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Population dynamics and resilience of green abalone *Haliotis fulgens* in Isla Natividad

Ph. D. Thesis
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Chapter 1

Introduction

1.1 Marine reserves as a tool for sustainable fishery management

Fishing the ocean is one of the most significant human enterprises directly benefiting from the provision of renewable resources of our seas. In 2009, marine wild fisheries and aquaculture supplied the world with about 100 million tons of food fish; of this total, aquaculture accounted for 20 percent. Total capture of marine fish reached 90 million tons in 2009, and in 2008, total world trade of fish and fishery products reached a record value of US $102 billions(FAO, 2010).

Unfortunately, however, many fisheries worlwide are not sustainable. Nowadays, it is estimated that about half of the stocks (53 %) is fully exploited and therefore producing catches that are at or close to their maximum sustainable limits, with no possibility for further expansion (FAO, 2010). Another 32% is either overexploited, depleted or recovering from depletion with no possibilities in the short or medium term of further expansion and with an increased risk of further declines and need for rebuilding. Only the 15% of the stock groups remain underexploited or moderately exploited (FAO, 2010). Furthermore, the rate of fisheries collapses, defined as catches dropping below 10% of the recorded maximum, has been accelerating over time, with 29% of currently fished species considered collapsed in 2003 (Worm et al., 2006). The negative economic effects of overfishing are detrimental especially for small-scale artisanal fisheries that directly rely on marine resources for their livelihoods (FAO, 2010).

In recent years, Marine Reserves (hereafter MRs) have gained popularity on global scale as a management tool for marine conservation, fisheries management and other uses of marine environments (Halpern, 2003). Many papers, reviews and meta-analyses have documented the efficacy of MRs in terms of recovery of fish populations within their boundaries (Halpern and Warner, 2003; Halpern, 2003). Observed ecological benefits of MRs include increase in fish density, mean size and size at age, increase in species richness, reestablishment of trophic interactions and improvement in habitat quality (Micheli et al., 2004; Guidetti, 2006), and have been shown to be positively correlated with reserve size and age (Claudet et al., 2008). In addition, marine reserves are predicted to benefit fishermen by promoting the recovery of overexploited stocks and by contributing to fishery yields outside the no-take area through export of adults or larvae, i.e., through the *spillover effect* (Holland and Brazee, 1996). However, the implementation of MRs is often fiercely opposed by fishermen communities legitimately afraid of losing revenues as a consequence of the reduction of the fishing ground (Kellner et al., 2007). Hence, while the conservation benefits of MR implementation have been proven in a significant number of cases, the efficacy of MRs as fishery management tool is still a mattern of concern. To date, very scarce empirical data exist to unquestionably prove that MR implementation may also benefit fishery management. Therefore, the analysis of the potential fishery benefits of MRs is often carried out by using theoretical models of fishery dynamics. A number of theoretical papers have indeed shown that suitably designed MRs may possibly enhance catches in single own fisheries (Gaines et al., 2003). However, the majority of existing studies has often neglected the effect of factors such as population size structure and size-dependent fertility, which are crucial aspects in determining the success of a MR. In addition, predictions from theoretical models are still largely untested and more work needs to relate theoretical hypothesis to empirical case studies. In fact, although conceptual and theoretical models have the great advantage of representing a wide variety of phenomena and ecological processes that are valid under a broad range of hypothesis, the results of these simulation are not always able to provide operative solutions to real case studies. The efficacy of a MR, in fact, depends on many factors -*in primis* the species' life history and the adopted fishery regulations- whose range of variability cannot be comprised in a single model. Every marine protected area is a single unit in which the potential benefits to the species of interests should be analyzed through opportunely calibrated models, basing on the specific characteristics of the study sites and on the available data.

Focusing on real case studies- as the abalone fishery in Isla Natividad- can contribute to reduce the lack of empirical evidences of the socioeconomic effects of the establishment of a marine reserve. This case study represents an excellent model system to analyze the effect of fishing on community structure and exploring the efficacy of marine protected areas. The analysis of small scale fisheries - of which this is a very important reference example - is extremely important as small-scale fisheries represent about 90% of the fisheries around the world and make up aggregately 50% of the annual catches (FAO, 2010).

1.2 Significance of the study system

Abalones (*Haliotis* spp.) are long-lived, slow-growing marine mollusks which natural populations have undergone dramatic declines all over the world. Abalones' life history and ecological traits- high longevity, slow growth rates, poor adult mobility and limited dispersal- make them particularly prone to population decline (Roberts and Hawkins, 1999), and several abalone species are now endangered or considered species of concern (Rogers-Bennett et al., 2007; Micheli et al., 2008). Understanding how abalone species respond to external pressure, especially to fishing mortality, is essential to prevent a further decline of current exploited populations and possibly to rebuild collapsed stocks. To this end, it is crucial to understand if marine protected areas could be effective tools in forstering population recovery and in promoting a sustainable management of the fishery.

In Baja California (Mexico), the fishery of green abalone (*Haliotis fulgens*) and pink abalone (*H. corrugata*) is still a high lucrative enterprise, worth approximately US $ 20,000,000 per year. However, after the dramatic declines in the 70s and 80s, the current catch levels of both species remain low and great concern exists regarding the sustainability of the fishery (Ponce-Díaz et al., 1998). In Isla Natividad, which is representative of the community-level abalone fisheries operating in the entire region, fishermen established in 2005 two marine reserve closing around 8% of their fishing grounds with the aim of protecting remaining populations of abalone and hopefully to enhance their fishery yields. In particular, it is crucial for the fishing community to understand I) if larval spillover effect can compensate for the decrease in abalone catches due to the reduction of the fishing grounds; and II) if yes, after how much time are the benefits likely to occur.

Isla Natividad represents the ideal system to explore how different management strategies, including the establishment of marine reserves, likely affect the future trends of abalone stock and fishery yields. In fact, the island is representative of the community-level cooperatives operating in the entire Baja California peninsula, as habitat characteristics, diving techniques and fishery management systems are similar throughout the region. Moreover, in the last twenty years, the fishermen of Isla Natividad carefully recorded detailed data on catch, effort and size-frequency distributions, providing thus valuable time series to be used for calibrate a population demographic model. Finally, more recently, a number of fishery-independent surveys around the island have been launched to characterize abalone population in terms of abundance and size structure inside and outside the protected area and to assess the spatial scale of abalone larvae dispersal.

What can be learn about the population dynamics of green abalone- in particular regarding its vulnerability to fishing, its recovery potential and its response to protection- may be valid also for other species belonging to *Haliotis* spp. that still support commercial fishery around the world and for lesser-known long-lived marine invertebrates that are expected to become increasingly important fisheries in California (Rogers-Bennett et al., 2007). Management indication derived by this system may also help to devise sustainable fishing strategies for many invertebrate fisheries that are rapidly expanding worldwide with limited stock and ecosystem-impact assessments, and for which enhanced management attention is needed to avoid negative consequences for ocean ecosystems and human well-being (Anderson et al., 2011).

1.3 Objectives of the thesis

Aim of my thesis project was to evaluate the efficacy of two marine reserves in Isla Natividad (Mexico) as a management tool for the abalone fishery, focusing mainly on green abalone *Haliotis fulgens*.

The first step was to develop and calibrate a demographic for green abalone to describe its dynamic when subjected to exploitation. To do so, I defined a size-based matrix model that allows incorporating information on growth, size-specific survival and size-specific fecundities; specifically, I conducted an extensive literary review to estimate the corresponding vital rates. I also used fishery data collected by fishermen on Isla Natividad to calibrate the model, i.e.

to estimate density-dependence in the larval stage and size-dependent fishing mortality. In particular, through this model, I intended to:

- examine recent trends in abalone abundance in Isla Natividad and compare the current status of the stock with theoretical carrying capacity;
- compute informative fishery reference points such as maximum sustainable yield (MSY) and effort that guarantees the MSY to compare them with current and historical fishery yields and exploitation rates;
- assess the recovery potential of abalone populations and investigate the likely trend of abundances and yields under different exploitation scenarios.

Then, I intended to investigate if the reserves can increase, or at least maintain, the catch of abalones in the fishable areas through larval spillover, that is, a net export of larvae during the planktonic stage from the protected toward the unprotected zones. The expected increase in abalone abundance inside the marine reserves and the increase in mean size of sexual mature individuals, in fact, could positively influence the reproductive output of the population with an enhanced production of eggs, which, through larval dispersal, can contribute to the recruitment also in the areas outside the reserve. To explore the likely trends in abundance and catches of these commercially important species both in the short and in the long term, I extended the above-mentioned model formulation by defining a spatially-explicit version of the model. I assumed that the populations were distributed along a linear array of contiguous patches, representing the fishable and the protected blocks along the perimeter of the island. As abalones are sedentary species, I assumed that the connectivity between subpopulations was driven by the exchange of larvae in the planktonic phase. Dispersal kernels for larval movement were defined to describe movement probability between more or less distant patches. In particular, I wanted to:

- examine the likely trends in abalone abundance and fishery yields catches under different assumptions of reserve establishment (intended as percentage of fishing grounds protected and size of individual no-take areas);
- assess if larval spillover effect can compensate for the decrease in abalone catches due to the reduction of the fishing grounds, and, if yes, after how much time are the benefits likely to occur;
- analyze if the results in terms of population trends and fishery benefits are sensitive to the spatial arrangement of the reserve, that is, to the level of overall protection (%) and to the size of individual reserves.

1.4 Outline of the thesis

The thesis is organized as follow:

In chapter number II, I presented a review of the major anthropogenic impacts occuring in the marine environment, with a particular attention devoted to the problem of overfishing.

I provided a brief description of the different political and management tools used to halt or avoid the overexploitation of marine resources. A paragraph was particularly dedicated to the role of marine reserves as a conservation and management instrument.

In chapter number III, I provided a detailed description of the case study of the marine reserves in Isla Natividad. I described the main biological features of the species of interest, i.e. abalone *Haliotis* spp., as well as the general characteristics of the fisheries that have developed along the Pacific coast of North America. I reported detailed information regarding the fishery of *H. fulgens* in Isla Natividad, and the results of an exploratory analysis of fishery data that I personally obtained from the fishermen cooperative during several field trips on the island.

In chapter number IV, I reported the results of a literary review on abalone mortality rates. This chapter has been published in peer reviewed journal: **Rossetto M., De Leo G.A. Bevacqua D., Micheli F. 2011. Allometric scaling of mortality rates with body mass in abalones. *Oecologia*, DOI 10.1007/s00442-011-2163-1**

In chapter number V, I described the demographic model developed to reproduce the population dynamic of green abalone when subjected to exploitation. I provided a detailed description of how the demographic model has been calibrated. The model was used to examine recent trends in population abundance and to compare the current status of the stock with theoretical carrying capacity; to compute informative fishery reference points such as maximum sustainable yield (MSY) and effort that guarantees the MSY; and to assess the recovery potential of abalone populations and the likely trend of abundances and yields under different exploitation scenarios. Materials of this chapter have been submitted to peer review: **Rossetto M. , Micheli F., Saenz-Arroyo A., Espinoza A., De Leo G. A. Population dynamics and resilience of an exploited marine invertebrate: combining models and long-term data to assess recovery. *Submitted***

In chapter number VI, I presented several results of a field survey conducted at Isla Natividad by the Hopkins Marine Station of Stanford University in collaboration with the ONG COBI (Comunidad y Biodiversidad), to which I contribute to the data analysis. Part of the chapter has been submitted to peer-review: **Micheli, F, A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto, G. A. De Leo. Marine reserves enhance population resilience to climatic impacts. *In review*** Then, I presented a spatially explicit version of the demographic model developed to assess how different spatial arrangements of marine protected areas can affect abalone fishery yields and population persistence. **Rossetto, M., G.A. De Leo and Micheli, F. No-take marine reserves can enhance population recovery and support the fishery of abalone. *In preparation***

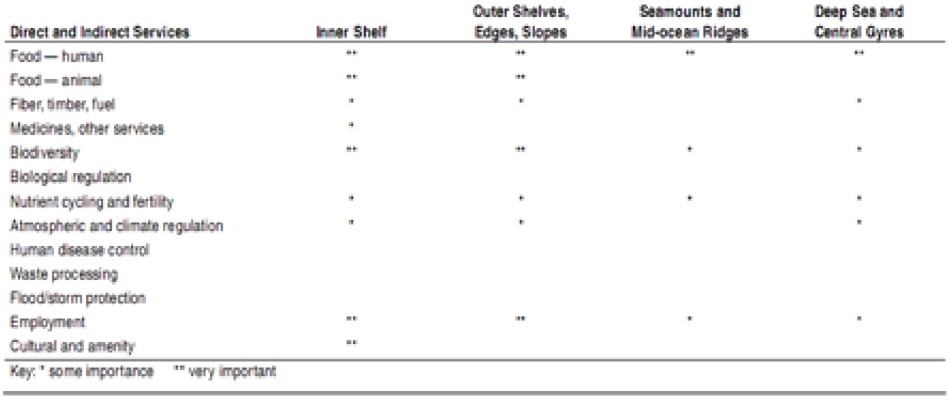
Chapter 2

Tradeoffs between fishery management and conservation of marine resources

2.1 The problem of sustainability in the exploitation of marine resources

The exploitation of marine resources allowed civilization to thrive since the beginning of human history. Societies developed on the coast have been able in past three millennia to achieve an incredible level of welfare: oceans provided for centuries the production of seemingly endless quantity of fish proteins for human diets, immensely vast areas to dump any quantity of waste and polluted waters, an effective pathway to transport any sort of goods by connecting geographically distant harbours through navigation. Several wars fought for gaining access to the sea remind us the strategic importance that coastal areas have always had in human civilization. In more recent decades, coastal areas became also an attraction for a highly lucrative tourism industry and, thanks to technological innovation, provide opportunities for offshore resource extraction (gas, oil, minerals), aquaculture (fish, bivalves, macro algae such as kelp) and energy production (offshore wind farm and wave energy production). Today, some 71% of the world's coastal people live within 50 kilometers of an estuary, 31% live within 50 kilometers of a coral reef system, 45% live within 50 kilometers of mangrove wetlands, and 49% live within 50 kilometers of seagrass ecosystems (MA 2005). This is obviously not accidental, as coastal and marine systems provide a wealth of ecosystem services used by human populations (Figure 2.1).

Fishing the ocean, in particular, remains one of the most significant human enterprises directly benefiting from the free provision of renewable resources from our seas. In 2009, marine wild fisheries and aquaculture supplied the world with about 100 million tons of food fish; of this total, aquaculture accounted for 20 percent. Total capture of marine fish reached 90 million tons in 2009, and in 2008, total world trade of fish and fishery products reached a record value of US $102 billions (FAO, 2010).



Direct and Indirect Services	Inner Shelf	Outer Shelves, Edges, Slopes	Seamounts and Mid-ocean Ridges	Deep Sea and Central Gyres
Food — human	**	**	**	**
Food — animal	**	**		
Fiber, timber, fuel	*	*		*
Medicines, other services	*			
Biodiversity	**	**	*	*
Biological regulation				
Nutrient cycling and fertility	*	*	*	*
Atmospheric and climate regulation	*	*		*
Human disease control				
Waste processing				
Flood/storm protection				
Employment	**	**	*	*
Cultural and amenity	**			

Key: * some importance ** very important

Figure 2.1: Summary of ecosystem services provided by different marine system subtypes. Source: MA 2005

Unfortunately, this lavish feast does not come at no cost. A large number of scientific reports shows beyond any reasonable doubt that coastal habitats are becoming more and more degradated around the world and that marine resources are increasingly over-exploited. A recent analysis by Halpern et al. (2008) synthesizing 17 global data sets of anthropogenic drivers of ecological change for 20 marine ecosystems indicated that no marine area around the world is unaffected by human influence and that 41% is strongly influenced by multiple stressors (Figure 2.2). This intense activity on land and on waters is affecting ocean systems through both direct and indirect effects and the consequences are now measurable not only in terms of loss of habitat and biodiversity but also in terms of negative impacts on economic activities and human welfare.

