

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 harvesting 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.

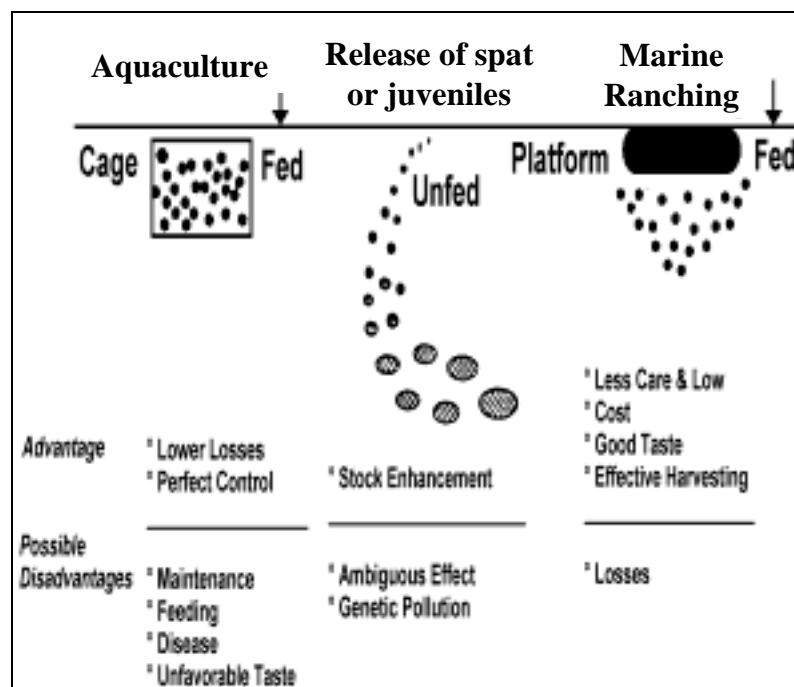


Figure 1.2 Illustrating the functional transition between cage culture (aquaculture) through stocking of public waters by releasing juveniles collected in the wild or produced in hatcheries, to marine ranching within exclusive access (after Masuda and Tsukamoto, 1998).

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.

