooperation, and promote the identification and exclusion of non-contributing users. Thus, trust among fishers and group cohesion is necessary conditions to improving co-management (Pomeroy and Williams, 1994).

6. Allocation of TURFs has proved an effective tool where geographically restricted harvesting occurs. When accompanied by co-management, allocation of TURFs ameliorates the weaknesses of enforcement regulations, diminishing information and enforcement costs (Mantjoro, 1996). In these cases, fishers play an outstanding role in the implementation and surveillance of regulations, improving the status of shellfisheries, increasing abundance, individual sizes of the specimens and the economic benefits derived from the enhanced stocks (Seijo, 1993; Castilla, 1994, González, 1996; Castilla *et al.*, 1998). Given the current state of most benthic shellfish stocks around the world and the continuing declining trend or collapse of many resources, effective management is likely to be a hybrid of traditional and modern arrangements. The community may allocate extraction quotas, access rules and self-policing strategies among fishers, whereas the government should retain the authority to modify the management plan by setting or modifying operational management measures (e.g. legal sizes, closures, gear regulations: Castilla and Defeo, 2001). The local relevance of a given mix of management strategies will depend on the kind of resources to be enhanced and managed, and the nature of the ecosystem inhabited by the species. Some pros and cons of different management schemes in shellfish populations are discussed in Chapter 2.

7. Co-management improves the results of enhancement experiments and the application of spatially explicit management tools (e.g. reproductive refugia, rotation of grounds, natural restocking). Management experiments without the help and advice of fishers are nonsense. The joint venture into enhancement experiments between fishers, scientists and managers promotes a better understanding of the biology of shellfish stocks and leads to adequate administration of wild resources and/or habitats for conservation and management. Experimental management units (e.g. involving TURFs), with dissimilar effort levels in each, could be the subject of a rigorous experimental design in which the spatial and temporal coupling of operational management tools (i.e. management redundancy) could be evaluated through specific “area-season windows” (Caddy, 1999a) to consolidate a sustainable management framework for shellfish. Participation of fishers is of critical importance in assuring unbiased reporting of results and implementation of an up to date information flow from fishers to scientists, as well as in enforcing regulations through their participation throughout the enhancement experiment.

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ANNEX I

A BRIEF OUTLINE OF THE TRAFFIC LIGHT METHOD

A precautionary management framework was proposed by Caddy (1999b, c), originally intended for use in data-poor situations and where age-reading methodologies were impossible (in particular, for shrimp, and other invertebrate populations, of the North Atlantic Fisheries Organization, NAFO). This was subsequently developed further and applied in eastern Canada to groundfish management (see especially Halliday, Fanning and Mohn, 2001). For practical applications on shrimp stocks, see recent research documents of DFO Canada (e.g. Koeller *et al.*, 2000).

As originally proposed, this method was seen as a development of the limit reference point approach whereby multiple measures of biomass, fishing mortality, productivity, fleet performance etc, were each considered “Characteristics” of the fishery, and measured by one or more indicators on an annual basis. This approach could simply be to provide an index of stock status, as used by Koeller *et al.* (2000). A further development could be to develop a Traffic Light Precautionary Management Framework (Caddy, 2002) based on reliable indicators, with minimal use of modelling to define RPs; thus, the traffic light (TL) approach could be integrated into a Control Rule for use in routine fishery management, or in a stock recovery plan. Judgements as to which indicator to choose, and what value of the indicator should correspond to a Limit Reference Point, could be arrived at by analysis and/or by “oracle” sessions between experts and stakeholders. These sessions could review past annual values of the indicator from historical performance, especially during the declining phase of the fishery, (which presumably preceded the present need for a management recovery approach). This should help identify the conditions/indicator values in years immediately preceding stock collapse to below an agreed dangerous level. To simplify, each indicator value is then assigned a colour, separated by cut-off values, which may be considered equivalent to reference points, but which were referred to by Halliday, Fanning and Mohn (2001) as “traffic light boundary points”.

In Halliday, Fanning and Mohn (2001) several different approaches to defining colour boundaries were explored. The “Strict” cutoff approach proposed in Caddy (1999b, c), proposed a two-colour system with a sharp transition between green and red for each of a multiplicity of indicators. The management response would then be graduated in intensity depending on the proportion of indicators which showed as “red”. More elaborate “Ramp” and “Fuzzy” systems were explored by Halliday, Fanning and Mohn (2001), in which three colours were used, and they allowed the value of an indicator to progressively merge between adjacent colours (e.g. 30 percent yellow; 70 percent red), in a way that avoids the need for abrupt judgements and loss of information (for more details see Halliday, Fanning and Mohn, 2001).