Chemical pollution of ocean waters and of bottom sediments caused by heavy metals, POP, PCB and endocrine disruptors released in the environment may have dramatic effects on marine organisms and can pose serious threat also to human health because of the biological magnification of pollutant concentration through the trophic chain. Increase turbidity because of suspended sediments and solid transport can affect fish behavior and growth of primary producers, which can push local community to a tipping point. Discharge of organic load can cause water eutrophication, a problem that now affects a progressively larger fraction of coastal habitats in both developing and industrialized countries: in fact, an increase in nutrient load can boost primary productivity and, consequently, alter the ecological relationships that shape food webs and community structure. Algal blooms triggered by the excessive discharge of organic nutrients can cause deadly anoxic crises that kill any form of bentonic and pelagic animals and may wipe out the bivalve production with huge economic losses. Toxic algal blooms and infective pathogens released in wastewater can threaten the health of marine organism and of human population. Invasions of exotic species translocated on purpose or accidentally through ballast waters threaten local biodiversity and, in the case of parasites and pests, affect aquaculture productivity. Ocean farming, on the other hand, causes the dispersal in the environment of antibiotics and antifouling, increased the risk of

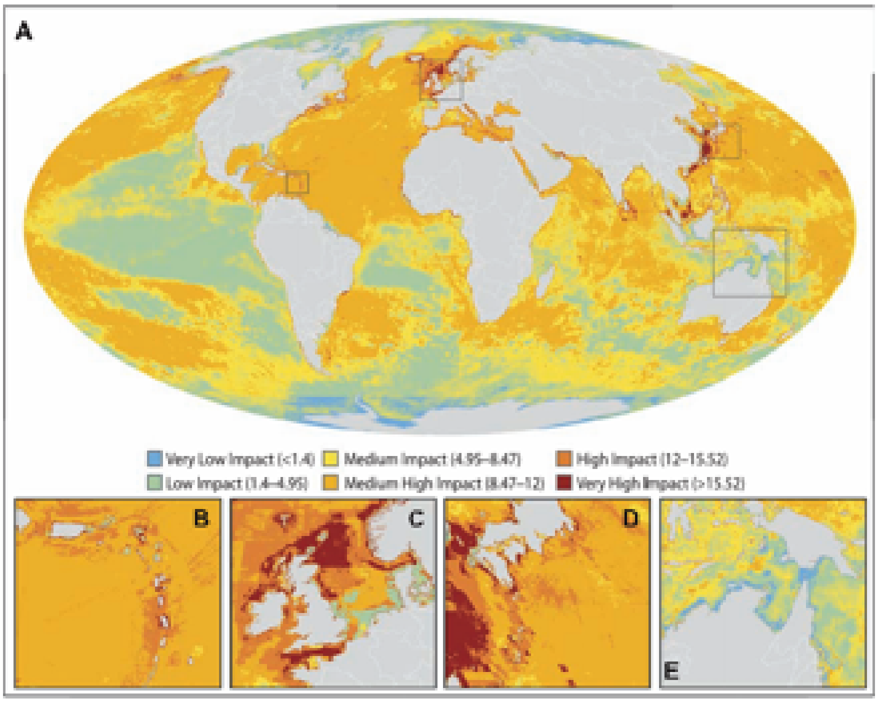
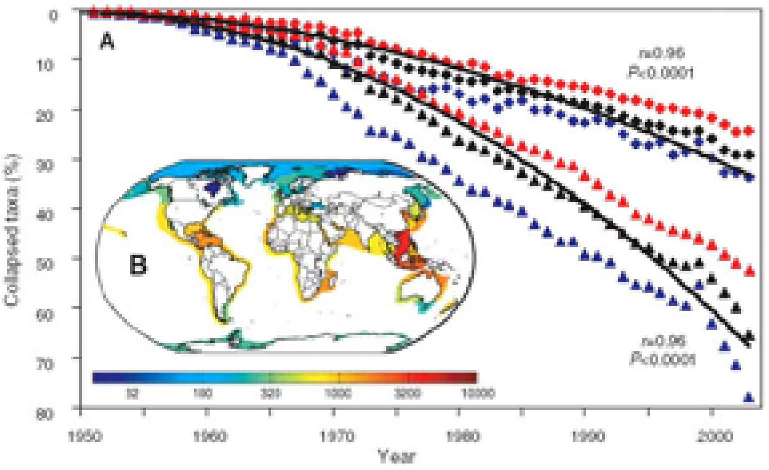


Figure 2.2: Global map of cumulative human impact across 20 ocean ecosystem types. Source: Halpern et al. (2008)

genetic contamination through accidental loss of farmed individuals and can locally cause high concentration of organic loads. The noise and vibrations produced by navigation, off-shore resource extraction and energy production through wind farm can negatively impact the survivorship and welfare of marine mammals. Along with the pressure that human activities directly impose on marine communities, a new major source of disturbance is about to impact of marine ecosystems, i.e. anthropogenic climate change which is now threatening the survivorship of many marine species and the functioning of entire ecosystems. The increase in CO_2 concentration, in fact, not only is causing a patchy increases of sea temperature that may displace species from their climatic envelop but it can potentially alter ocean circulation through the alteration of the convey belt, the strength and frequency of upwelling events, the increase in the dead anoxic zones of the oceans recently identified. CO_2 increases in the oceans is already triggering a significant increase in waters acidification, with potentially disastrous impacts on organism metabolism and physiology, reduction of calcification in bivalves and corals causing a decrease of survival, fertility and, more generally, in fitness. Coral reefs might not be able to cope with the joint cumulative effects of sea level rice and reduced calcification and thus, one of the most productive and diverse habitat might be doomed to extinction. The cumulative effects of climate change and other forms of anthropogenic pressures can pose unprecedented threats to the integrity of marine ecosystems and to the services that provide.

The list of stock collapses due to overharvesting or to a harmful combination of harvesting and unfavorable environmental conditions is disconcertedly long: text book cases include the sardine fishery of California and that of Japan in the late 1940s, the anchovy fishery of Peru and Chile in 1972 (Botsford et al., 1997), the Southwest African pilchard, the North sea herring. More recent examples are the collapse of the Canadian cod fishery and several New England groundfish stocks in the early 1990s. Nowadays, it is estimated that about half of the stocks (53 %) is fully exploited and therefore producing catches that are at or close to their maximum sustainable limits, with no possibility for further expansion (FAO, 2010). Another 32% is either overexploited, depleted or recovering from depletion (28%, 3% and 1%, respectively) with no possibilities in the short or medium term of further expansion and with an increased risk of further declines and need for rebuilding. Only the 15% of the stock groups remain underexploited or moderately exploited (3% and 12%, respectively)



Global loss of species from LMEs. (A) Trajectories of collapsed fish and invertebrate taxa over the past 50 years (diamonds, collapses by year; triangles, cumulative collapses). Data are shown for all (black), species-poor (<500 species, blue), and species-rich (>500 species, red) LMEs. Regression lines are best-fit power models corrected for temporal autocorrelation. (B) Map of all 64 LMEs, color-coded according to their total fish species richness.

Figure 2.3: Global loss of species from large Marine ecosystems. Source: Worm et al. (2006)

Furthermore, the rate of fisheries collapses, defined as catches dropping below 10% of the recorded maximum, has been accelerating over time, with 29% of currently (Fig. 2.3) fished species considered collapsed in 2003 (Worm et al., 2006).

Beside the decline of stock abundance, global landings also showed a decline of catch trophic level in the last fifty years (ca. 0.05-0.1 per decade, (MA, 2005)). This effect, widely known in the literature as 'fishing down the food web' (Pauly et al., 1998), evidence a gradual transition in landings from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish. In fact, the average biomass of predatory fishes declined by two-thirds through the second half of the 20th century. Extrapolation of present trends in commercial fishing implies massive expansion of bottom fisheries into increasingly deeper waters, with demersal fishes as orange roughly, chilean seabass, hagfish suffering the major impacts (Pauly et al., 1998). Depletion through overfishing is in fact extremely dangerous for species as the deep oceanic fishes with long life span and late reproductive maturity. Although it has often been assumed that overfishing does not impose any direct threaten of species extinction, the past few decades have shown a growing concern about this. The species particularly at risk are highly valued, large and slow to mature, have limited geographical range or sporadic recruitment (Pauly et al., 2002). Even where stock abundances remain high, fisheries can change the evolutionary characteristics of a population by reducing average age, size at age, and genetic diversity affecting future resiliency and sustainability . In addition to the threat of target species collapse, overfishing can exacerbate bycatch problems, that is, the accidental capture (and killing) of non-target species or undersized individuals of the target species (Sanchirico et al., 2002; Pikitch et al., 2004). Non-target species are discarded either because they do not have a valuable market or because existing regulations prevent them to be marketed, as in the case of marine mammals, turtles, sea horses and other endangered species. The use of fishing vessels of increasing power, or more sophisticated fishing techniques and of highly efficient but non-selective fishing gears (such as hooks and nets) caused an increase in bycatch and, consequently, of fishing mortality of non target species. Bycatch is estimated to be about 30% of global landings (Pauly et al., 2002) and it is only one component of the total amount of illegal, unreported and unregulated (IUU) catches.

Fishing activity results also in alteration of the trophic interactions that can propagate all through the food web (Scheffer et al., 2005). It has been observed that reduction of the number and length of pathways linking fishes and primary producers, and hence a simplification of the food web, has occurred as a consequence of removal of top predators. Frequently, losses of top predators and mammals have been the tragic consequence of the deterioration in ecosystem structure. For instance, the removal of top predators through fishing allows primary consumers to increase their abundance, which in turn produces a decrease of zooplankton grazers and, ultimately, causes massive blooms of phytoplankton, a phenomenon well know in the ecological literature as trophic cascade (Fig. 2.4). In tropical reefs, the overharvesting of top predators has caused a trophic cascade that, through elimination of sea urchin grazers, transformed highly productive coral reefs into biodiversity poor algal barrens. In the temperate waters of the Mediterranean Sea, on the contrary, the collapse of sea bream populations due to over-harvesting, has caused the transformation of macro-algal beds into sea-urchin barren.

2.2 Brief overview of policies and management strategies to regulate the exploitation of marine resources

Several methods of regulation and restriction are applied worldwide with the aim of avoiding the occurrence of negative impacts of fishing activity. Traditional fishery management tools include regulatory methods and limiting entry schemes. A set of voluntary approaches can be also implemented to achieve a more sustainable use of marine resources. Besides the more traditional instruments, the ecosystem-based management has been claimed as an optimal solution, as it explicitly recognizes the importance of ecological processes in the marine

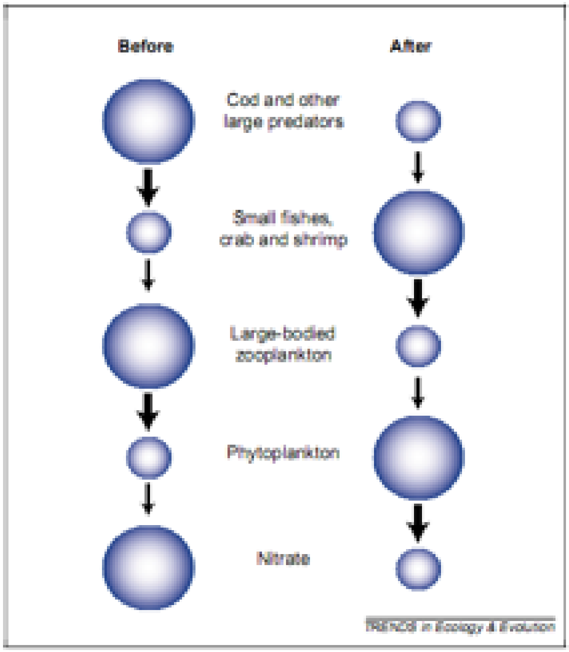


Figure 1. The cascading effect of the collapse of cod and other large predatory fishes on the Scotian Shelf ecosystem during the late 1980s and early 1990s. The size of the spheres represents the relative abundance of the corresponding trophic level. The arrows depict the inferred top-down effects.

Figure 2.4: A schematic representation of the effects of fishing activity on the community structure by the removal of top predators. Source: Scheffer et al. (2005)

resource management. The main tools can be classified as following:

- **Traditional fishery management** tools include the definition of **Total Allowable Catches**, other regulatory methods and limiting entry schemes. The Total Allowable Catch (TAC) is a catch limit set for a particular fishery, generally for a year or a fishing season, and it is actually defined in many countries on MSY single-species assessment. A large set of other **methods of regulation** (e.g. gear restriction, size limits, trip limits, closures) is applied worldwide, in order to regulate and limit fishing effort and to minimize the damage resulting from fishing activity. A common approach is also **limiting entry** to marine fisheries, attempting to overcome the problem of external costs through the creation and enforcement of property rights where they have not evolved naturally. It can been shown that limiting entry is a fundamental way to solve the so called 'Tragedy of the Commons', because it overcomes the problem of open-access resources; however, the method of limiting entry should be accompanied by regulations and restriction in order to avoid other harmful consequences on marine ecosystem.

- **Ecosystem-based management** represents a more holistic approach to marine resource management as it explicitly recognizes the importance of ecological and ecosystem processes in determining the response to human exploitation. The overall objective of EBM is to sustain healthy marine ecosystem and the fishery they support, generating knowledge of ecosystem processes sufficient to understand the likely consequences of human activity (Pikitch et al., 2004). The main goals of EBM are to restore and maintain an ecosystem in a healthy, productive, and resilient condition in order to guarantee the providing of ecosystem services and to evaluate cumulative impacts across sectors, resolving trade-offs among sectors or activities. An ecosystem-based management should support the scientific research, and when dealing with uncertainty, rely on the precautionary principle and on the adaptive management.

- **Co-management strategies** are suitable instruments to reduce the negative impacts of extractive use of marine resources, promoting the involvement of greater stakeholders in the decision-making processes in a collaborative manner. The co-management approach can be facilitated by the adoption of codes of practice. Other alternative approach includes the adoption of accredited environmental management systems, implemented through the promotion of environmental performance certification.
- **Marine Reserves (MRs)** aim at the protection of biodiversity protection, at a sustainable fishery management, and at the development of non-extractive uses of the ecosystem (recreational activities, ecotourism).

2.2.1 Total Allowable Catch

The Total Allowable Catch (TAC) is a catch limit set for a particular fishery, generally for a year or a fishing season, and it is defined in many countries on MSY single-species assessment. Catch limits are generally used in most fisheries, with the general aim of preserving fish stocks from overexploitation and to ensure the largest yield that can be taken from a species stock over an indefinite period. This system is appealing because of the simplicity of its implementation: the fishery is fundamentally open-access (no licensing system required), the TAC is usually derived as a fraction of the overall population that maximizes long term catches (i.e., MSY or other bioeconomic indicators of fishery performance), only landed catches need to be monitored and fishing is allowed as long as the TAC is not exceeded. Yet, as the fishing season is closed as soon as the TAC is attained, fishermen are inevitably prompted to a so-called 'olympic' race to fish as much as possible as fast as possible, as any share of fish not harvested by an individual fisherman will be invariably removed by somebody else. In absence of cooperation, a common problem of TAC-regulated fisheries is that fishing effort (such as the number of operating fishermen, or the power/size of the fishing fleet) is doomed to increases well above the level required by a single owner to achieved MSY; as a consequence, the fishery is eventually overcapitalized. Definition of TAC is habitually made considering one species, uniformly distributed in space, lacking age-structure and trophic interactions. Often, the likely consequences of this simplification are decline in stock abundance and harmful effects on other species. Static interpretation of MSY puts stocks at too much risk, because it ignores that populations undergo natural fluctuations in abundance and can become severely depleted under constant-catch rates. Whenever the rate of harvest exceeds the natural rate growth, the population biomass level will decline (Clark, 1990). Furthermore, there has been severe violation of the assumption of the compensatory response, which represents the ecological basis of the sustained net production (Pauly et al., 2002). Compensatory responses to reductions in stock size consist in increasing juvenile survival rate, through behavioral or ecosystem-scale shifts in foraging time and predation risk. Some stocks have shown recruitment failure after sever harvest, possibly associated with cultivation-depensation effect, competition-predation trade-offs among species at the same trophic level or presence of predators feeding on multiple trophic levels (Walters, 2000). A thorough knowledge of the biology and ecology of the species (including age-structure and trophic interaction) is hence of primary importance in order to maintain long-term socioeconomic benefits in commercial fishery. Multi-species and eco-trophic models can be helpful to better evaluate the consequence of fish removals. Another crucial aspect about TAC assessment regards direct interaction of the fishing gears with other species. In many fisheries, in fact, some mix of species is inevitably fished together, and this necessitates transfers of quotas or other changes by fishers to match their catches with their quota holdings (Karagiannakos, 1996). In most cases TACs are set for individual species without considering the mix of species jointly harvested. If the TAC of a species is reached before the TAC of other jointly harvested species is achieved, then discarding at sea is likely to occur, and the TACs of some species will be exceeded. To manage species aggregations, Multi-species Total Allowable Catch (MSTAC) can be defined. If the species in the complex are caught in the same ratio, setting a total catch provides control over the harvest of each individual species. Another possible approach would be setting MSTAC to the level of the most vulnerable species in a mixed fishery catch (Karagiannakos, 1996). The problem of discarding at sea is aggravated by highgrading, that is, the fact that under a TAC system a certain marketable fish length or size is required. Especially in structured fish populations, some fish may be more valuable per unit weight than others (Clark, 1990). Hence, fishermen will attempt to fill their quotas with the most valuable types, concentrating their effort on the most productive and convenient fishing grounds. Finally, fishery management has often ignored TAC assessment results provided by scientists. Managers, under constant political pressure for greater short-term benefits to society, allow harvest to increase when scientists cannot specify with certainty that the next increase will lead to overfishing and collapse (so called 'burden of proof' problem) (Botsford et al., 1997). Moreover, in some cases catch is more affected by the conditions of the stocks in nature rather than the agreed or recommended TAC (Karagiannakos, 1996).

2.2.2 Methods of regulation

Regulatory approaches are widely used in many fisheries and include different instruments, like seasonal and area closures or gear restriction. Regulatory methods attempt to limit fishing effort and are essential in the conservation and preservation of habitat and vulnerable species. Closed seasons, no take zones can be successfully applied in protecting juveniles, vulnerable population, and to diminish bycatch levels during fishing operations. The effectiveness of closed areas and seasons as a mean to reduce negative biological effects depends on the importance of the time or zone protected for the at risk species. Size or sex selectivity measures introduce minimum or maximum size limits, or penalties for possession of spawning females. The objective of size and sex limits is to allow young fish to grow, in order to increase spawning rates and recruitment into the fishery. Gear restrictions try to limit the use of fishing gears that have negative impacts on habitats. Bottom trawling and mining, for example, are among the greatest sources of anthropogenic disturbance of seabed habitats worldwide. Gear limitations also attempt to limit the level of bycatch. Accidentally caught fish can include species that may be targeted in other fisheries, undersized fish in the target fishery as well as endangered or protected species; removing them affects the food chain and ultimately the economic and social aspects of the fishery in many ways. Bycatch Reduction Devices (BRDs) are defined as any device, trawl modification, or combination of devices that attempt to reduce bycatch, and are designed to allow fish that are not targeted to escape from the net before it is hauled back into the boat.

Although regulatory methods are useful in protecting critical species and habitats, they are not efficient when used to restrict harvest or effort. These methods increase the costs and adjusted them to meet the revenue curve at the MSY point, which then becomes the point of regulated bioeconomic equilibrium.