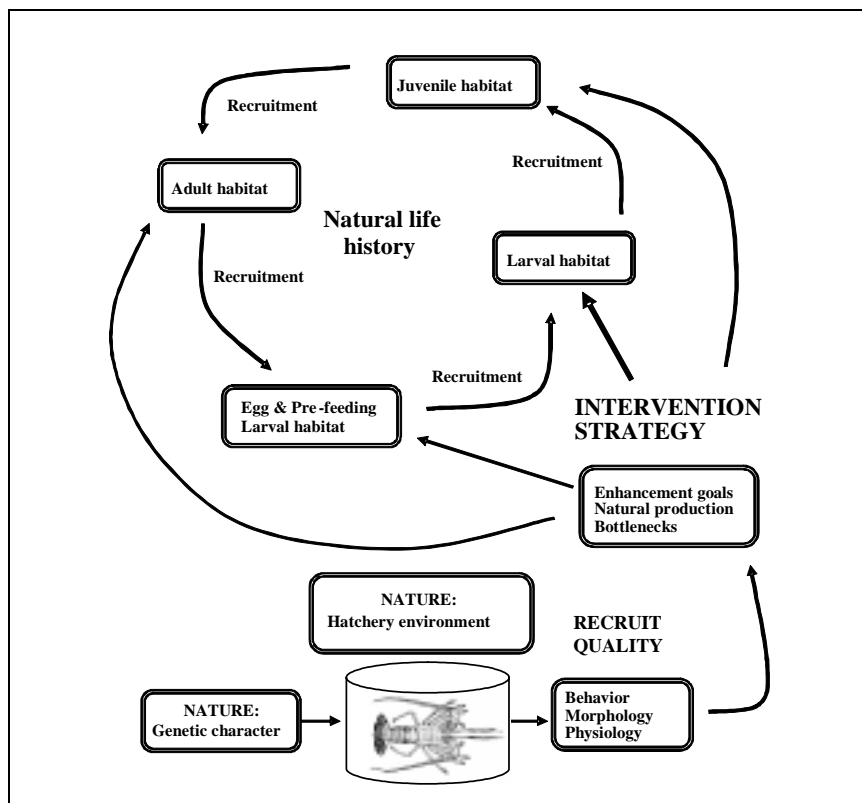


Figure 1.3 A generalized scheme for invertebrate stock enhancement using hatcheries (after Olla, Davis and Ryer, 1998).

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*.

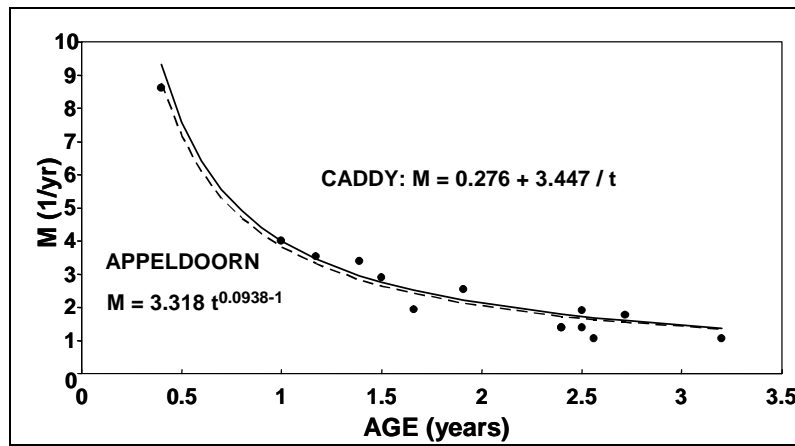


Figure 2.1 Appeldoorn (1988) and Caddy (1991) models fitted by non-linear least squares to M -at-age data for the queen conch *Strombus gigas*. Data in Appeldoorn (1988).

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).