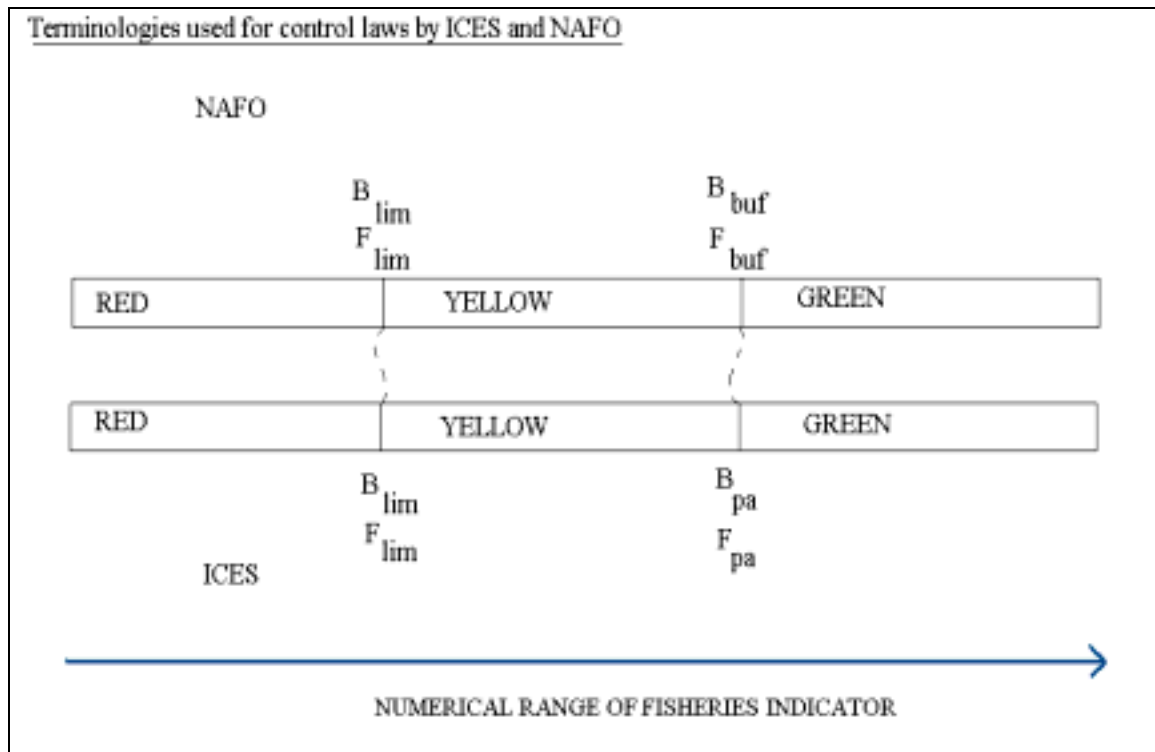


Figure A.1 The range of an indicator and boundary point nomenclature usage in two fisheries organizations, and the colour values assigned to each segment of the indicator range. See text for details on abbreviations.

As suggested by Figure A.1, two boundary points may be envisaged; between green (safe) and yellow (uncertain) conditions, and between yellow (uncertain) and red (unsafe) conditions. This approach is directly analogous to the definitions of “decision points” in a fisheries law, such as were suggested for management purposes by two fisheries bodies, ICES and NAFO, (see Figure A.1). As noted in Caddy (1998), terminologies such as “buf” (buffer), “lim” (limit), “pa” (precautionary), and “tr” (target) as in B_{lim} , B_{buf} , B_{pa} , B_{tr} , F_{tr} , F_{lim} , F_{buf} , F_{pa} , and more generally, the terms TRP (Target reference point) and LRP (Limit reference point), do not of themselves define a specific level of fishing mortality or biomass. What they do represent, are decision points in a Harvest Control Rule or Law, such as is shown in Figure A.2. These RPs will then need to be defined operationally from a precautionary point of view. The point we were making above, was that these “traffic light boundary points” should primarily be values agreed on by the fishing industry and managers, based on their past experience of the fishery, if (as seems likely for most invertebrate stocks), such boundary points cannot be simply derived from a population modelling procedure. Thus, a boundary point in a TL approach, could be based on expert judgement or experience, instead of, (but not exclusive of) analysis, or can represent a previous state of the system which by common opinion marked the onset of unfavourable conditions, such as B_{1966} , where 1966 was the year when conditions in the fishery started to deteriorate for example.