Economists studying fishing industry have severely criticized such regulatory methods, stating that they achieve a primarily biologically oriented goal by introducing deliberate economic inefficiency (Becker and Choresh, 2006). Gear restrictions and prohibitions tend to induce economic inefficiency by forcing fishermen to use more expensive and less productive fishing techniques. Even if fishing mortality were initially reduced by gear restriction and prohibitions, it would not necessarily be maintained at a reduced level because with open-access there could be a long-term increase in the number of fishermen, each using the restricted gear. Annual quotas and seasonal closures encourage fishermen to seek more effective ways to maximize their shares before the quota is reached and the season is closed. Fishermen would fish more intensively earlier in the season and would likely seek out and adopt new gear, larger vessels, or different technologies. Managing a fishery by controlling effect through season shortening inevitably produces an excess of fishing capacity: the fishing vessels are used only during a brief annual season; otherwise the fleet sits idle at the dock. This extreme 'overcapacity' in fisheries is widespread, and increases the difficulty of management in various ways. Accurate control becomes extremely hard, and vessels owners would ask for large catch quotas, on the basis of financial necessity (Clark, 2006). Unrestricted access methods of regulation are therefore not able to prevent overfishing, as fishing effort tends to increase in the long term. In fact, these regulations treat the symptoms of the problem and not the fundamental cause (Sanchirico et al., 2002). A consequence is that signs of recovery in fish populations can often attract additional fishing effort; as a result, any short gain in stock levels and profits are not sustainable due to the policy-induced responses of the fishermen (Waters, 1991; Clark, 2006).

2.2.3 Methods of limiting entry

Regulations that restrict access to a fishery are classified as limited-entry methods of management, which introduce elements of property rights into the fishery. These methods attempt to overcome the problem of external costs through the creation and enforcement of property rights where they have not evolved naturally. Use rights can be classified in two categories, namely access rights and withdrawal rights (Waters, 1991). Access rights refer to the capability to enter a fishery and participate in it. Access right can be associated to constraints on how, where and when participation is allowed. The best-known forms are Limited entry licenses and Territorial Use Rights in Fishing (TURFs).

Withdrawal rights refer most often to the intensity of resource use, as reflected in the level of effort (input rights, such as Individual Vessel Quotas (IVQs) or the quantity of harvest (output rights, such as Individual Transfer Quotas (ITQs), Individual Quotas (IQs), Community Development Quotas (CDQs).

Another crucial aspect about use rights is the choice between individual and collective rights, and that between market-based and community-based rights. A choice between these should depend on both the historical context and the fishery objectives. Individual right are perhaps most suitable for recently developed fisheries, which have an industrial focus, while collective rights can be most feasible in longstanding, cohesive traditional fisheries. Furthermore, in economies dominated by market, fishery participation and allocation of allowable catch or effort can be easily determined through the buying and selling of rights. In contrast, in traditional, historical fisheries, rights can be assigned in a more deliberate manner, through multi-objective decision-making process carried out at community, regional or national scale. According to several authors (Sanchirico et al., 2002) there is an emerging focus on use rights as crucial to success in fishery management. In some fisheries, particularly with a long history, use rights have naturally evolved over time. It is not surprising that use right would have emerged, since there are clear benefits to defining the group of fishers entailed to fish in a certain location, both for the fishers themselves and for well-being of the fishing community. The agreement about use rights in fishery management is accompanied by a parallel interest on management rights, that is, the right to participate in management decision processes.

Access rights

Limited entry licenses are a management system in which the right to enter the fishery is restricted to those with licenses, and the number of licenses is restricted by the regulating agency. Licenses could be distributed by random drawing or according to a criterion usually based on the historical participation and investment in the fishery (Waters, 1991). A reduction in the number of participants, however, does not entail an overall decrease in fishing effort. The partial recovery of the fish stock will motivate license owners to invest in vessel improvements, so as to increase their own catches (Clark, 1990). In particular, this management system does not overcome the rush for fish (in which each fisherman seeks to catch the fish first) or the corresponding incentive for capital stuffing (that is, the expansion of each vessel's fishing capacity). Territorial Use Rights in Fishing (TURFs) involve the assignment of rights to individuals and/or groups to fish in certain location, generally based on long-standing tradition. This management system is not usually feasible for marine stocks and has been commonly associated with relatively sedentary species, like shellfish, lobster or oyster leases (Waters, 1991).

Withdrawal rights

Input (effort) rights restrict the right to deploy some units of effort to those with licenses. They involve the assignment to individual fishers, group or communities of allowable levels of effort such as time fished, vessel size, amount of gear, gear attributes. A known form is the Individual Vessel Quota, IVQ. Controlling the individual effort through the number of vessels can be a viable approach to management, as long as two key problems are dealt with. First, limitations on the number of vessels would encourage fishermen to increase their fishing power through improvements in other, unrestricted components of effort. For example, new, larger vessels could replace old, smaller vessels. This implies the need for a multi-dimensional approach, in which not one, but a combination of inputs is subjected to restriction. Although most licenses limitation program restrict several components of effort (vessel tonnage, number of vessel) it is impossible to control all aspects of fishing effort (Waters, 1991). Second, there is a natural process of technological improvement that gradually increases the effectiveness of any set of inputs over time. An input program must therefore adjust for such increases in efficiency. However, effort rights can be a good approach for stocks for which biomass estimates are unreliable, or for which regular catch monitoring is too expensive.

Output (catch) rights are able to avoid these negative outcomes and are now in place in many fisheries. In this system, each fisherman or group of fishermen receives a transferable certificate that allows him to catch a fixed proportion of the total allowable catch. Rights may be assigned to communities, as CDQs (Community Development Quotas), so that collective control is exerted and decision on use of quota can explicitly reflect community values and objectives. Otherwise, catch rights may be allocated to individual fishers, as Individual Quotas (IQs) or Individual Transferable Quotas (ITQs). Individual quotas, especially if transferable, are generally judged to be successful in reducing the race of fish, as they can improve the economic and biological performance of a fishery in several ways. The fisherman can in fact arrange to catch his quota in the most cost-efficient way, and is not compelled to compete with other fishermen to obtain a share of the total catch (Waters, 1991). In this way quotas can solve the problem of overcapacity. If quotas are transferable, fishing costs can be reduced as quotas are traded from less efficient to more efficient fishermen. Finally, because the value of the quota depends on the state of the fish population, fishermen will support conservation activities and research programs to maintain and increase the fish stock (Clark, 2006). Clark (1990) demonstrated that individual transferable quotas are equivalent to taxes in terms of economic efficiency, and that both systems are capable in theory to achieve the optimal allocation of effort (Clark, 1990). Several difficulties are associated with taxation in fishery: first, fishermen are always opposed to it, and a second difficulty regards calculation of the optimal tax, which would require the management authority to know the operating costs of each vessel, as well as the biological characteristics of the fish population. For these reasons, regulation by taxation has almost never been seriously considered as a viable practical approach to fisheries management, and ITQs system is mainly preferred. However, ITQs also raise several problems. First, the incentive to exceed the amount of the quota always exists; therefore, the government must enforce the monitoring of catches. Substantial enforcement costs are then required to achieve a rigorous monitoring. Furthermore, if individual quotas are transferable, they will take on a value determined by the future rents of the fishery and in many cases quota values have skyrocketed once the quota system has been established. Therefore, the initial allocation of the quotas is often strongly contested, as the quota owners quickly become wealthy. Individual quotas assume high values because they have the effect of capitalizing the future value of the fishery at the time that the quotas are issued. Many economists hence recommend limited-duration quotas, which only capitalize the value for that duration. It has been also recognized by most countries that the governments should retain a portion of the resource rents. In fact, marine resource belongs in principle to the nation at large, so that a share of the rents should be collected for the public purse (Clark, 2006). The resource in question- the fish- remain a public good, and as such, the public should be compensated- or at least not taxed- for their use. Thus the cost of fishery management, and the windfall profits of fishery conversion, should be shared (Hilborn et al., 2005).

2.2.4 Voluntary approaches

The political instruments seen in the previous sections rely mostly on the principle of 'command and control': the attempt to limit the race for fish has been carried out in many countries through regulations such as limited entry licensing, gear restrictions or fishing grounds closures. Their modest overall level of success have driven policy makers to look for alternative solutions. One approach can be encouraging greater stakeholders participation in fisheries management in a collaborative manner (co-management). The co-management approach can be facilitated by the adoption of codes of practice. Other alternative approach includes the adoption of accredited environmental management systems, implemented through the promotion of environmental performance certification.

Co-management

Co-management presents a new challenge for the management of natural resources. Co-management shares management responsibility between the state and local communities or resource user groups. A basic principle of co-management is thus self-governance within a legal framework established by government. Various forms of co-operative stakeholder groups have been established in the fisheries sector along a continuum of co-management, depending on the degree of government participation in decision-making. By including a range of stakeholder input and values, co-management has the potential to transform the current extractive and single-species management focus to a more sustainable, ecosystem-based approach. Such an approach would recognize the marine environment as an ecosystem linked to the land and air, not just a 'fish basket' for human consumptive purposes.

Co-management provides a number of potential benefits for marine management, including the problem of managing environmental externalities. Bringing different stakeholder groups together to communicate helps these groups to both redefine their own problems, and to gain understandings of the problems of other groups. The inclusion of stakeholders within a management process can provide a wider base of information and knowledge, particularly in respect of local and regional fish patterns, and the identification of key issues. Legitimacy of any regime is essential to encourage fishers and other marine stakeholders to voluntarily advance their collective interests at the partial expense of their private interests.

By involving different stakeholders in the management process, and by establishing a pattern of co-operation based on reciprocity, co-management has the potential to enhance legitimacy. Increased legitimacy is also likely to procure increased levels of compliance with rules and regulations.

The opportunity for participation in decision-making should encourage stakeholders to see themselves as collective managers or stewards of the resource. This may provide the incentive for adopting sustainable fishing practices, and for action in conservation spheres such as habitat protection and rehabilitation. When fully developed, the co-management process should drive stakeholders to take an ecological approach to management rather than focusing purely on single species management.

Several factors may influence successful co-management. Firstly, co-management tends to operate more favorably when stakeholder groups already have a cohesive social system. Secondly, co-management is likely to be more easily implemented if there is already a degree of trust among the various stakeholder groups. Thirdly, other exogenous factors may be important, such as having a facilitative political mechanism, and the absence of strong external threats to the legitimacy of the co-management agreement. Codes of practice may be described as a particular variant of a co-management agreement. A code of practice is a document negotiated and agreed by interested stakeholders on best practice for a particular industry. Codes are generally voluntary and establish principles and recommendation to implement sustainable fishing activities.

Market based standards and labels

Market based standards and labels, such as eco-labeling, are voluntarily adopted certifications of the environmental performance of a firm. Several factors contribute to the development of market standards and to their possible expansion. On one hand, food demand has been changing with the evolution of lifestyles and demographics. Increasingly demanding consumers expect not only safe and high-quality foods but also a transparent and informative trail that can be used to trace the origin of food, its quality, and the environmental and/or social conditions current during its production, processing and distribution. Hence, government and public authorities have been increasingly engaging the responsibility of the industry for ensuring food safety and quality, and many fishing firms have agreed that food safety is a competitive issue of high importance. On the other hand, there is increased concern that expanding international fish trade may further strain the sustainability of fish stocks and the marine environment. Campaigns seeking to reduce or eliminate consumption of particular overfished stocks or endangered species are becoming more common. Other issues of global concern, such as environmental protection, social requirements and IUU fishing, are likely to be increasingly governed through market-driven standards and schemes. The eco-labeling schemes are extremely useful to create market-based incentives for environmentally friendly products and production processes.

2.2.5 Marine Reserves as a management tool

Many fisheries scientists and managers are at present promoting the use of Marine Resreves (MRs). Three types of purposes can be assigned to a creation of a MR: biodiversity protection, sustainable fishery management, and development of non-extractive uses of the ecosystem (recreational activities, ecotourism) (Ablan et al., 2006).

Regarding the role of MRs in preserving biodiversity and healthy ecosystems, scientific research overall a large set of reserves shows that these goals are consistently accomplished. Within the boundaries of a MR, biomass and species diversity generally increase, and it has been observed that heavily fished stocks often show the most considerable increase in density and body size. When exploitation is ceased in an area, resident fish populations begin to recover. As the populations recover, the abundance of fish increases, including the number of older and larger fish that would have been caught if fishing were allowed to continue (Sanchirico et al., 2002).

It is hypothesized that MRs can help to sustain fisheries external to them by becoming net exporters of adults (the *spillover effect*). The extent to which spillover effects are significant in rebuilding external fish populations depends on the dispersal characteristics of the populations that reside in the reserve. For sedentary population, for example red sea urchin, juvenile or adult dispersal cannot be expected. On the other hand, if the population more mobile, then spillover of juveniles and adults is more likely to occur. The effectiveness of a spillover effects in increasing catch rates beyond its boundaries is still controversial. In theory, MRs could increase fish catches in the zone neighboring the no-take area only if they can overbalance the negative effects resulting from reduction in the size of the fishing zone (Ablan et al., 2006). However, the benefits derived from the recovery of the population could be not high enough to compensate for the loss of some fishing zone. In particular, an increase in yields is likely to occur when fishing effort outside cannot be controlled and populations would otherwise overfished, but this might not be the case when a management system already exists. Under TAC system, for example, establishment of a MR requires a reduction in the total catch, in order to avoid an increase in fishing pressure on the stock outside the MR, with the result of a decrease in catch (Hilborn et al., 2006).

Nevertheless, several studies suggest the existence of positive effects of MRs in adjacent fishing zones. A case study in Philippine, for example, shows that after the reopening of a reserve to fishing, landings began to decrease (Hilborn et al., 2006). MRs can also be effective as they can bring stability in catches, by making fish stocks less vulnerable to overfishing (Charton and Ruzafa, 1999). According to several authors, the use of large marine protected areas is the most effective risk management strategy, and the uncertainty characterizing fisheries management is the major factor justifying the use of MRs as fisheries management tools (Botsford et al., 1997; Clark, 2006). MRs can in fact decrease the risk of fishing catastrophes, because they increase the resilience of the population, that is, they increase the speed it takes a population in recovering from a negative shock. MRs provide a number of opportunities for recreational users to practice non-extractive activities like diving, sailing, or marine mammals watching. Recreational fishery also benefits from the establishment of marine protected areas, resulting in change in the frequency of official records concerning sport fishing (Roberts et al., 2001).

Tourism related to this kind of activities is often called ecotourism. Benefits provided from the development of ecotourism could be used to compensate the costs incurring from restricting fishing activity. Beside its positive contribution, ecotourism in MRs may also have some negative impacts on the environment. Uncontrolled tourism could generate congestion and be a source of pollution, and alter the behavior of fishes. These factors may decrease the attractiveness of MRs, contradicting the objectives of protection assigned to them. To avoid these negative impacts, the development of tourism in a MR should be kept within the limit of the carrying capacity of the environment.

From society's perspective, MRs are a public investment of marine resources and their implementation include a large number of stakeholders. The decision to establish a marine reserve can be guided by a benefit-cost framework that measures whether the potential benefits of protection outweigh the potential costs.

2.2.6 Ecosystem Based Management (EBM)

Besides the traditional instruments described above, the Ecosystem Based Management (EBM) represents a more holistic approach to marine resource management as it explicitly recognizes the importance of ecological and ecosystem processes in determining the response to human exploitation. One of the overarching principles of Ecosystem Based Management is that healthy, fully functioning ecosystems provide the basis for sustaining communities, economies, cultures and the quality of human life. Ecosystem based management can be considered a new direction for fishery management, essentially reversing the order of management priorities to start with the ecosystem rather than the target species. The overall objective of EBM is to sustain healthy marine ecosystem and the fishery they support, generating knowledge of ecosystem processes sufficient to understand the likely consequences of human activity (Pikitch et al., 2004). The main goals of EBM are to restore and maintain an ecosystem in a healthy, productive, and resilient condition in order to guarantee the provision of ecosystem services and to evaluate cumulative impacts across sectors, resolving trade-offs among sectors or activities.

The increasing attention to the integrity of the whole marine ecosystem proceeds from the awareness that oceans provide a set of fundamental ecosystem services upon which human life depends. Marine habitats provide the public with a valuable and diverse set of goods and services, including seafood, recreational enjoyment, carbon sequestration, storm protection, and opportunities for pharmaceutical discoveries (Sanchirico et al., 2002). In the Mediterranean Sea, for example, shipping and fishing activities heavily endanger sea-grass meadows of *Posidonia oceanica.* The destruction of sea-grass has direct effects not only on fish production, but also on the stability of the seashore, as the meadows act as breakwater, holding sediments and reducing swell. In many places the disappearance of sea grass meadows has soon been followed by the disappearance of sandy beaches, with significant economic losses also for all the activities related to the beaches. This example is to highlight the tight connection among the health of the ecosystem and the potential of human development and well-being.

In order to preserve the health of the oceans and to maintain their capability of supplying essential ecosystem services, the consequences of any human activity should be analyzed, both at biotic and abiotic level. One aspect of the EBM is hence the development of models that take into account direct and indirect ecological interactions among species and their environment. Multi-species and eco-trophic models are necessary to better evaluate the consequence of fish removals. Different models can predict biomass trajectories over time and under various fishing pressures, with different spatial, temporal, and biological resolution, quantitative or qualitative nature of the results, and insight into system function (Latour et al., 2003). Major oceanographic processes should be integrated in these models. Fisheries scientist focused on variability on yearly time and on changes in the atmosphere and in oceanic conditions occurring every few years (like El Niño Southern Oscillation, ENSO, or the Northern Atlantic Oscillations, NAO), in order to make year to year adjustments in managements. More recently, awareness of broad scale regime shifts occurring across entire oceans every few decade has led to increased understanding of changes in distribution and abundance of fish stocks (Botsford et al., 1997). Variations in temperature and nutrients concentration significantly influence primary productivity and hence survival and growth of fishes like anchovies, mackerel, or salmon. Oceanographic variables may explain also global patterns of distribution of greater predators, like tunas and billfishes.