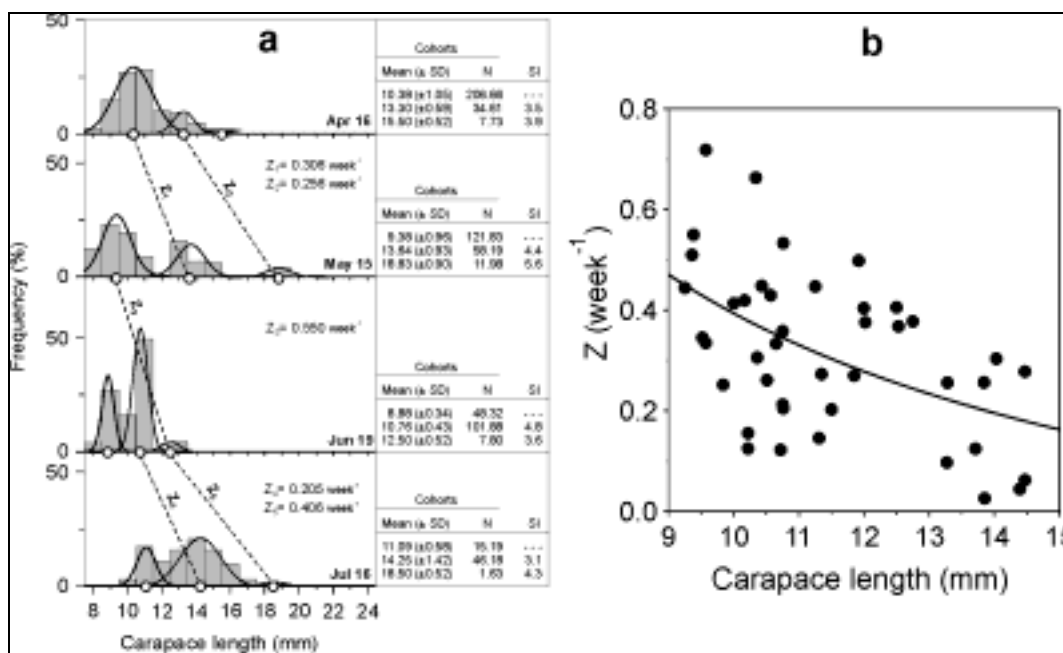


Figure 2.2 (a) LFDs of selected sampling dates (April-July 1997) for *Farfantepenaeus brasiliensis* of Celestun lagoon (Mexico), with separation of cohorts by NORMSEP. Mean (\pm SD) carapace length (CL), cohort size (N) and the separation index (SI) of contiguous cohorts are shown. Dashed lines link 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.

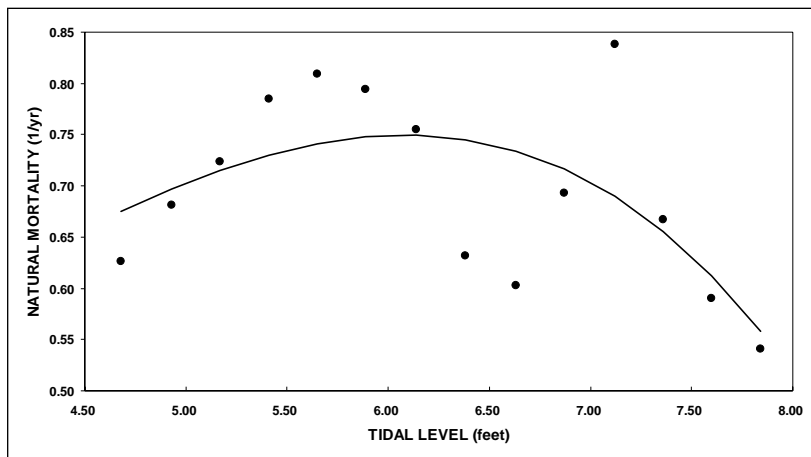


Figure 2.3 Bivariate distribution of M and the corresponding tidal level for the Manila clam *Tapes philippinarum* in Puget Sound, Washington (after Hall, 1983).

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.