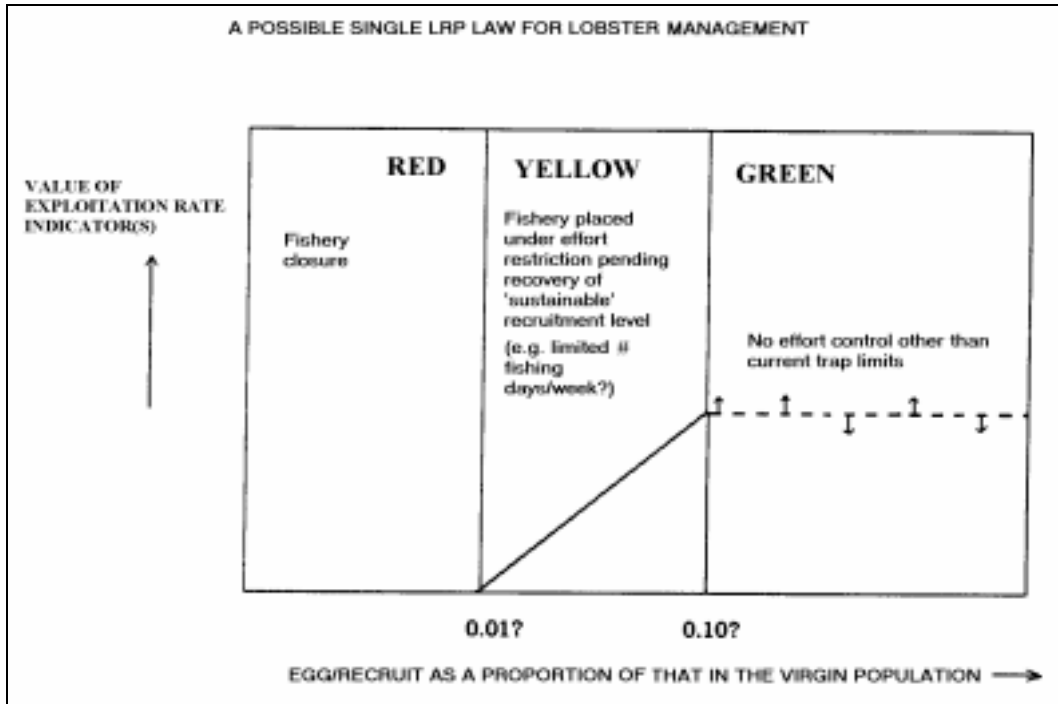


Figure A.2 Illustrating a hypothetical fishery control law for *Homarus americanus* in which a single factor, the egg/recruit for the population decides on the overall exploitation rate to be exerted.

Thus, B_{LIM} could be defined as a proportion of the virgin biomass B_0 (e.g. $0.2 \cdot B_0$), the frequently chosen (if arbitrary) minimum level of biomass it is felt it would be unsafe to allow the stock to drop below. F_{pa} could be defined for example as $F_{0.1}$, a level of fishing mortality defined as “one tenth of the initial rate of increase in yield per recruit with fishing mortality” (Gulland and Boerema, 1973).

Another point that could be made here in relation to the TL system as originally conceived, is that it was seen as integral to a fisheries control law, and not just a way of presenting the state of a resource. Perhaps this makes more explicit the need for judgement in applying fisheries science to management, instead of the former illusion that science was occupied with “quantitative analysis” and judgement was an activity reserved solely for managers! The judgement as to appropriate control points in a fisheries law will require input from “stakeholders” with the technical assistance of scientists, and this is in essence what the “co-management approach” is all about. As noted by Halliday, Fanning and Mohn (2001), the assignment of boundary points to indicators in the TL approach can be made precautionary, in that a wide range of indicators can be incorporated, making for some necessary redundancy in information inputs. This approach also allows an “objective-based” management approach to be developed, whether this is aimed at controlling fishing under “normal” stock conditions so that “normal” stock conditions prevail, or stock rebuilding, in that the definition of boundary points, their weightings, and their use in the Control Law, is cleared with stakeholders, and corresponds to some economic or ecological optimum. One immediate advantage of this system for communicating with the fishing industry is ease of understanding, and the sense of urgency and immediacy the colour coding provides.

Some definitions of terms used in the TL system

Elements of a fishery were conceptualized by Halliday, Fanning and Mohn (2001), as having “attributes”, such as biomass, growth rate and the mortality due to fishing.