Knowledge of physical variations in oceanic conditions, jointly with information of habitat use, spawning areas, migration pattern, and fishing mortality, could be used to define different areas, in which type and level of allowable human activity are specified. Ocean zoning is useful in identifying priority areas for ocean conservation where non-selective or destructive gear can be prohibited (Pikitch et al., 2004; Worm et al., 2006). Recently, Halpern et al. (2008) developed a global map of human activities on marine ecosystem, which provide a helpful tool for management of fishery activities through the identification of the most sensible areas. From this study emerged that, besides fishing activity, the management of the oceans has to deal with the effects of climate change, and negative interactions with terrestrial environment. The need of advanced marine spatial planning is necessary to resolve conflicts across different sectors such as fisheries, aquaculture, marine mammal conservation, shipping, oil and gas: zoning would not replace existing regulations but would add an important spatial dimension by defining areas within which compatible activities could occur (Crowder et al., 2006). The Marine Spatial Zoning is a planning instrument that considers marine protected areas as a necessary but not sufficient instrument by which to manage the complexity of human activities that insist on marine ecosystems. The ecosystem based management indicate rather a principle than a practical way to operate: it is made up of several instruments and actions, and the spatial approach to the use and exploitation of marine resource is necessary to control not only the single impacts, but the joint effect and the interactions among the different human sectors.

Because ecosystem management involves a wide range of objectives and great ecosystem complexity, it requires a quite broad amount of data. EBM has therefore to deal with a high level of uncertainty, due to the complexity of marine ecosystems, the difficulty and expense involved in sampling them, and their susceptibility to environmental variability. Scientists now use to include confidence intervals to stock abundance estimates, or bayesian methods are used to quantify various forms of uncertainty. More recently, also uncertainty related to model structure has been taken into account. However, complexity will always limit the extent to which the effects of fishing can be understood or predicted. A prerogative of an ecosystem based management is hence precautionary principle should be adopted. The precautionary principle states that if the consequences of an action are potentially adverse, the action should not be allowed to proceed, even if cause and effect relationships have not been fully established scientifically (Boesch, 2006).

EBM can be facilitated by adaptive management, which relies on the progressive accumulation of knowledge for improved fisheries management (Pikitch et al., 2004). An example could be is the long established practice in fishery management of protecting at least some small forage for their value in supporting larger piscivorous (Walters, 2000). Adaptive management approach is based on deliberate experimentation followed by systematic monitoring of the results, from which the fisheries managers and fishermen can learn. Applications can range from passive adaptive management, which focuses on monitoring and evaluating outcomes from a particular policy option, to active adaptive management, which includes experiments to test competing models of system behavior or alternative solutions (Boesch, 2006).

Chapter 3

The case study of abalone fishery at Isla Natividad

3.1 Brief description of *Haliotis* spp.

Abalones (Fig. 3.1) are marine gastropod herbivourous molluscs (family Haliotidae, genus *Haliotis*) that are found along the coastal waters of every continent, with about one hundred of species recognized worldwide (Lindberg et al., 1992).

The shells of abalones have a low and open spiral structure, and are characterized by several open respiratory pores in a row near the shell's outer edge. The muscular foot has a strong suction power permitting the abalone to clamp tightly to rocky surfaces. A column of shell muscle attaches the body to its shell. The mantle circles the foot as does the epipodium, a sensory structure and extension of the foot which bears tentacles. The epipodium projects beyond the shell edge in the living animal. The epipodium surface may be smooth or pebbly in appearance and its edge may be frilly or scalloped. It is the most reliable structure for identifying abalone species.

The internal organs are arranged around the foot and under the shell. The most conspicuous organ, the crescent-shaped gonad, is gray or green in females and cream colored in males. It extends around the side opposite the pores and to the rear of the abalone. The abalone has a pair of eyes, a mouth and an enlarged pair of tentacles. Inside the mouth is a long, file-like tongue called the radula, which scrapes algal matter to a size that can be ingested.

The gill chamber is next to the mouth and under the respiratory pores. Water is drawn in under the edge of the shell, and then flows over the gills and out the pores. Waste and reproductive products are carried out in the flow of water. Since it has no obvious brain structure, the abalone is considered to be a primitive animal. However, it does have a heart on its left side and blood flows through the arteries, sinuses and veins, assisted by the surrounding tissues and muscles.

In abalones, the sexes are separate and the sex ratio is approximately 1:1. Abalones are broadcast spawners, that is, the eggs or sperm are released direcly in the water column, through the pores with the respiratory current. Spawning may be controlled by the water

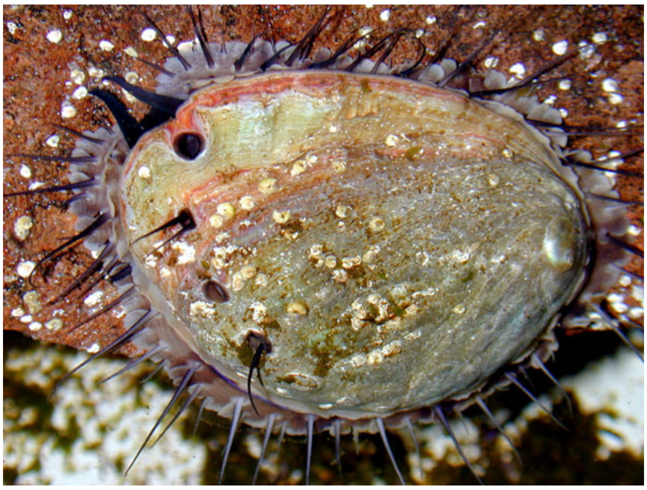


Figure 3.1: A picture of red abalone *H. rufescens* in natural environment

temperature or length of the day, and during a single spawing event, millions of gametes can be realesed. As fertilization occurs in the water column, the degree of fertilization can be a limiting factor to succesfull recruitment, especially at low population denisties.

In North America, seven species of abalone can be found: pink abalone *H. corrugata*, red abalone *H. rufescens*, green abalone *H. fulgens*, black abalone *H. cracherodii*, white abalone *H. sorenseni*, flat abalone *H. walallensis*, and pinto abalone *H. kamtschatkana* (Fig. 3.2). Californian abalones occur on rocky reefs among forests of kelp *Macrocysitis pyrifera*, mainly between 0 and 20 m depth. Post-larvae of genus abalones graze diatoms and crustose coralline algae (McShane, 1992). Young juveniles occupy crevices in the daytime, moving out to forage at night and returning to their homesites before dawn (Tutschulte and Connell, 1988). Adults occupy more exposed positions and feed on drift algae (Tutschulte and Connell, 1988).

Abalone have sustained lucrative fisheries worlwide, as the meat is a valuable food especially for the Asian markets. Also, the shells of abalone are a source of mother of pearl for jewelry and other decorative items. In Mexico, the species of most commercial importance are *H. corrugata* and *H. fulgens*, and, to less extent, *H. cracherodii* and white abalone *H. sorenseni*. Along the Pacific coast of Mexico, the fishery of *H.corrugata* and *H. fulgens* is a lucrative enterpise, worth approximately US $ 20,000,000/year.

3.2 The abalone fishery at Isla Natividad

3.2.1 Study site

The Natividad Island is a little island on the Pacific coast of Baja California, Mexico. The California Current is a northwesterly current that causes strong upwelling from February to June, (T=12-13°C). The Davidson Current occasionally brings tropical waters northward from October to January, and elevates temperatures to about 19- 20°C. Fishing grounds at

Isla Natividad extend into the kelp forest up to 25 m from the coastline, and are divided in 44 blocks of about 500x500 m, grouped in 6 zones: A, B, C, D, E, and F (Figure 3.3). Green abalone *Haliotis fulgens* occurs on rocky reefs among kelp beds mainly between 0 and 10 m depth, whereas pink abalone, *Haliotis corrugata*, is more abundant in deep waters, from 10 to 25 m water depth.

3.2.2 History and management of the fishery

In the period 1956-1970 four abalone species were exploited in Isla Natividad: the pink abalone *H. corrugata* (70-80% of the catch), the green abalone *H. fulgens*, the white abalone *H. sorenseni* (heavily exploited from 1970, after the decline of pink abalone), and the black abalone *H. cracherodii* (lightly exploited, about 1.5% of the catch). In 1976 the fishery of white abalone suffered a strong collapse, and from 1995 *H.sorenseni* became formally protected. In the period 1980-1984, the fishery sector in the Natividad Island underwent a strong decline associated with El Niño event (Fig. 3.4). *Macrocystis* disappeared from Isla Natividad in 1983 and in 1991. A second collapse occurred in 1997, in concomitance with another El Niño event.

Size limits for both green and pink abalone were formally established in 1956 (145 mm shell length (SL) for *H.fulgens* and 135 mm for *H. corrugata*), although they began to be effectively observed only after 1984. From 1984 to 1997, size limits were increased to 150 and 140 mm for green and pink abalone, respectively, and, from 1997, after the second collapse, they were brought to 155 and 145 mm. For *H. fulgens*, current size should be increased up to 165 mm to avoid recruitment overfishing (Shepherd and Guzmán del Próo, 1991).

In 1985, a marine reserve of about 15 ha was established at the southeastern coast of the Island, and it remained closed until 1990. In 1981 catch quotas were introduced; preliminary surveys were carried on in 1985 to assess the state of the populations. In 1988, annual surveys were started to assess the density of abalone populations: reefs to 20 m depths were divided into 500x500 m blocks. In each block 8-10 samples (each at 5x2 m transects) were taken to estimate total density, density of individuals above the legal size, and density of individuals below legal size. In the period 1990-1995, catch quotas for each block were fixed at 30% (in 1995 between 15 and 30%) of the biomass of fishable individuals, i.e. organisms at or larger than the minimum legal size. In 1996, the quotas were established basing on the estimates of prerecruits predicted to recruit into the fishery during the year. Prerecruits were animals smaller than 10 mm for green and 5 mm for pink abalone. In 1997, the (Hilborn and Walters, 1992) dynamic version of Schaefer surplus production model, modified to include the environmental effect of mean sea temperature anomalies (SST), were applied to fix annual quotas. Bayesian techniques were used to revise the estimates based on the comparison of catches of the previous year and the calculated surpluses estimated from the survey data. Selected TACs were those resulting in projected biomass equal to current levels.

In 2006, two marine reserves, La Plana-Cueva and Punta Prieta, were created around Natividad Island. The fishermen from Natividad Island voluntary closed 5% of their fished area as marine reserves, corresponding to 4 and 7% of spiny lobster and abalone catch, respectively. The receptivity of the fisherman community to this marine reserve initiative supervised by the private Mexican organization Comunidad y Biodiversidad (COBI) was facilitated with their own experience (as cited above, the cooperative closed a small area at the southern end of the island from 1985 to 1990 to recover from a decrease of abalone stock). Currently, about 80% of total catches are made up of abalone (60%) and lobster (40%), and the remaining 20% is made up of red urchin, sea cucumber, sea snails, and red algae.

3.2.3 Exploratory analysis of fisheries data

Fishermen on Isla Natividad systematically record catches and effort for green (*H. fulgens*, figure 3.6) and pink (*H. corrugata*, figure 3.5) abalone from 1994. Information about catch (number of harvested individuals) and effort (hours spent in fishing activities) permits to analyze temporal trends in catch per unit effort. Independent surveys on density of green and pink abalone show that CPUE is a good proxy of abundance for pink abalone (Fig. 3.7B, r^2=0.67, $p< 0.01$) while the relationship was not significant for green abalone (Fig. 3.7A, r^2=0.02, NS). Despite the non-significant result obtained for *H. fulgens*, CPUE can be considered as a good proxy of abundance for both species. Indeed, surveys were carried out almost at depth greater than 10 m, where green abalones are scarce, and hence are likely not representative of the real occurrence of *H. fulgens*.

CPUE for *H.fulgens* is high especially at depths in the range of 0-10 m, reflecting its higher abundance at shallow depths (Fig. 3.8), while CPUE for *H.corrugata* is instead highest at depths greater than 10 m (Fig. 3.9). CPUE for *H.fulgens*, in addition, shows a clear decreasing trend from 1994 up to now (Fig. 3.8), while no temporal patterns were detected for *H. corrugata* (Fig. 3.9).

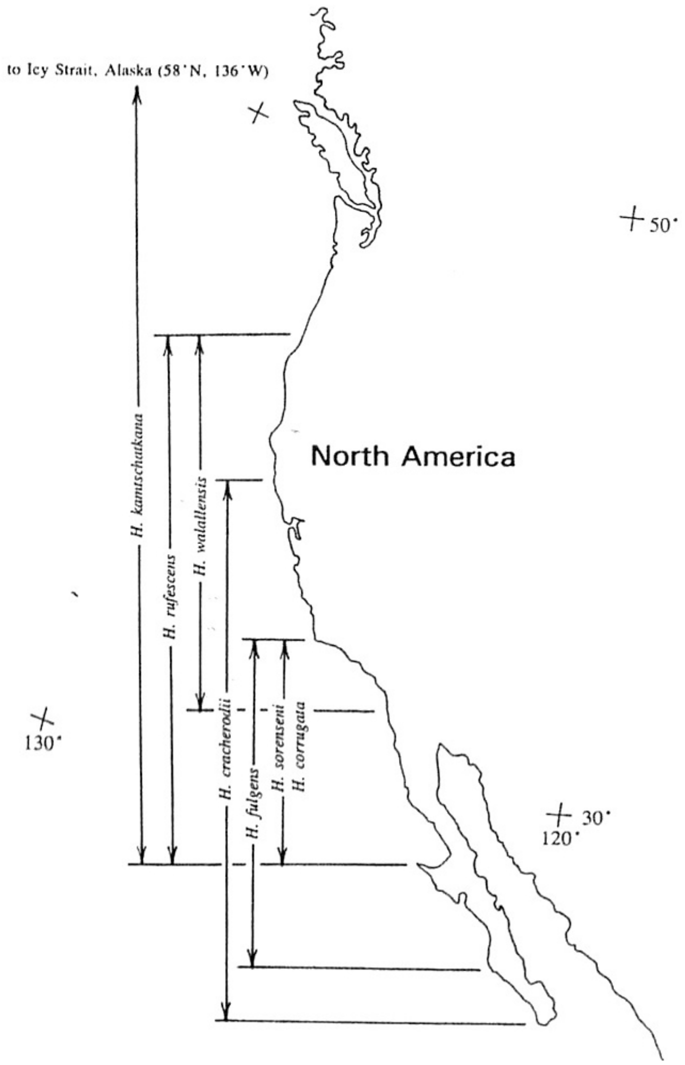


Figure 3.2: Biogeographical distribution of *Haliotis* spp. along the west coast of North America

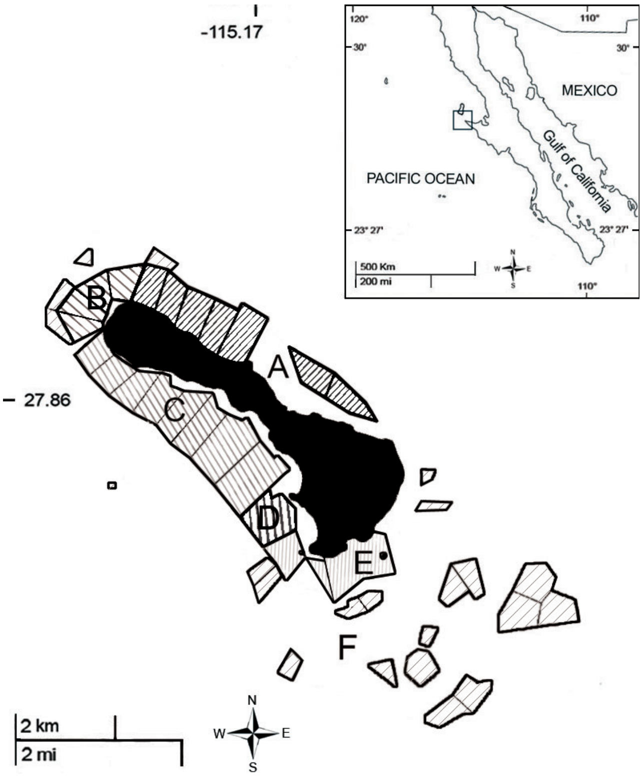


Figure 3.3: Location of Isla Natividad, Baja California Sur, Mexico. The six zones (A, B, C, D, E and F) in which fishing grounds are divided are indicated

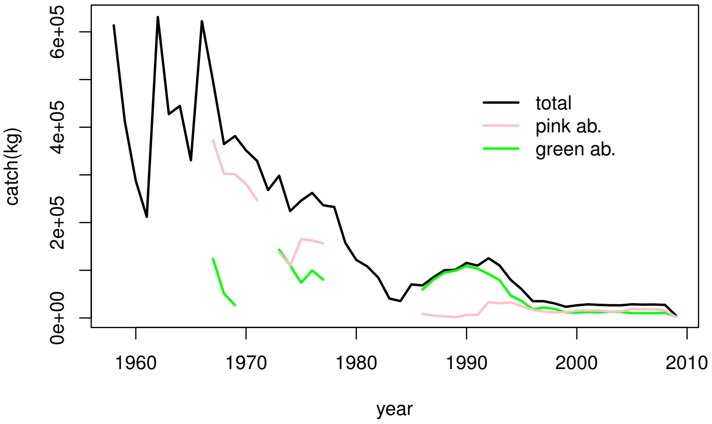


Figure 3.4: Trend in pink and green abalone catches for Isla Natividad

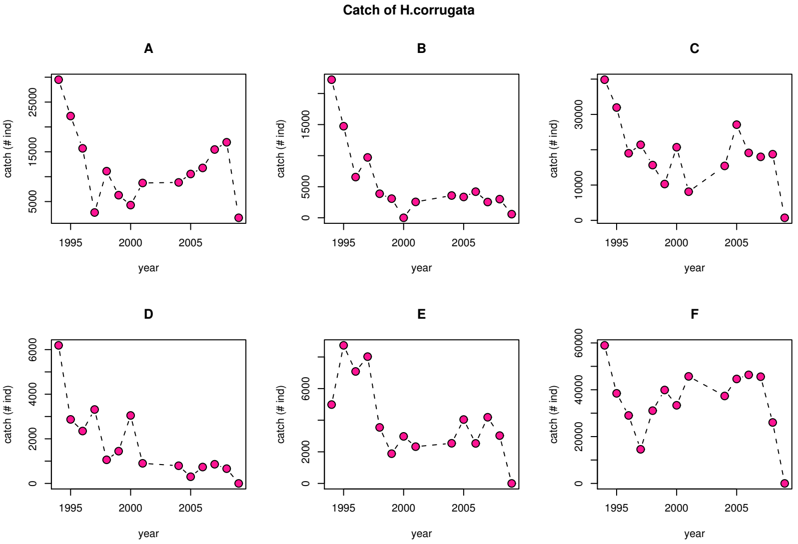


Figure 3.5: Trend in pink abalone catch for Isla Natividad for the six fishing zones in the period 1994-2010