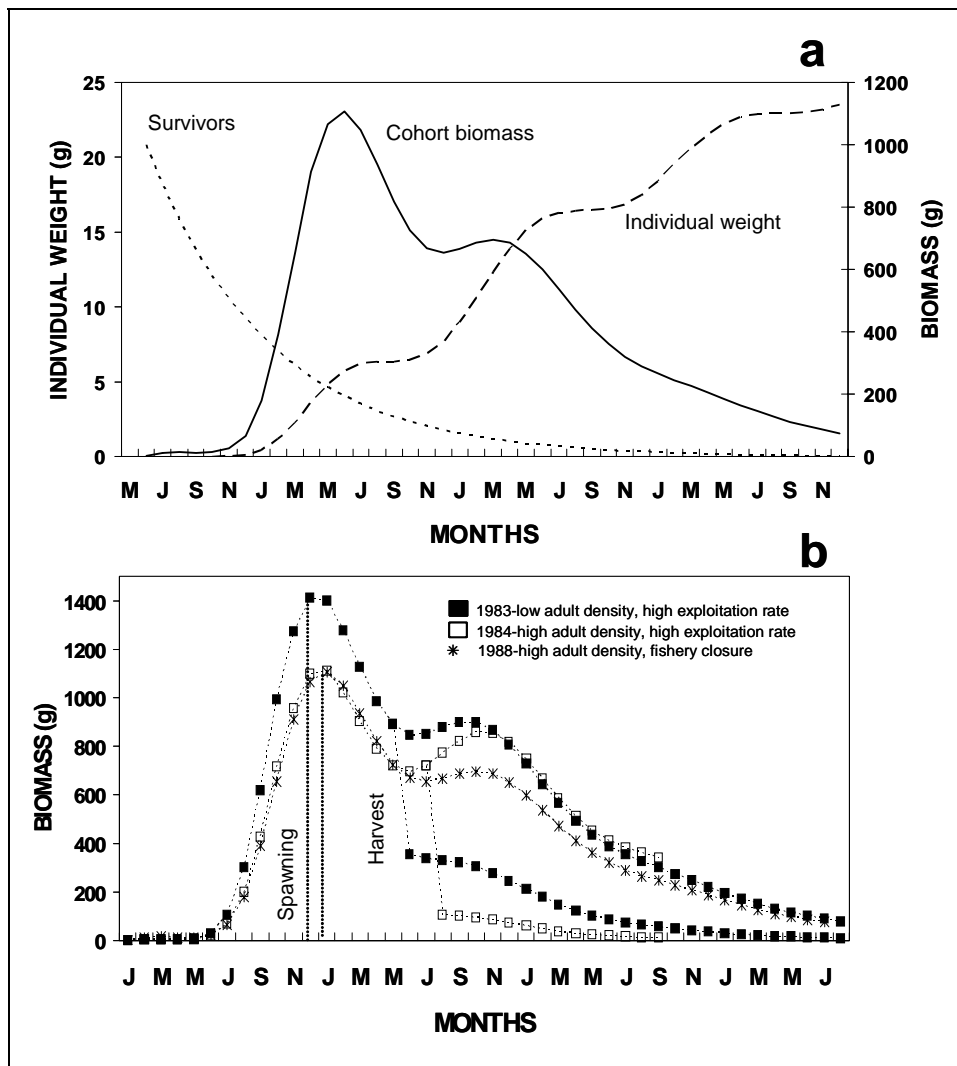


Figure 2.4 (a) Monthly trajectories of growth in weight, decline in numbers and biomass projections for an idealized biomass projection based on monthly predicted lengths estimated by seasonal growth curves of the generalized von Bertalanffy model, a length-weight relationship, natural and fishery mortality 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).

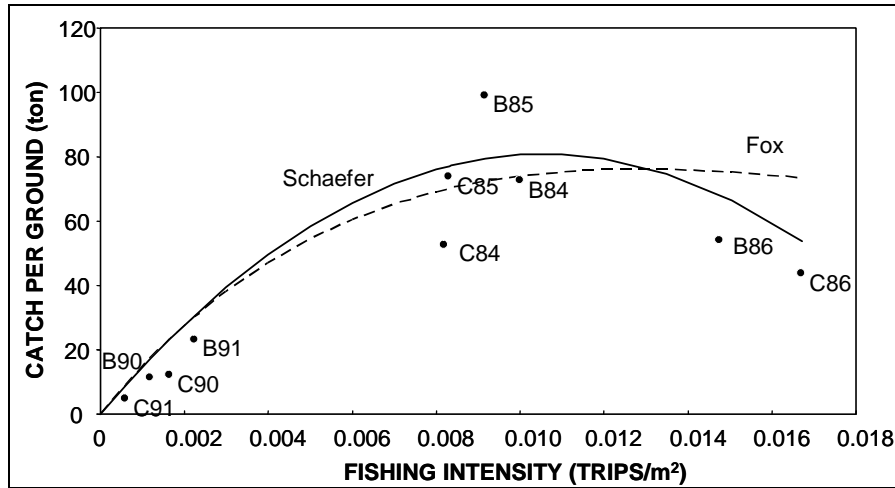


Figure 2.5 Composite production models (Schaefer and Fox) for a clam fishery in Uruguay, from fishing grounds denoted as B and C (comparable in terms of productivity) and years 1984-86 and 1990-91. (Data from Defeo, unpublished).

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 f_{\max} 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 Ducrotoy *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.