“Attributes” of the population or fishery are monitored by one or more indicators. For example, mean weight per tow of a research vessel survey is a “relative” indicator of population biomass. A normalized summation of two or more indicators for may be referred to as measuring a system “characteristic” of the stock, such as: (a) abundance, (b) production, (c) fishing mortality and (d) ecosystem/ environment. (Note that conventional stock assessments usually only deal with (a) and (c), while the TL system potentially allows much wider ecosystem, or even socio-economic, contexts, to be incorporated into a fishery control law).

A “template” for outlining a TL Indicator

Halliday, Fanning and Mohn (2001) suggest some aspects of indicators which require description:

- data sources, ranges, transformations or smoothings and software used in calculation
- statistical properties (variance, bias, skewness), transformations used, consistency with other estimators
- Interpretability in terms of the characteristic measured
- Sensitivity to changes in stock status

The overall value of an indicator may be scaled relative to other indicators by a weighting factor, so as to reflect the importance of the attribute being measured, or the proven reliability of the indicator. No firm rules have been derived as yet for what in effect is an empirical results-based system, but for example, two indicators derived from the same data source should perhaps each be given a weighting of 0.5, compared with a single indicator based on an independent data source, given a weighting of 1.0.

In general, we start by defining the yellow-red boundary as corresponding to the onset of dangerous conditions, using one of the criteria employed for deciding on LRPs (see e.g. Caddy and Mahon 1995, or examples in the above Table A.1). In judging where to place the green-yellow boundary, one approach is to choose a value taking into account an estimate of the variance of the data series the indicator is based on. That is, choose a boundary point that corresponds to an acceptably low (e.g. five percent), probability that the indicator value, by error, will exceed the LRP established at the yellow-red boundary. An assessment of the performance of an indicator and its boundary points should be carried out periodically, and checked against new findings on resource status, and on those critical factors influencing the risk of stock collapse.

Table A.1 An example of some considerations that might influence the choice of indicators and their LRPs for the fishery for the lobster *Homarus americanus*.

Indicator of:	Level indicator	Change indicator	LRP Triggered by:
Recruitment:	Annual recruitment versus long term average: (R_T/R_{AV})	Annual trends in CPUE of “shorts” in commercial traps	$R_T < R_{AV}$ for three successive years?
Exploitation rate: (Ratios of numbers in successive moult groups should change with F)	Overall mortality rate indicator as a log ratio of numbers per moult group: [$Z_m = - \ln (N_{m+1}/N_m)]$	Slice size composition using moult increments to estimate approximate numbers of each moult group (m) in the catch?	Define a limiting value for overall mortality rate per moult group
Exploitation rate: (Ratio of mature males/mature females should decline with exploitation, where berried are females returned and survive)	Estimate sex ratio of mature males/mature females	Examine trends in ratio: (# mature males/ # mature females).	Decide on a value of this ratio below which mature females would have low probability of finding mates within their typical size of individual territory?
Exploitation rate: (Calculate mean number of eggs/size on berried females in the commercial catch)	Smaller animals are lower fecundity – Estimate number of eggs produced per female/mean CPUE	Examine trends in mean individual fecundity in commercial catch.	Set a minimum percentage for females in the catch of a size that should have spawned at least twice
Prevalence index: (Has the species range decreased?)	Percent non-zero sub-areas in original low exploitation meta-population range, as established from surveys or geographically displayed log book data	Shrinkage/expansion of range can be a useful indicator of population health when abundance data are doubtful.	Set percent of original “pre-decline” stock range or area as LRP
Economic data: (As catch rate declines, revenue per trip (NR) falls to a level where costs (ΣC) are not covered)	Estimate $NR/\Sigma C$ (= Net revenue per cost of a trip)	Examine trends in NR through season and annually.	Set LRP at value of $NR/\Sigma C = 1.0-1.05$?

A broad review is provided of factors relevant to enhancing populations of invertebrate resources and methods promoting their recovery by natural recruitment, restocking or habitat restoration. The review focuses on the biological, technical, environmental, economic and biological factors affecting the feasibility of restoring or enhancing productivity of commercially valuable local invertebrate populations. Three categories of enhancement activity are recognized: restoring or enhancing stocks by conventional management methods, transplanting or seeding, and the use of juveniles produced from collectors in the wild or from hatcheries. Some guidelines are provided on issues related to enhancing recruitment, site selection, experimental closures and ecosystem considerations including predator control, as part of a stock management and enhancement programme. Ownership and co-management issues, and the necessary decisional rules for successful management, are discussed, as well as how to reconcile the enhancement programme with other uses of the coastline. Spatial and geographical considerations are addressed, including allocation of areas for enhancement, rotational harvest schemes, use of refugia for protecting juveniles and the spawning stock, and the impact of the use of coastal zones for other human activities.