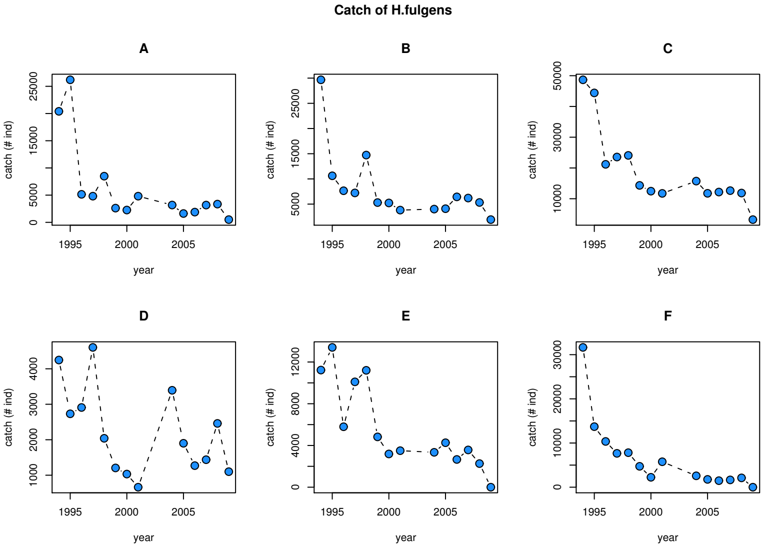


Figure 3.6: Trend in green abalone catch for Isla Natividad for the six fishing zones in the period 1994-2010

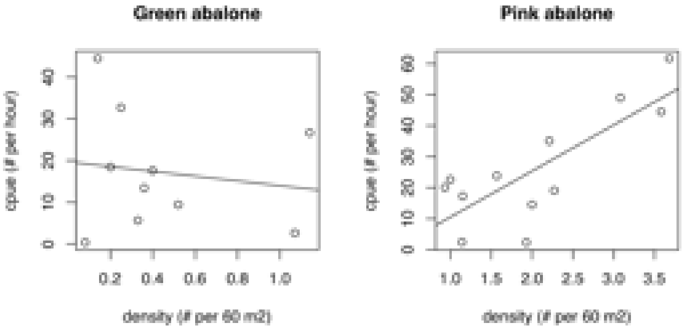


Figure 3.7: Relationship between catch per unit effort and density for *H.fulgens* and *H.corrugata*

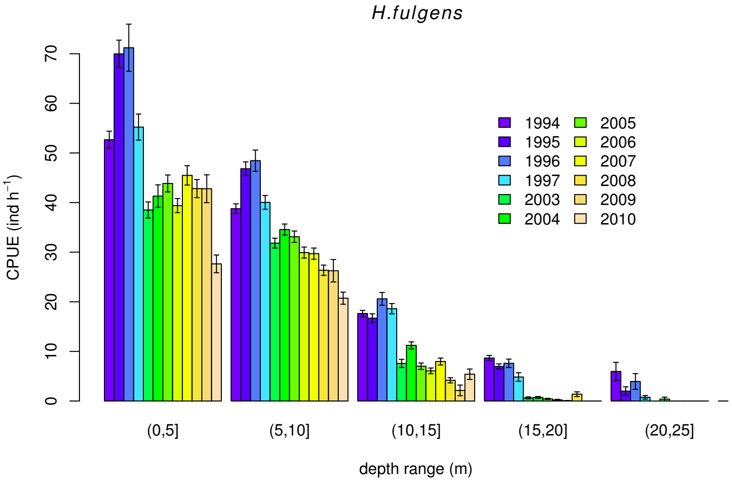


Figure 3.8: Catch per unit effort (number of individual per hour) for *H. fulgens* at different depths in different years

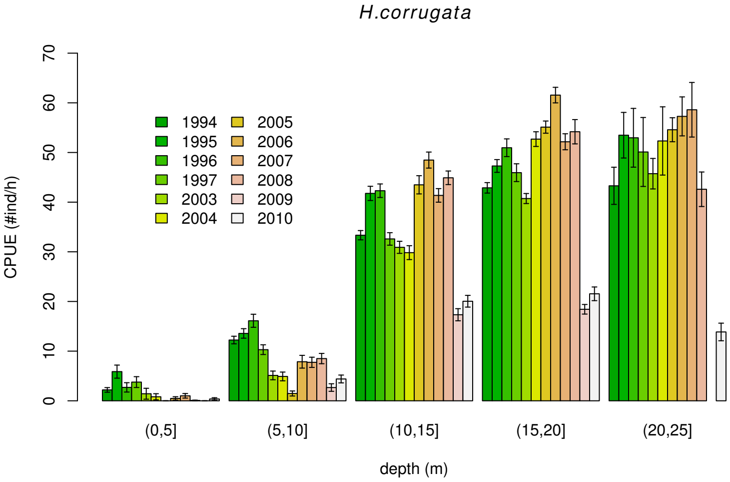


Figure 3.9: Catch per unit effort (number of individual per hour) for *H. corrugata* at different depths in different years

Chapter 4

Allometric scaling of mortality rates in abalone

This chapter has been published in peer-reviewed journal [1]

4.1 Introduction

Identifying the relative importance of the factors that control mortality rates in natural populations is fundamental to understanding and predicting their dynamics (Gulland, 1987). Mortality, as most vital rates, is governed by a combination of physiological and environmental factors, and shows highly regular relationships with organisms body masses at different levels of biological organization (Blueweiss et al., 1978). In most marine invertebrates, mortality rates are often size dependent, with smaller individuals having lower survival probabilities than larger individuals (Gosselin and Qian, 1997). Such inverse correlations are typically attributed to greater vulnerability of small individuals to predation, resource competition and environmental stressors (Byström et al., 2006). Negative relationships between mortality and body can also be related to trade-offs in energy allocation between growth and maintenance (West et al., 2001), with young, fast growing individuals having a lower investment in processes such as immunological competence, resistance to physiological stressors, or developmental stability (Mangel and Stamps, 2001; Hou et al., 2008).

Theoretical and empirical studies suggest that an allometric relationship of the form $\mu = a \cdot M^b$, where a is a normalization constant and b is a negative scaling exponent, subsists between mortality rate (m) and body mass (M) at different levels of biological organization (McGurk, 1986, 1996; Lorenzen, 1996; Brown et al., 2004). Most empirical assessments of the allometry between mortality rates and body size have been conducted at the interspecific level or across different taxa, suggesting negative scaling exponents varying from -0.27 to -0.43 in fish (McCoy and Gillooly, 2008; McGurk, 1986, 1996; Lorenzen, 1996), of -0.26 in invertebrates, -0.20 in birds, -0.24 in mammals (McCoy and Gillooly, 2008), and from -

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[1] Rossetto M., De Leo G.A. Bevacqua D., Micheli F.2011. Allometric scaling of mortality rates with body mass in abalones. *Oecologia*, DOI 10.1007/s00442-011-2163-1

0.22 to -0.30 in plants (Marbà et al., 2007; McCoy and Gillooly, 2008). Empirical studies conducted within population have also highlighted a negative scaling of mortality versus body mass (Bevacqua et al., 2010; Lorenzen, 1996); however, the existence of a consistent allometry between mortality rates and body mass at the intraspecific/ontogenic level remains still unclear.

In this study, I investigate the intraspecific allometric relationship between mortality rates and body mass in marine mollusks characterized by broad distribution, i.e. abalones *Haliotis* spp. In abalones, a decreasing relationship between mortality and body mass has been observed in the field (Shepherd and Breen, 1992), and young abalones are expected to be more exposed to different source of mortalities compared to adults given their weaker shells and a weaker power of attachment to the substratum (Prince et al., 1988). Predation, in particular, can be a major driver in the determination of a higher natural mortality of young abalones compared to adult individuals in the field (Hines and Pearse, 1982; Tegner and Butler, 1985), as larger individuals may attain a refuge from predation because of their stronger foot muscle, their thicker shells and the difficulty that predators have in handling them (Leaf et al., 2007). Because abalones have high commercial value and support both wild capture fisheries and aquaculture operations in several nations, a suite of laboratory and field studies have investigated mortality rates and their relationship with individual size or age. The plethora of published field and laboratory studies conducted on this molluskan genus provides an opportunity to: 1) compare the relationship between mortality rates and body mass among different species, and 2) compare this relationship between natural and laboratory conditions. In particular, I address the questions i) Do mortality rates scale with body mass in multiple abalone species? ii) Does the relationship between mortality and body mass differ between natural and laboratory conditions?

4.2 Materials and Methods

4.2.1 Dataset

Estimates of age-specific, length-specific or mass-specific mortality rates of abalones obtained in the field and under laboratory condition were searched both in the peer-reviewed and grey literature. Data presented in graphs were extracted using the software Plot Digitizer 2.5. All measures of survival and mortality were converted into instantaneous yearly mortality rates μ (y^{-1}). Estimates of abalone mortality were collected for seven species, i.e. the three Californian, USA, species, pink (*Haliotis corrugata* Gray), green (*H. fulgens* Philippi) and red (*H. rufescens* Swainson) abalone; the two Australian species blacklip (*H. rubra* Leach) and greenlip (*H. laevigata* Leach) abalone; the Japanese Ezo abalone (*H.discus hannai* Ino) and the green ormer (*H. tubercolata tuberculata* Linneaus and *H. tuberculata coccinea* Reeve).

For estimates of mortality rates in the field, I include all experiments that monitor natural or transplanted populations of given age or size in natural environment. Only the 8% of the studies reported the initial body weight of individuals, which was hence calculated from shell length through published length-mass relationships. In addition, in the 20% of cases, I calculated shell length from individual age through Von Bertalanffy growth equations. Length-age and length-mass relationships, when available, were extracted from the same data source; otherwise, they were selected from studies carried out in the same region. In total, 101 data points reporting mass-specific mortality rates in the field were collected from 27 studies. For estimates of mortality rates in the laboratory, I considered all experiments conducted in closed systems under controlled conditions. I include studies that exposed individuals at different diet, light, density or temperature treatments, while studies in which abalones were starved or exposed to infectious agents as part of the experiments were excluded from the analysis. The 54% of laboratory experiments reported the initial weight of individuals; in all other cases, the mass was calculated from the shell length of reared individuals using published length-mass relationships. In total, 274 data points reporting mortality rates at different body sizes in the lab were extracted from 46 studies.

4.2.2 Statistical analysis

The significance of the relationship between log transformed mortality rates and log transformed body mass was individually tested for each species both in the field and in the laboratory using ordinary least-square regression. Analysis of covariance (ANCOVA) was used to test whether the relationship between body mass and mortality rates varies among species and between natural and laboratory condition. First, ANCOVA was separately performed on field and laboratory studies and included log-transformed mortality rates ($\ln\mu$) as the response variable and two explanatory variables with their interaction: log transformed body mass $\ln M$ (covariate) and species (7 levels: *H.corrugata*, *H.discus hannai*, *H.fulgens*, *H.rufescens*, *H.laevigata*, *H.rubra*, *H.tuberculata*). In addition, ANCOVA was used to test whether the relationship between body mass and mortality rates varies between natural and laboratory condition. The model included log-transformed mortality rates ($\ln\mu$) as the response variable and three explanatory variables with all first order interactions and multiplicative terms: log transformed body mass $\ln M$ (covariate); species (7 levels: *H.corrugata*, *H.fulgens*, *H.rufescens*, *H.laevigata*, *H.rubra*, *H.tubercolata*); condition (2 levels: laboratory or natural conditions).

4.2.3 Sensitivity analysis

In the dataset, individual body weight was calculated from shell length through published length-mass relationships (of the form $W = aL^b$, where W is weight in g and L is length in mm) in the 92% of field studies and in the 46% of laboratory studies. In addition, in about 20% of field studies, the individual shell length was derived from individual age through the Von Bertalanffy growth equation (of the form $L = L_{inf}(1 - e^{-k(t-t0)})$, with k in y^{-1}, L_{inf} in mm and t_0 in y).

Given the extensive use of these conversion equations, a sensitivity analysis was performed to evaluate how the uncertainty in the estimates of parameters a, b (of the length-mass relationship) and of parameters L_{inf}, k (of the Von Bertalanffy growth equation) can affect the results of this analysis. Typical standard errors associated with the estimate of k in abalone can vary from 0.3 to 25% relative to the mean, whereas errors associated with L_{inf} vary from 0.5 to 5% relative to the mean (see for example Shepherd and Guzmán del Próo

Table 4.1: ANOVA table for the statistical model relating log-transformed mortality rate (lnμ) to variation in log-transformed body mass (ln$M$) and species in field studies

Source of variation	Df	Sum Sq	Mean Sq	F	p
lnM	1	89.68	89.68	137.69	<0.001
species	6	36.15	6.02	9.25	<0.001
lnM:species	6	1.99	0.33	0.51	0.80
Residuals	87	56.66	0.65		

(1991)). Standard errors in the estimates of a and b for abalone are generally of the order of 1-7%. We evaluated the sensitivity of the results to five levels of uncertainty - defining for each parameter five conservatives ranges of variation corresponding to the mean ± 5, 10, 20, 30 and 40% - first varying one parameter at time and then varying all parameters simultaneously.

To evaluate the sensitivity of the result to a given level of uncertainty, I randomly sampled the parameter value(s) from the uniform distribution over the range of variation considered. Using the sampled parameter value(s), I generated a new dataset, performed the analysis of covariance (including ln$M$, Species, Condition and their interaction as explanatory variables) and recorded i) the estimates of the allometric exponent in the field and in the lab; ii) the significance level of the allometric relationship; iii) the significance level of the difference between the field and laboratory intercepts; iv) the significance level of the difference between the field and laboratory slopes. I replicated the process 100 times, calculated the mean and standard deviation of the obtained allometric exponents, and computed how many times the three explanatory terms were significant at the 0.05 level.

4.3 Results

Log-transformed mortality rates in the field were negatively correlated with individual log-transformed body mass for all seven species considered (Fig. 4.1). The relationship was significant for *H.corrugata* ($p<0.05$), *H.discus hannai* ($p<0.001$), *H.laevigata* ($p<0.05$), *H.rubra* ($p<0.001$), *H.rufescens* ($p<0.001$); nearly significant for *H.fulgens* ($p=0.064$); and not significant for *H.tuberculata* ($p=0.121$). Mean estimates of allometric exponents in the field range from -0.524 for red abalone to -0.303 for blacklip abalone, with wide overlapping confidence intervals (Fig. 4.2).

Analysis of covariance on field data indicates that the slopes of the log-log relationships did not differ significantly among species ($p=0.799$) indicating similar scaling of mortality with body mass across the seven species considered (table 4.1). Common allometric exponent was -0.400 (95% CI -0.466, -0.335). The intercept of the log-log relationship, representing the mortality rate at unit weight, was significantly different among species ($p<0.001$, table 4.1), indicating that individuals of the same body size belonging to different abalone species experience different mortality rates.

Log-transformed mortality rates in the laboratory also scaled negatively with individual log-transformed body mass (Fig. 4.1). Allometric relationships were highly significant for

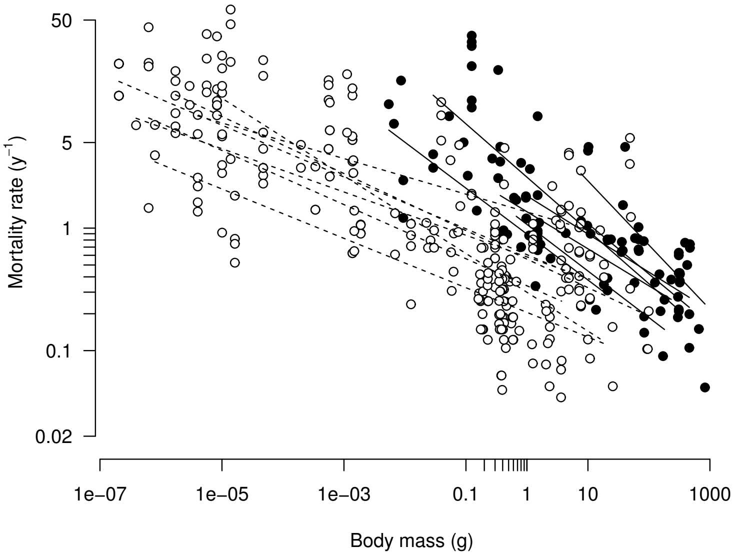

Figure 4.1: Scatter plot of mortality rate versus body mass (both natural log transformed) for seven species of abalone, along with the fitted regression line for each species, for laboratory studies (white circles, dashed lines) and for field studies (black circles, solid lines)

all seven species considered ($p<0.05$ for *H.rubra* and $p<0.001$ for all other species). Mean allometric exponents range from -0.258 for Ezo abalone to -0.145 for blacklip abalone (Fig. 4.2). The slopes of the log-log relationship were not significantly different among species ($p=0.137$, ANCOVA on laboratory data, table4.22) and estimated common slope was -0.221 (95% CI -0.242 -0.200). As in the case of field studies, intercepts of allometric relationships were significantly different among species ($p<0.001$, table 4.2).

For all seven species considered, mean estimates of allometric exponents were consistently more negative in natural than in laboratory conditions (Fig. 4.2). Although the differences in allometric exponents among field and laboratory conditions were not significantly different at the species-level given the wide confidence intervals (with the exception of *H.rubra*), the common estimate of the slope in the laboratory was significantly lower than that estimated in natural conditions, as indicated by the significant interaction term between $\ln M$ and condition (table 4.3).