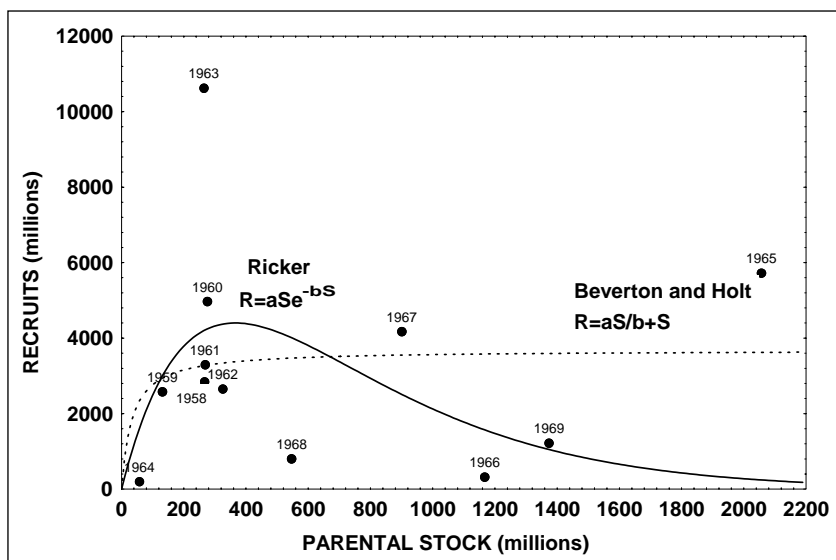


Figure 2.6 Stock-recruitment relationships for the cockle *Cerastoderma edule* of Burry Inlet (data from Hancock, 1973). Ricker and Beverton-Holt stock-recruitment relationships are presented for comparative purposes.

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.

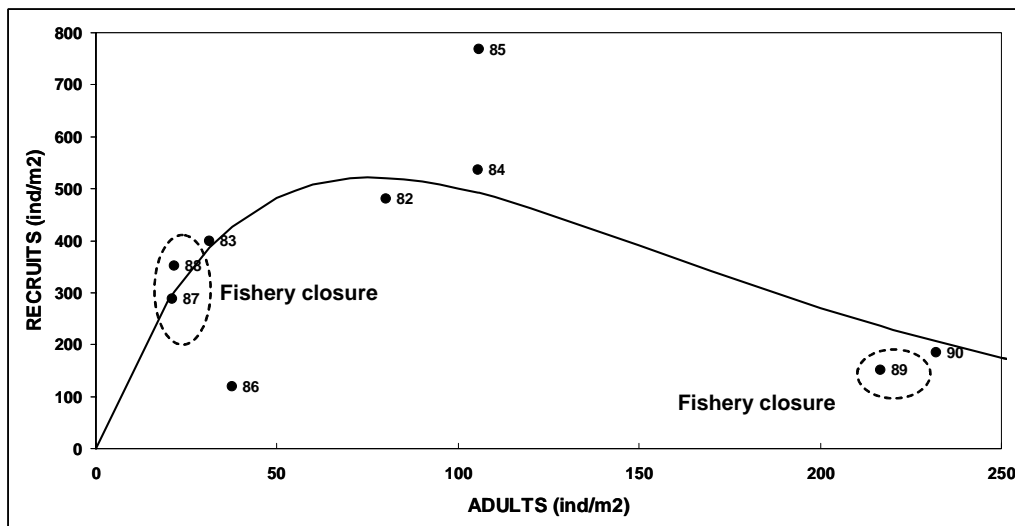


Figure 2.7 SRR for the yellow clam *Mesodesma mactroides* of Uruguayan beaches. The fishery was closed between 1987 and 1989 (highlighted in the figure). Detection of strong overcompensation was possible because of the rapid population build-up as a result of the experimental closure, and recurrently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