In natural conditions, the intercepts of allometric relationships estimated in the laboratory were smaller than the estimates obtained in natural conditions (table 3, figure 3) indicating that mortality rates at unit weight are generally higher in the field than in the lab; however, the significant interaction term between the two factors species and condition suggests that the differences between mortality rates at unit weight in laboratory and natural conditions

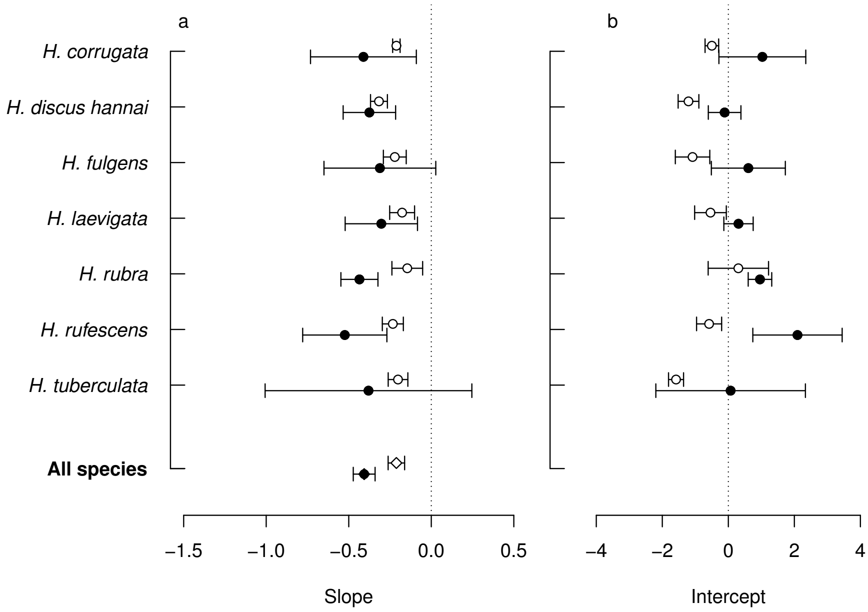

Figure 4.2: Estimates of a) slopes and b) intercepts of linear regressions of the logarithm of mortality rate versus the logarithm of body mass for abalone species along with 95% confidence intervals in the laboratory (white circles) and in the field (black circles). Diamonds represent common estimate of allometric exponents for laboratory (white) and field (black) studies with 95% confidence intervals

are variable among species.

4.3.1 Sensitivity analysis to parameter uncertainty

Results of the sensitivity analysis to variation of single parameters on field and laboratory allometric exponents are shown in figure 4.4 and 4.5, respectively. For field data, uncertainty in Von Bertalanffy parameters does not affect the value of the common slope or the significance level of the differences between the field and laboratory allometries (results not reported). Conversion from age to shell length through Von Bertalanffy growth curve was performed on the 20% of field data and for only three of the seven species considered; therefore, small variations in the estimated shell length on these individuals would have negligible effects on calculated log-weight and on final slope. On the other hand, uncertainty in length-mass relationship could significantly affect the estimates and the associated uncertainty of allometric exponents, both in the field and in the lab, as well as the significance levels of the explanatory variables considered in the model (Fig. 4.4 and 4.5). Results were particularly sensitive to error in the estimate of b, and field data were more sensitive than laboratory data to uncertainty in length-mass relationship. Variation of b greatly affects the calculation of body mass given that it is the power to which individual body lengths are to be raised and it is

Table 4.2: ANOVA table for the statistical model relating log-transformed mortality rate ($\ln\mu$) to variation in log-transformed body mass ($\ln M$) and species in laboratory studies

Source of variation	Df	Sum Sq	Mean Sq	F	p
lnM	1	489.03	489.03	495.36	<0.001
species	6	39.22	6.54	6.62	<0.001
lnM:species	6	9.70	1.62	1.64	0.137
Residuals	260	256.68	0.99		

Table 4.3: ANOVA table for the statistical model relating log-transformed mortality rate ($\ln\mu$) to variation in log-transformed body mass ($\ln M$) and species in laboratory studies

Source of variation	Df	Sum Sq	Mean Sq	F	p
lnM	1	471.42	471.42	522.07	<0.001
Species	6	101.82	16.97	18.79	<0.001
Cond	1	59.68	59.68	66.10	<0.001
lnM:species	6	5.43	0.91	1	0.423
lnM:Cond	1	6.10	6.10	6.75	<0.001
Species:Cond	6	17.352.89	3.20	<0.001	
lnM:Species:Cond	6	4.11	0.68	0.76	0.603
Residuals	347	313.34	0.90		

likely to affect the results given the extensive use of this length-mass conversion equation in this analysis. Results obtained when simultaneously varying all parameters were also likely determined by the effect of uncertainty on parameter b (fig. 4.6). However, given the actual errors generally associated with a and b, I expected a low bias in the actual estimate of the allometric exponents and a good robustness of these results to current parameter uncertainty.

4.4 Discussion

Results of these analyses show that body mass is an important predictor of mortality rates in a group of marine invertebrates. First, the logarithm of mortality decreases significantly and linearly with the logarithm of individual body mass both in natural and laboratory conditions, indicating the size-dependence of different sources of mortality for abalone. Second, allometric exponents are remarkably similar among seven species of the same genus. Third, the comparison between field and laboratory studies shows that in the natural environment factors such as predation and environmental stress have additional contribution to mortality, particularly for younger individuals.

In the field, allometric exponents of mortality-weight relationship were similar among species and I estimated a common exponent of -0.400, which falls in the range of observed intraspecific allometric exponents obtained in previous studies on marine organisms (within populations, Lorenzen (1996, 2000) suggest weight exponents between -0.12 and -0.55). In laboratory condition, allometric exponents were less variable among species and estimated common slope was -0.221, that also falls in the range of weight exponents obtained within species in culture conditions (Lorenzen, 1996). In this study, allometric exponents were remarkably similar among the different species of *Haliotis* spp., despite the wide geographic distribution spanning from America to Europe to Japan to Australia, the different water depth ranges, i.e. low to mid intertidal for *H.fulgens* and *H.rubra* and subtidal for *H.corrugata*, *H.discus hannai*, *H.laevigata*, *H.rufescens* and *H.tubercolata* (Guzmán del Próo, 1992; James et al., 2007) and variation in maximum adult sizes. Mortality rates at unit weight, on the contrary, were significantly different among species both in the laboratory and in the field, suggesting that individuals of the same body size belonging to different abalone species experience different mortality rates. Results of previous studies on allometric scaling of mortality versus body mass among species also found more variability in mortality at unit weight than in allometric exponent Lorenzen (1996, 2000).

Comparison of allometric relationships between natural and laboratory studies suggest that mortality rates are significantly higher in the field than in controlled conditions. This is consistent with the expectation that in the natural environment mortality may be higher because organism are exposed to temperature extremes, storms, disease, starvation, and to ecological interactions, e.g., predation and competition, which all may cause mortality in abalone (Shepherd and Breen, 1992). In contrast, in laboratory conditions, predation, interspecific competition, starvation and physical or chemical stresses are usually absent (abalones are raised in monospecific cultures, maintained in well aerated tanks and typically fed *ad libitum*). Intraspecific competition, however, may still be present in the laboratory and hence contribute to mortality under controlled conditions. The likely absence of ecological interactions in the laboratory studies (except perhaps for intraspecific competition, though even this might have been weak because food was given ad libitum), suggests that something intrinsic to the animals causes the body-size scaling of mortality rates in the laboratory. Energetic trade-offs between growth rates and maintenance (Mangel and Stamps, 2001; Hou et al., 2008) could partially be responsible of the higher mortality rates of young, fast growing individuals with respect to adult individuals. The higher mortality rates of smaller individuals in the laboratory with respect to adults can be due to ontogenic development of the immune system, different ability to face environmental stress, or available energy reserves. Studies on the energy allocation of abalone show that the component of energy budget used for somatic growth decreases with increasing body mass, whereas the budget allocated to mucus production, which is important for locomotion, protection and signal transmission, increases with increasing body mass. The degree by which the amount of energy allocation to maintenance could be a direct predictor of mortality rates, however, still requires further investigation.

The steeper slope of the relationship of $\ln\mu$ versus $\ln M$ fitted on data from natural populations compared to laboratory studies suggests that natural causes of mortality present in the field may be more severe for juveniles than for adults. The only previous comparison of allometric scaling of mortality rates in wild and culture fish populations (Lorenzen, 1996) concludes that mortality rates are lower overall in the laboratory, as in this study, but that allometric scaling is more negative in the laboratory than in natural populations, the opposite of the results for abalone. Lorenzen (1996), in the light of his results, suggests that non-predation mortality (i.e., that observed in laboratory condition) should be more strongly size dependent than predation mortality in order to determine a more negative scaling exponent in natural population. The outcomes of this study would indeed suggest the opposite, that is, that predation mortality is more size-dependent that non-predation mortality. I believe that predation mortality for abalone is strongly size dependent as juveniles are know to be more vulnerable to predators given their weaker shell and lower power to attach to the substratum (Prince et al., 1988); indeed, size-dependent predation has historically advocated as the main factor causing the scaling of mortality rates with body mass in abalone. In this study, all species are represented both in natural and in culture conditions, thus avoiding possible confounding factors due to variability in allometric exponents among species or families. Nevertheless, I am aware that, because the estimates of natural mortality in the field are typically lacking for the smallest size classes, the magnitude of the interaction term between $\ln M$ and condition may have been slightly biased in the analysis, i.e. actual juveniles mortality rates in the natural environment could be higher or lower that predicted from the linear model. Further comparisons on allometric scaling between laboratory and culture studies could contributing to the understanding of the size dependence of different sources of mortality.

Other factors are likely to influence the mortality rates in abalone besides body mass. In this study, the residual variability in mortality could be due to different diets, densities, and temperature conditions both in natural and in laboratory environment as well as random variation among studies. In addition, chronic diseases, e.g. the withering syndrome, can tremendously increase mortality rates leading to precipitous population declines (such as mass mortality events observed in California for the black abalone *H.cracherodii* (Raimondi et al., 2002). Understanding the circumstances under which mortality is likely to increase is fundamental to guide management and restoration efforts.

Abalones are representative of a suite of marine invertebrates including mollusks and echinoderms that share similar life history and characteristics, such as size refuges from predation associated with the development of shells, tests, and spines, and benthic, sedentary juveniles and adults. Thus, I hypothesize that my results could be broadly applicable to other taxa. Additional investigations are needed to clarify the relationship between mortality and body mass in a suite of different taxa.

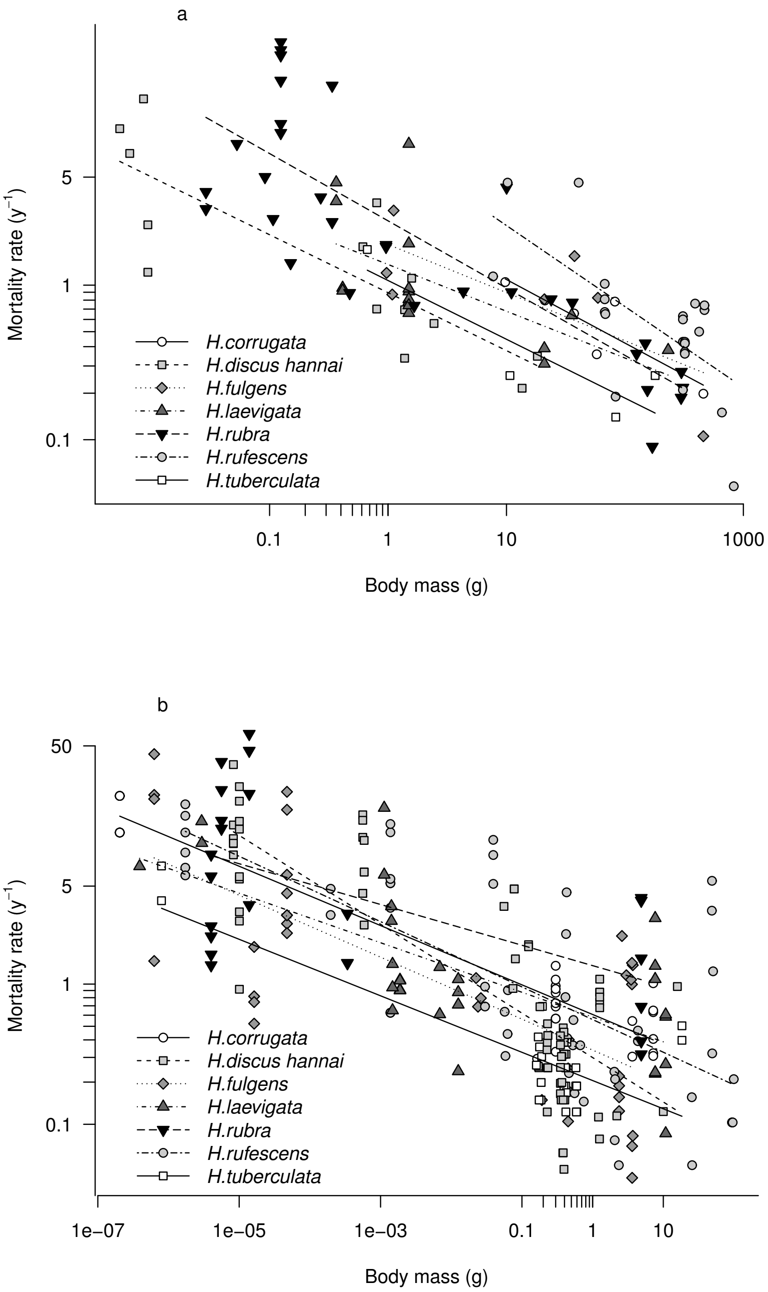

Figure 4.3: Scatter plot of mortality rate versus body mass (both natural log transformed) for seven species of abalone, along with the fitted regression line for each species, for field studies (upper panel) and for laboratory studies (lower panel)

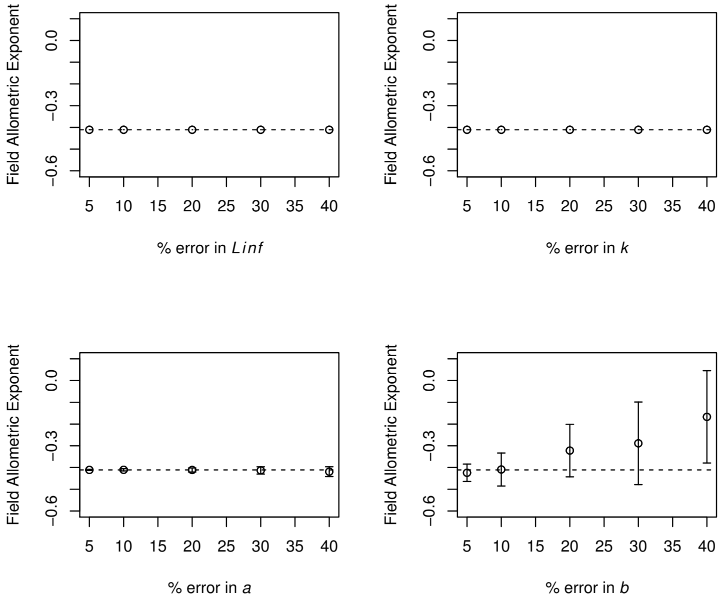

Figure 4.4: Sensitivity of common allometric exponent for field data to variation in parameters L_{inf}, k, a and b. Dashed line represents the allometric exponent estimated when no varying the parameter values.

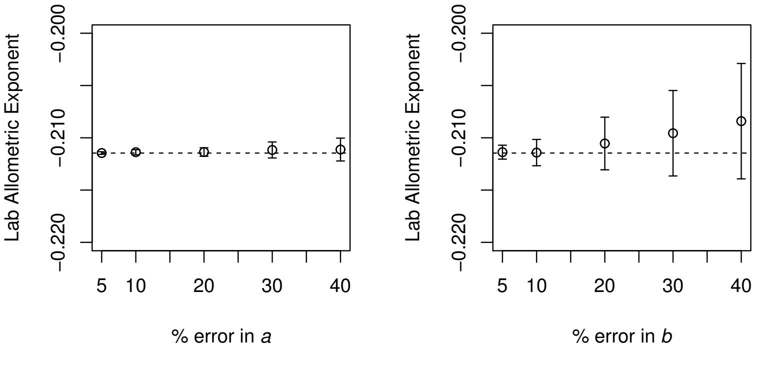

Figure 4.5: Sensitivity of common allometric exponent for laboratory data to variation in parameters a and b. Dashed line represents the allometric exponent estimated in the lab when no varying the parameter values

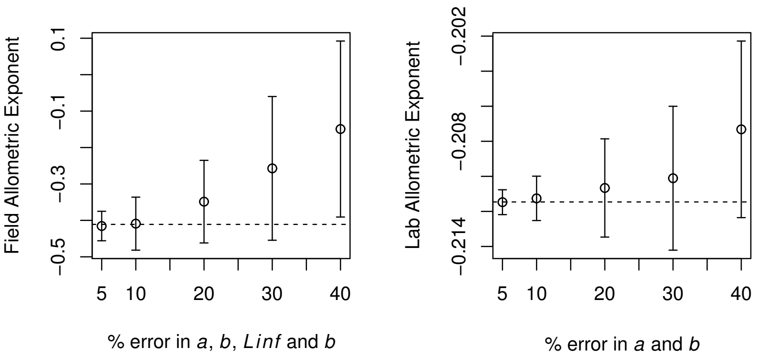

Figure 4.6: Sensitivity of common allometric exponents to simultaneous variation in parameters L_{inf}, k, a and b for field data and to simultaneous variation in a and b for laboratory data. Dashed lines represent the allometric exponent estimated when no varying the parameter values

Chapter 5

Definition of a population dynamic model for green abalone *Haliotis fulgens*

Part of this chapter has been submitted to peer review.[1]

5.1 Introduction

Abalone populations, once sustaining lucrative fisheries, have collapsed in many countries all over the world. Decline of *Haliotis* has been recorded in Canada (Sloan and Breen, 1988), Japan (Masuda and Tsukamoto, 1998), Mexico(Shepherd et al., 1998), USA (Karpov et al., 2000; Hobday et al., 2000), Australia and South Africa (Dichmont et al., 2000). Overfishing, ocean warming, and the spread of disease are accredited as the main factors responsible for the decline, and several *Haliotis* species are now endangered or considered species of concern (Rogers-Bennett et al., 2007; Micheli et al., 2008). Given the high economic value of this fishery, there is considerable interest in improving the understanding of the demography and ecology of this species to rebuild collapsed stock and to prevent the decline of current exploited populations (Dixon et al., 2006).

Matrix models are flexible and powerful tools for analyzing the dynamic of age or size-structure populations and can be used to address management and conservation issues of exploited populations (Rogers-Bennett and Leaf, 2006). Size-based matrix model are considered particularly appropriate to describe the dynamic of *Haliotis* spp., as many demographic traits of abalone are known to scale with body size (Bardos, 2005; Rogers-Bennett and Rogers, 2006; Bardos et al., 2006; Rogers-Bennett and Leaf, 2006). To date, existing matrix models on abalone have been used in a prospective way, highlighting that adult survival has the most influence on population growth (Rogers-Bennett and Leaf, 2006) and that the dynamical re-

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[1] M. Rossetto, F. Micheli , A. Saenz-Arroyo, A. Espinoza, and G. A. De Leo Population dynamics and resilience of an exploited marine invertebrate: combining models and long-term data to assess recovery *Submitted*

sponse of abalone to fishing pressure can be sensitive to the assumptions of the compensatory density-dependent processes (Bardos et al., 2006). Such models include quantitative information on growth, survival and fecundity derived from field or laboratory survey of specific populations (Bardos et al., 2006; Rogers-Bennett and Leaf, 2006), with particular attention devoted to the estimation of growth transition from length-increment data (Bardos, 2005; Rogers-Bennett and Rogers, 2006). Information on larval survival, carrying capacity and/or density-dependent mechanisms of abalone population are instead generally set in arbitrary way (Bardos et al., 2006; Rogers-Bennett and Leaf, 2006) given to the inherent difficulties of directly measuring them. Information on these parameters and processes are however critical as they affect both the long-term equilibrium of the population and the dynamical response to external pressure, and hence are essential for a realistic description of species dynamics. A possible way to fill this gap is the inference of individual demographic rates on the basis of population dynamics, but to date, none of existing studies on abalone has attempted to tightly reproduce the dynamic of a specific fished stock or to infer unknown parameters from abundance and catch time series.

Here, I present a size-based matrix model for green abalone *Haliotis fulgens* in which model parameters have been calibrated on available data on catch and abundance gathered between 1994 and 2010 in Isla Natividad, Baja California Sur (Mexico). Native populations of this mollusk have undergone a dramatic decline all along the California peninsula since the 1970s (Guzmán del Próo, 1992). In USA, green abalone has been identified as species of concern in 2004, and no fishing is allowed south of San Francisco since 1997. Along the Mexican coast of the California peninsula, green abalone, along with pink abalone, still represents about 95% of commercial catches, but after the dramatic collapses in 1983-1984 and in 1996-1997, the current catch levels of both species remained low and great concern exists regarding the sustainability of the fishery (Ponce-Díaz et al., 1998).

Isla Natividad represents the ideal site to study the population dynamic of green abalone. First, a number of field studies have been historically carried out in the area to estimate the vital rates of green abalone. Second, in the last twenty years, the fishermen on the island recorded detailed data on catch and effort, providing thus a valuable time series to be used for parameter estimation. Thirdly, more recently, fishery independent surveys around the island have been initiated to characterize the abalone population in terms of abundance and size structure. My approach aims at combining this quantitative information in a demographic model calibrated on Isla Natividad able to describe the dynamic of green abalone when subjected to exploitation. The model includes basic demographic processes such as growth, size-dependent survival and size-dependent fertility, which were derived from the considerable accumulated research on green abalone population. In addition, the model explicitly includes density-dependence in the larval stage and size-dependent fishing mortality, which parameters were estimated on temporal population surveys and fishery data by using an Approximate Bayesian Computation method.

5.2 Materials and methods

5.2.1 Dataset

Information on catch (number of abalone) and effort (number of fishing trips) on Isla Natividad was available at different temporal and spatial resolution. Total abalone catch (including both pink and green abalone) and effort were recorded for the whole island since the 1969. For 17 years, namely from 1994 to 2010, information about catch of green abalone (number of individuals, ind) and fishing effort (trips) was recorded in each of the six fishing zones A, B, C, D, E and F. For a subset of these years, namely from 1994 to 1997 and from 2002 to 2010, the depth (m) and the time (h) of each fishing dive, along with the number of collected abalones, were also recorded. Fishermen monitored the length-distribution of abalone (in mm) in the six fishing zones in the period 2000-2009. Fishery-independent surveys on green abalone density were conducted in Isla Natividad every year from 2006 to 2010.

5.2.2 Demographic model

The population dynamic of green abalone *Haliotis fulgens* in each fishing zone was described by means of a pre-breeding, birth-pulse size-based matrix model. According to the timing of the biological events and fishing activities, the sequence of subprocesses experienced by individuals was assumed to be reproduction, growth, harvest, and natural survival (Fig. 5.1).

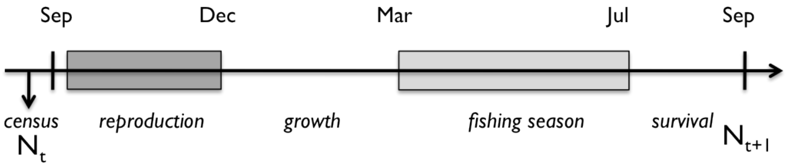

Figure 5.1: Graphical description of the processes experienced by individuals of green abalone during a year. Spawning begins in September and last through the autumn, ending in December or January. Growth was assumed to occur before the fishing season begins, whereas natural mortality was assumed to be concentrated in summer

The model consists of 8 size classes, i.e., two juveniles classes (25-50, 50-75), three classes including unfished adults (75-100, 100-125, 125-155 mm) and three classes including individuals above the minimum legal size of 155 mm (155-180, 180-205, 205-250 mm). Explicitly, the model representation is:

$$\begin{pmatrix} n_{1,z,t+1} \\ n_{2,z,t+1} \\ n_{3,z,t+1} \\ n_{4,z,t+1} \\ n_{5,z,t+1} \\ n_{6,z,t+1} \\ n_{7,z,t+1} \\ n_{8,z,t+1} \end{pmatrix} = \begin{pmatrix} g_{1,1}s_1 & 0 & 0 & \phi_4 s_4 & \phi_5 s_5 & \phi_6 s_s & \phi_7 s_7 & \phi_8 s_8 \\ g_{1,2}s_2 & g_{2,2}s_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ g_{1,3}s_3 & g_{2,3}s_3 & .. & 0 & 0 & 0 & 0 & 0 \\ g_{1,4}s_4 & g_{2,4}s_4 & .. & .. & 0 & 0 & 0 & 0 \\ g_{1,5}s_5 & g_{2,5}s_5 & .. & .. & .. & 0 & 0 & 0 \\ g_{1,6}s_6v_{6,z,t} & g_{2,6}s_6v_{6,z,t} & .. & .. & .. & g_{6,6}s_6v_{6,z,t} & 0 & 0 \\ g_{1,7}s_7v_{7,z,t} & g_{2,7}s_7v_{7,z,t} & .. & .. & .. & g_{6,7}s_7v_{7,z,t} & g_{7,7}s_7v_{7,z,t} & 0 \\ g_{1,8}s_8v_{8,z,t} & g_{2,8}s_8v_{8,z,t} & .. & .. & .. & g_{6,8}s_8v_{8,z,t} & g_{7,8}s_8v_{8,z,t} & s_8v_{8,z,t} \end{pmatrix} \begin{pmatrix} n_{1,z,t} \\ n_{2,z,t} \\ n_{3,z,t} \\ n_{4,z,t} \\ n_{5,z,t} \\ n_{6,z,t} \\ n_{7,z,t} \\ n_{8,z,t} \end{pmatrix} \tag{5.1}$$

where $n_{i,z,t}$ and $n_{i,z,t+1}$ are the abundances of individuals in the size class i in fishing zone z at time t and $t+1$, respectively, s_i is the natural survival of individuals in class i, $v_{i,z,t}$ is the fraction of individuals of class i that remains after fishing activities in zone z at time t, $g_{i,j}$ is the growth transition from class i to class j, σ_0 is the survival from eggs to recruits in the first size class and ϕ_i is the fecundity of an individual in class i. The time unit is one year and the units of n are individuals per hectare of available habitat at a reference depth between 5 and 10 m (ind ha^{-1}).

Growth transitions

Growth transitions (i.e. fraction of individuals in a given class that remain in the same size class or recruit to the following ones) were derived from length-increment data on *H. fulgens* collected in Bahia Tortugas by Shepherd and Guzmán del Próo (1991) and Guzman del Proo (*personal communication*) and in Bahia Asuncion by Guzmán del Próo and Salas. The transition probabilities $g_{i,j}$ (i.e. probability that individuals in a given class remain in the same size class or recruit to the following ones) are often calculated basing on the parameters of the Von Bertalanffy growth curve (Sladek Nowlis and Roberts, 1999; Rogers-Bennett and Rogers, 2006). However, body growth has been shown to significantly deviate from the Von Bertalanffy model for different species of abalone, such as blacklip, red and black abalone (Bardos, 2005; Rogers-Bennett et al., 2007; Micheli et al., 2008). Hence, before calculating the transition probabilities for *H. fulgens*, I first compare four different growth models fitted on length-increment data available for *H.fulgens*. Three deterministic models, i.e.Von Bertalanffy, Richards and Logistic, (Fig. 5.2 A) and the probabilistic Gompertz model used by Bardos (2005) (Fig. 5.2 B) were fitted on length-increment data obtained in tag-recapture experiments.

The results of the fitting are presented in table 5.1. The best model was chosen basing on the Akaike Information Criteria (AIC). Among the four models, the probabilistic Gompertz model better represents the empirical data, having the lowest AIC.

Annual survival

A review of literature on abalone mortalities estimated in natural environment suggests that instantaneous mortality rates scale allometrically with body size (see Chapter 4). Accord-

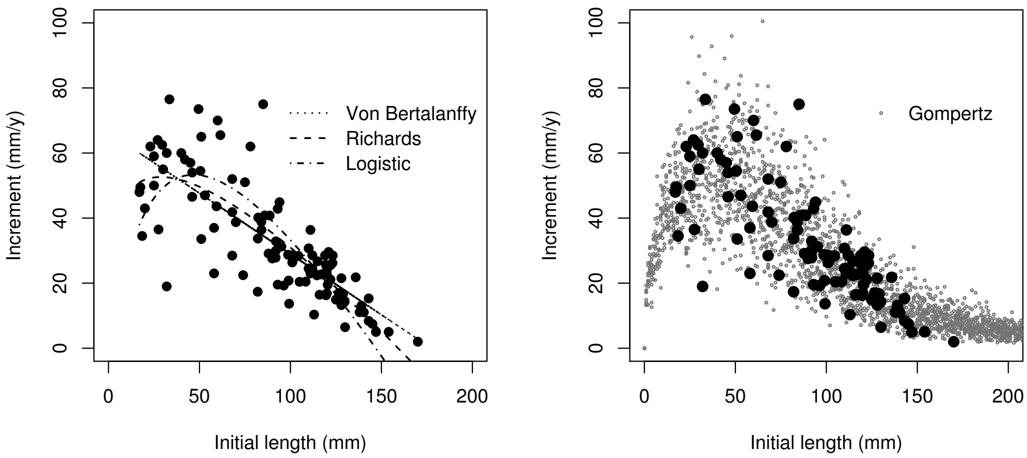

Figure 5.2: Deterministic models (panel A) and probabilistic model (panel B) fitted on length-increment data (black points). Grey dots in panel B are the result of stochastic simulation of the Gompertz curve.

Table 5.1: Results of the fitting of four different models on tag-recapture data obtained for *H.fulgens*

Model	Equation	AIC
Von Bertalanffy	$\Delta l = L_\infty \cdot (1 - e^{-k}) + l \cdot (e^{-k} - 1)$	796.88
Richards	$\Delta l = L_\infty^{-1/n} \cdot (1 - e^{-k}) + l^{-1/n} \cdot (e^{-k} - 1)^{-1/n} - l$	790.93
Logistic	$\Delta l = L_\infty^{-1} \cdot (1 - e^{-k}) + l^{-1} \cdot (e^{-k} - 1)^{-1} - l$	805.73
Probabilistic Gompertz	$p(\Delta \mid l) \sim gamma(L_\infty(l) - l, \mu(l), \sigma(l))$	767.68

ingly, I calculate mortality rate $\mu_i(y^{-1})$ in each size class from mean body mass in each size class M_i (g) by:

$$ln\mu_i = -alnM_i + b \tag{5.2}$$

where a=-0.35 0.06 and b=0.490.28. Body mass M_i (g) was calculated from mean shell length in each size class l_i (mm) using the length-weight relationship for green abalone reported in Shepherd et al. (1998):

$$M_i = 2.24 \cdot 10^{-5} l_i^{3.36} \tag{5.3}$$

Annual survival s_i, i.e. the fraction of individuals in each size class that survive to the following year, was then calculated from mortality rates:

$$s_i = e^{-\mu} \tag{5.4}$$

Fecundity

Mean fecundities φ_i were calculated multiplying the number of eggs e produced by a mature female by the proportion of fecund individuals ξ_i in each size class accounting for a sex ratio 1:1:

$$\phi_i = 0.5 \cdot \xi e \tag{5.5}$$

Several studies on abalone suggest that the number of eggs produced by a mature individual increases linearly with individual weight (Tutschulte, 1976; Litaay and Silva, 2003). Accordingly, in my study, the number of eggs e produced by each mature female in each size class was assumed to be a linear function of body mass with a first occurrence of maturity at 70 mm (≈35 g) (Shepherd and Guzmán del Próo, 1991), using a mean fecundity of 2.67 million eggs at 172 mm length (≈727 g) (Shepherd et al., 1998): The fraction of sexually mature individuals ξ in each size class was calculated using the experimental data of Shepherd et al. (1998), reporting sexual maturity as a function of individual size l (mm). I fit Shepherd's data with the sigmoid curve:

$$\xi_i = \frac{1}{1 + e^{-\frac{l-\eta}{\tau}}} \tag{5.6}$$

where l is the length of individual (mm), η (in mm) represents the size at which 50% of individuals are sexually mature, and τ is a parameter inversely proportional to the slope of the curve at $l = \eta$.

Larval survival

First-year survival σ_0 (representing fertilization success, survival in the larval stage, and early post-settlement survival during the first year) was assumed to be a density dependent process. Density-dependent survival in the early life stages has been observed in laboratory for greenlip abalone *Haliotis laevigata*, blacklip abalone *H.rubra* and European abalone *H.tubercolata* (Daume et al., 2004; G. et al., 2010), and in the field for *H. rubra* (McShane, 1991). In this study, I assume a Beverton-Holt density dependent function to describe survival from larvae to the first size class:

$$\sigma = \frac{a}{1 + b \sum \xi_1 n_{i,t}} \tag{5.7}$$

where a and b are unknown parameters to be estimated by using available data.

Harvest rates

Harvest rates $h_{i,z,t} = 1 - v_{i,z,t}$ (i.e. the fraction of individuals of i size class removed in zone z in year t) were calculated from fishing intensity $E_{z,t}$ (trips ha^{-1}) and catchability coefficients q_i (ha trips^{-1}) in the following way:

$$h_{i,z,t} = 1 - e^{-q_i \cdot E_{z,t}} \tag{5.8}$$

For individuals above minimum legal size (MLS), I assume catchability coefficient be an increasing function of length li (mm), as larger abalones are known to be more susceptible to harvest than smaller ones:

$$\begin{array}{ll} q_i = 0 & if l < MLS \\ q_i = \rho \cdot e^{\alpha(l_i - MLS)} & if l \geq MLS \end{array} \tag{5.9}$$

with ρ and α unknown parameters to be estimated by using available data.

Abalones catches (ind) in each fishing zone in each size class were calculated as:

$$C_{z,t} = A_z \sum \sum g_{i,j} n_{i,z,t} h_{i,z,t} \tag{5.10}$$

where A is the area in fishing zone z normalized to account for between-zone differences in mean water depth.

5.2.3 Parameter estimation and model fitting

The four unknown parameters a and b of the Beverton-Holt density dependence first-year survival and ρ and α of the catchability function were estimated using an Approximate Bayesian Computation (ABC) method with a rejection sampler (Pritchard et al., 1999). Two sets of observations were used for parameter estimation, namely the 17-years time series (1994-2010) of abalone catch (hereafter referred to as $C^{obs}_{i,z,t}$ with z=1, 2..6 indicating the zone level) and the 10-years time series (2000-2009) of size frequency distribution above the minimum legal size (hereafter referred as $\pi^{obs}_{i,z,t}$). The selection criterion was to minimize the square difference between observed and simulated catch and size distributions above the minimum landing size, so as to reproduce the available historical series of catch and size distribution in each zone.

Simulated proportions of individuals in the size classes above the minimum legal sizes in each zone in each year were computed as the ratio between the number of individuals in the j (j=6, 7, 8) class divided by the total number of fishable individuals, that is:

$$\pi_{z,t} = A_z \sum \sum g_{i,j} n_{i,z,t} h_{i,z,t} \tag{5.11}$$

Four zones (B, C, E and F) were randomly selected for calibration and the remaining two (A and D) used for validation. Calibration was performed as follows: a) uninformative (i.e. uniform) prior distributions were defined over a plausible range for each of the four unknown parameters; b) at each replicate j, a parameter vector θ_j=[a, b, ρ, α] was drawn according to the prior distributions of the parameters and then plugged in model (1) to derived estimation of catch $C^{sim}_{i,z,t}$ in years 1994-2010 and size distributions $\pi^{sim}_{i,z,t}$ in years 2000-2009 by using Eq. 6 and Eq. 7, respectively; c) the simulated variables $C^{sim}_{i,z,t}$ and $\pi^{sim}_{i,z,t}$ were compared with the experimental data $C^{obs}_{i,z,t}$ and $\pi^{obs}_{i,z,t}$ by using a combined distance metric based on the sum of squared errors. Steps (b) and (c) were replicate twenty millions of times (j=1,, $2 \cdot 10^7$) and the parameter vectors θ_j corresponding to the 1000 smallest distance metrics were accepted and used to derive the posterior distributions. The mean, mode and median, as well as the 2.5th and 97.5th percentiles for confidence intervals of the posterior distributions were computed for each parameter from a kernel density estimate using the function 'density()' in R version 2.9.2. To assess model performance, I simulated the harvests and size distributions for each of the 1000 parameter vectors and compared theirs mean with the observed datasets of the four fishing zones used for model calibration as well as for the two zones selected for validation. Pearson correlation coefficients were computed between the mean simulated catches and the observed harvests.