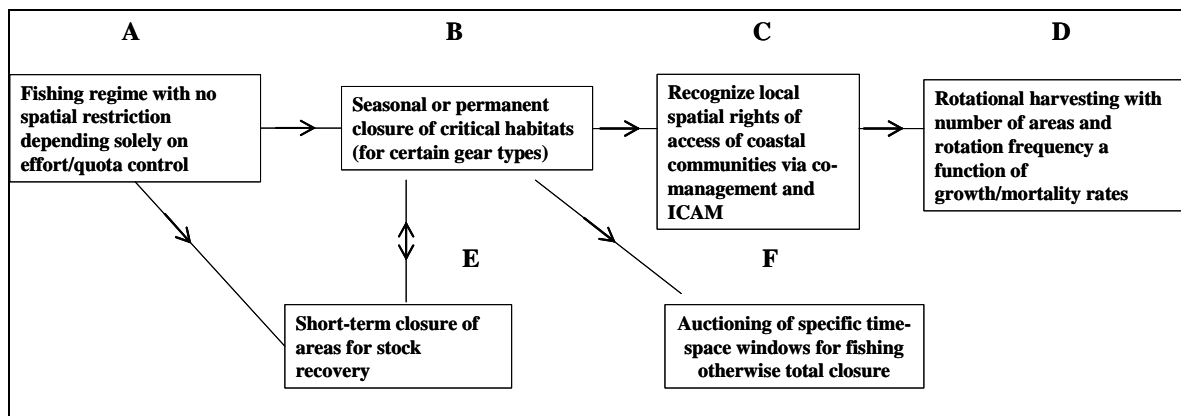


Figure 2.8 Illustrating progressive introduction of spatial components into a harvesting scheme for shellfish populations.

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.

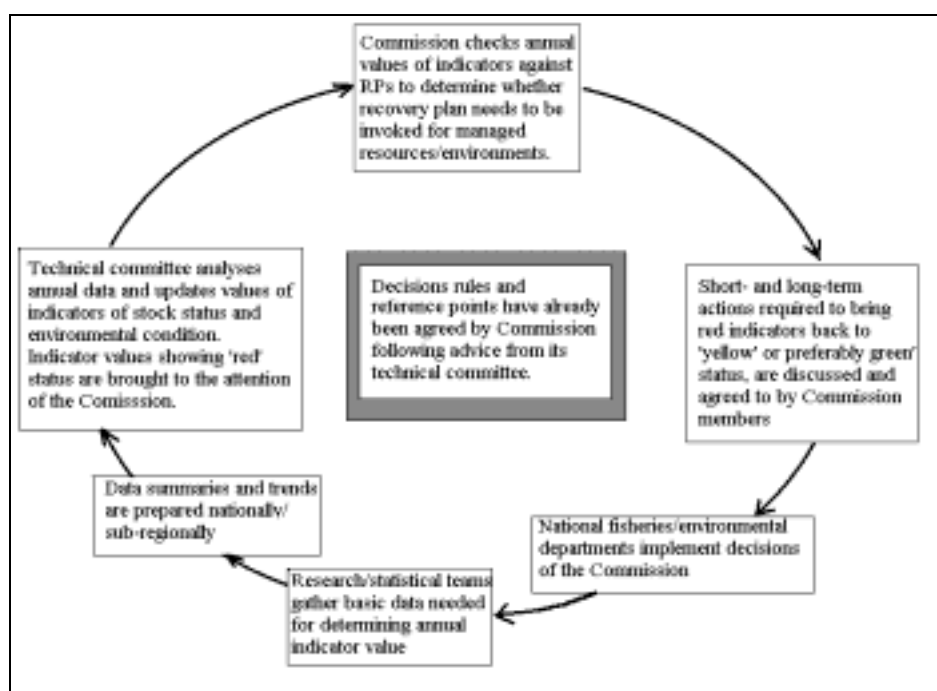


Figure 2.9 An idealized fisheries management cycle in which data on selected indicator values are collected and analysed annually by a technical working group, and values indicating dangerous conditions brought to the attention of managers and stakeholders in an overview management body referred to here 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 (*Mercuria 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 $\text{SPR} \geq 1/s^*$, 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).

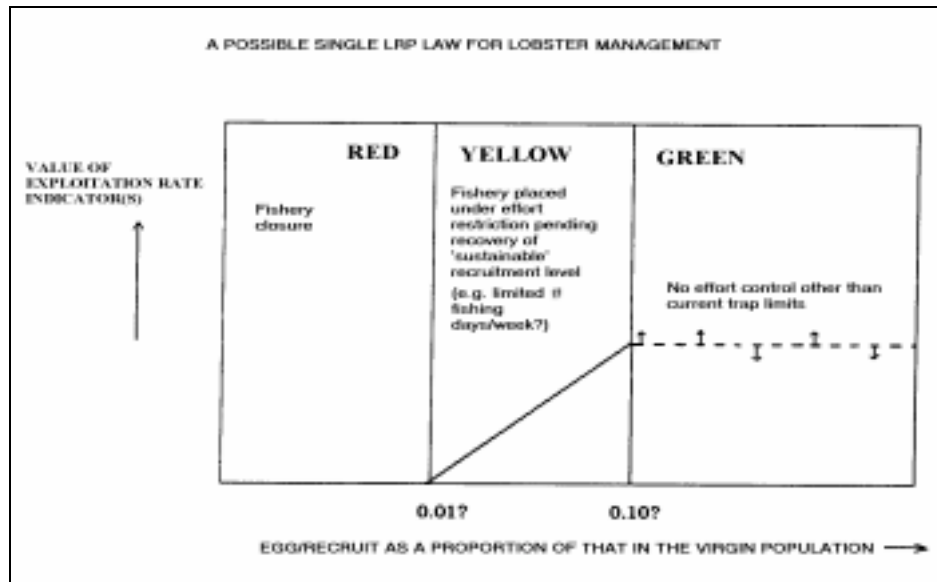


Figure 2.10 A hypothetical fishery control law for a lobster fishery, expressed in terms of its calculated egg production, as a fraction of that in the virgin population (horizontal axis). The fishery is placed under progressively more severe controls of exploitation rate (the descending ramp) until 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).

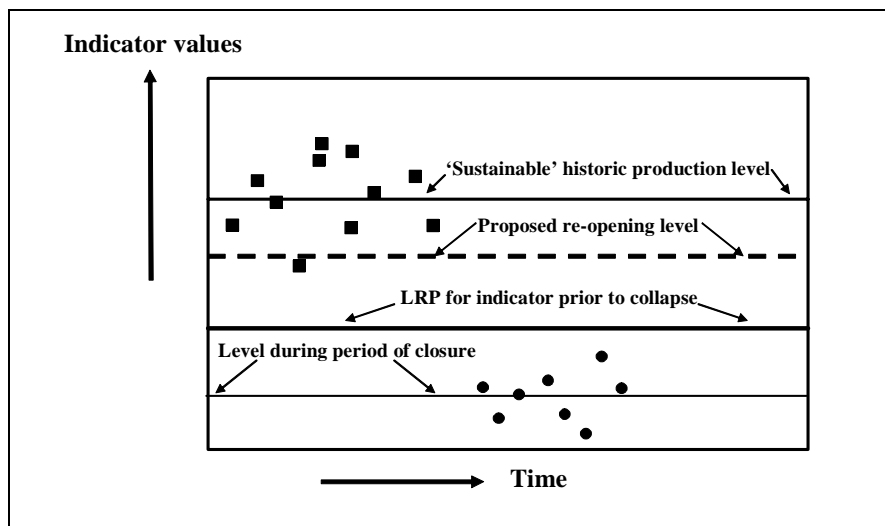


Figure 2.11 After a population collapses below a LRP set earlier, based on the mean value of the indicator during earlier sustainable production, the fishery is closed once the minimum value specified in some harvest control law is infringed. Reopening the fishery should not occur until the stock (and 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