5.2.4 Projections of population dynamics and fishery reference points

To characterize the current and future status of abalone fishery at Natividad, I used the best 1000 parameters vectors to derive the following demographic and fishery management parameters: the mean and 95% CI of carrying capacity under natural conditions (i.e. without harvesting); the mean and 95% CI of catchability function above the minimum legal size and the mean fraction of individuals yearly removed in the time frame considered; the maximum sustainable yield (MSY, ind ha^{-1}), the fishing intensity at MSY (trips ha^{-1}) and population abundance level at MSY (ind ha^{-1}). I also computed the maximum population growth rate as the magnitude of the dominant eigenvalue of the transition matrix when parameter b in Eq. (3) is set to zero and the maximum reproductive number at low densities, i.e. the average number of females abalone offspring that a females abalone is expected to produce during its entire life cycle. Finally, I used the model to simulate in each fishing zone the trajectory of abalone abundance and catches from current density levels under three different scenarios of fishing intensity, i.e. i) a business-as-usual BAU scenario in which fishermen continue to harvest with a fishing intensity equal to the average intensity exerted in the last 17 years; ii) a MSY scenario in which fishermen reduce the fishing intensity to the level that would guarantee the maximum yield in the long term; iii) an intermediate scenario in which fishermen reduce the fishing effort to a third of the average exerted in the last 17 years. The above simulations were used to assess the rate of recovery of population abundance under different scenarios.

5.3 Results

5.3.1 Size-based matrix model

The Gompertz growth model estimated on available data provided length increments that closely resemble the observed ones 5.2. Statistics on the fitting outcome and the corresponding matrix of growth transitions $g_{i,j}$ are reported in Appendix A. The fraction of mature females as a function of length is depicted in Fig. 1B: the estimated value of parameters of the sigmoid curve (2) are μ=11.27±0.55 and η=102.050.61. Table 1 shows the overall transition matrix $\mathbf{M}$ (eq. 2) accounting for growth, survival and fecundities, i.e. for a non-exploited population.

5.3.2 Model fitting and parameter estimation

The demographic model was able to successfully reproduce the observed dynamic of the exploited stock in all fishing zones, being able to capture the overall declining trend in observed catches from about 300 ind ha^{-1} in 1994 to 26 ind ha^{-1} in 2010 as well as most of the peaks in harvests 5.3. Pearson correlation coefficients between the mean simulated harvests and the observed ones were very high, spanning from 0.896 for zone D to 0.952 for zone F. The predicted stage distributions above the minimum landing size were also consistent with the observed data 5.3.

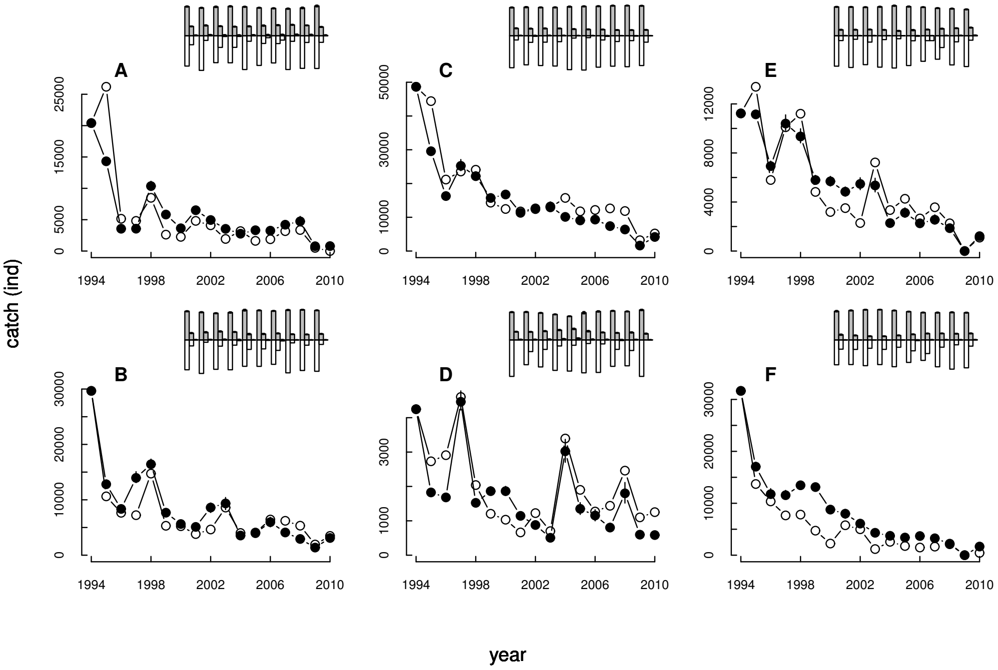

Figure 5.3: Model performance illustrated as visual comparison between observed (black dots) versus mean simulated (solid line) catch rates in the six fishing zones. Barplots in the upper region of each graph compare the observed (gray bars) and simulated (white bars) size distribution above the minimum landing size

Posterior distributions for the four parameters *a* and *b* of the Beverton-Holt density dependence first-year survival (Eq. 3) and ρ and α of the catchability function (Eq. 5) are shown in Fig. 5.4 along with their prior distributions, with mean, median mode and the 2.5th and 97.5th quantiles reported in Table 2.

The two-dimensional scatter plot (Fig. 5.5) shows that the posterior distributions of parameters were characterized by a negative correlation (-0.98) between the parameters ρ and α and by a positive correlation (0.86) between parameters *a* and *b*.

Mean value of *a*, which represents survival from egg to about one-year settlers at low population density, was equal to $5.150 \cdot 10^{-7}$ (95% CI $4.150 \cdot 10^{-7}$-$6.446 \cdot 10^{-7}$). Posterior for parameter b, representing the strength of density-dependence, was less informative, with the 95% interval spanning almost one order of magnitude from a $1.363 \cdot 10^{-10}$ to $1.184 \cdot 10^{-9}$. Jointly, the joint distributions of *a* and *b* indicate a mean carrying capacity of 4489 individuals per hectare, with the 95% interval spanning from 2283 to 12642 individuals per hectare. The

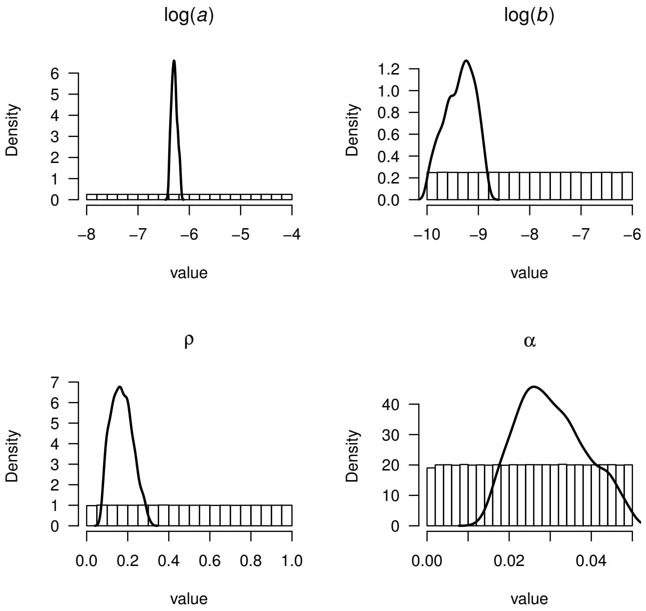

Figure 5.4: Priors (white bars) and posterior density curves (black line) for parameters a, b, ρ, α based on 1000 accepted replicates on $2{\cdot}10^7$ iterations

95% posterior distribution for parameter ρ, representing the catchability of individuals at the minimum landing size, was comprised between 0.093 and 0.265, while that of α was between $1.796{\cdot}10^{-2}$ and $4.490{\cdot}10^{-2}$. Joint estimates of ρ and α indicates that mean catchability was equal to 0.243 ha trip^{-1} (95%CI 0.164, 0.328) for individuals comprised between 155 and 180 mm; 0.507 (95%CI 0.476, 0.538) for individuals between 180 and 205 mm; and 1.525 (95%CI 0.957, 2.466) for individuals bigger than 205 mm.

Fig. 5.6a shows that confidence interval of the estimated catchability was quite narrow for individuals below 200 mm shell length and then it sharply increased for individuals well above 200 mm. The estimated catchability values indicate that over the time frame considered, the average harvest rates was ca. 30%, 52% and 86% for individuals in size class 155-185 mm, 185-205 mm, and ¿205 mm, respectively (Fig. 5.6b). Population finite growth rate at low density, computed from an undisturbed population (i.e. with fishing effort = 0) by setting the density-dependent parameter b of eq. (3) to zero, was equal to 1.135±0.018 (min: 1.095; max: 1.182; median: 1.133) which corresponds to a maximum theoretical doubling time (i.e. number of year for the population to double its initial density) of 5.58 years±0.69 (min: 4.15; max: 7.64; median: 5.55). The reproductive number at low density was equal to 3.84±0.51 (min: 2.79; max: 5.29; median: 3.78) while mean life expectancy for abalone in the first size class was 5.11 years.

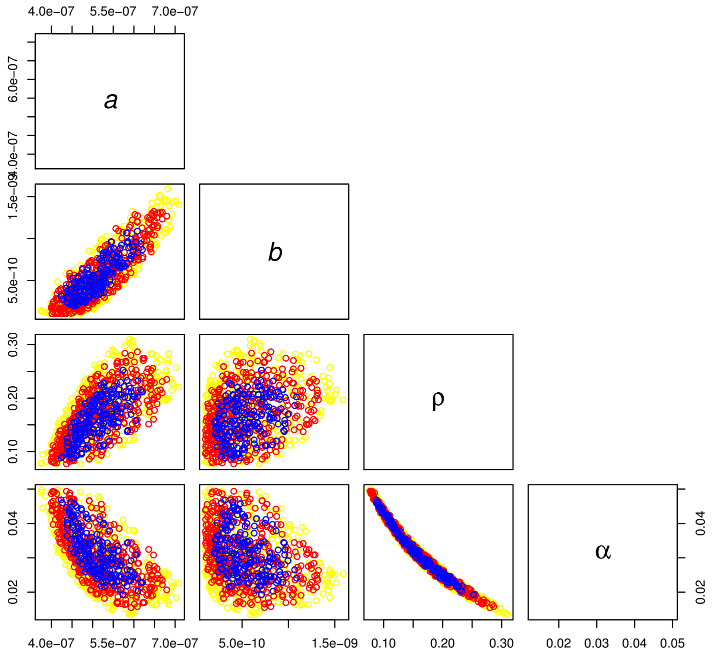

Figure 5.5: Two-dimensional scatterplots of the 1000 accepted parameters vectors

5.3.3 Abalone population dynamic and fishery reference points

The model suggests that the decline in catches in the period 1994-2010 was accompanied by a corresponding decline in abalone densities in all fishing zone considered, from a mean of 1744 (1363-2540) ind ha^{-1} in 1994 to current levels around 330 (331-404) ind ha^{-1} (Fig. 5.7). The simulated population dynamic in absence of fishing starting from estimated total density levels would be characterized by a slow growth rate especially in the early phase of recovery (first 20 years of simulation) and by high uncertainty in the further trajectory (Fig. 5.8); for instance, the model predicts that about ten years of fishing ban would be necessary to allow the population abundance to duplicate from current density levels, whereas 60 years would be necessary to approach the carrying capacity 5.8.

I estimated that the maximum sustainable yield calculate at current MLS (155 mm) would be 94 ind ha^{-1} (95%CI 45-204) corresponding to a fishing intensity of 0.15 trips ha^{-1} and to abundance levels of 2070 ind ha^{-1} (95%CI 979-4424) (Fig. 5.9). The fishing intensity at MSY corresponds to harvest rates equal to 3.3%, 6.8% and 17.8% of individuals in size class 155-185 mm, 185-205 mm, and ¿205 mm, respectively. Exerting the effort at MSY would allow the population to recovery (Fig. 5.10); however, current levels of abundance are so low that corresponding catches would keep low at least in the short term, approaching the maximum yield in no less than 50 years (Fig. 5.10). An intermediate fishing effort of 0.5 trips ha^{-1} would maintain the population and the catches at low levels, whereas I estimate

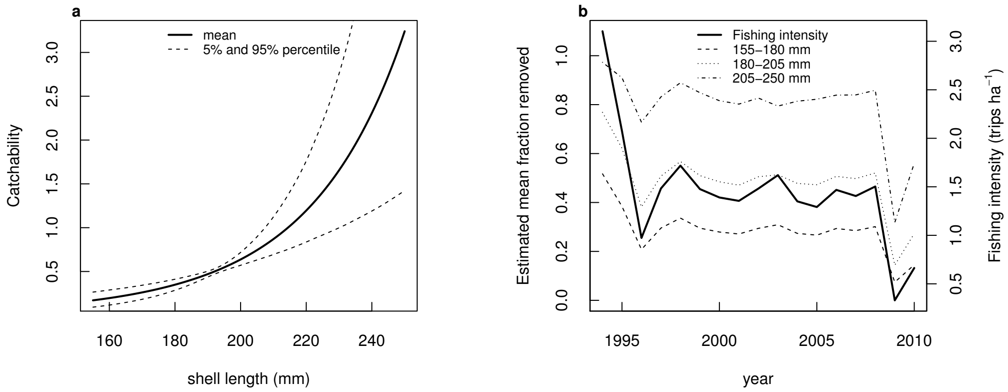

Figure 5.6: Panel a: estimated catchability function above the minimum legal size computed on the 1000 accepted parameters. Panel b: estimated mean fraction removed of the three fished size classes (dashed lines) along with observed fishing intensity (solid line)

that at current abundance level, the BAU scenario would rapidly lead to a continue decline in abalone population and to a complete collapse of the fishery in about 20 years (Fig. 5.10).

5.4 Discussion

5.4.1 Biological insights

The present analysis suggests that remaining populations of *H. fulgens* at Isla Natividad are highly depleted, with current densities lower than 10% of the estimated carrying capacity, and that the very high exploitation rates have significantly contributed to the observed decline of the abalone stock. For such depleted populations, I showed that the development of opportunely calibrated demographic models is of crucial importance to evaluate management and conservation scenarios. My quantitative approach has allowed merging a large amount of information available for *H. fulgens*, including information on key vital rates that have been extensively studied in this mollusk (especially growth and natural survival) and replicate time series of catch, effort and size distribution, providing a good fit to observed data and reliable estimates of demographic parameters. The so calibrated model indicates that continuation of current exploitation trend is likely to lead to a complete eradication of the green abalone population in the area. Therefore, results of the present study would recommend a drastic reduction of fishing effort to foster the recovery of the abalone stock; recovery at densities close to that at MSY, however, could take a very long time, of the order of 20 years or more, even if fishing activities would be completely closed.

The demographic model was able to successfully reproduce the observed dynamic of the exploited stock of green abalone in Isla Natividad. The model efficiently captures the 90% decline in green abalone catches occurred from 1994 to 2010 and suggest that this decline

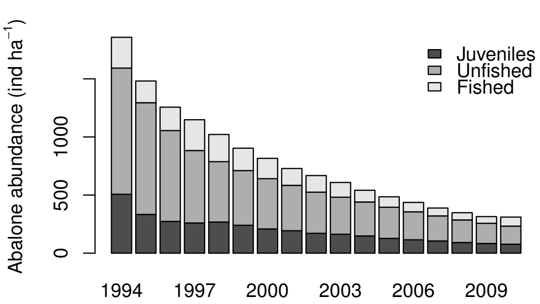

Figure 5.7: Reconstruction of trends in abalone densities for the six fishing zones considered in the period 1994-2010

was accompanied by a corresponding drop of almost 70% in overall population densities. I estimated that abalone densities are now about at less than 10% of the carrying capacity under undisturbed conditions and between 15 and 20% of densities at maximum sustainable yield, an indication that the remaining population of green abalone in Isla Natividad is currently very small and potentially at the verge of a collapse. Few field surveys are available to compare my estimates with observed abalone densities. An intensive field campaign carried out in the Baja California region between 1969 and 1970 showed that green abalone densities were between 230 and 2080 ind/ha. The model for Isla Natividad provided a density estimate of ca. 1750 ind/ha in 1994 and 300 ind/ha in 2009. Recent fishery-independent surveys conducted around the island in the period 2006-2009 found green abalone densities around one hundred ind/ha [between 11 and 112 ind/ha] (Micheli, unpublished data, a value smaller than, yet still in the same order of magnitude of, that estimated by my model in recent years. The difference between my estimation and the fishery independent surveys by Micheli could be at least partially ascribed to the fact the surveys took place mainly in deep waters (below 10 m) where green abalone are significantly less abundant than in the first ten meters (Micheli, unpublished data).

Estimation of parameter a suggests a mean survival from reproduction to one-year settler equal to $5.150 \pm 0.688 \cdot 10^{-7}$. The relatively narrow range of the estimate of larval survival is probably due to the fact that this parameter greatly determines the dynamic of the system under present low-density conditions. The mean value of a seems quite small considered that a single mature abalone can produce more than three million eggs during a spawning event. Yet, the parameter a accounts not only for survival in the larval stage but also for fertilization success and post-settlement survival during the first year of life up to the first size class (i.e. between 25-50 mm). Nevertheless, the overall reproductive success at low density, combined with size-dependent fecundity and size-dependent natural mortality, yields a reproductive rate at low density of about 3.8 offspring produced by one abalone in its entire

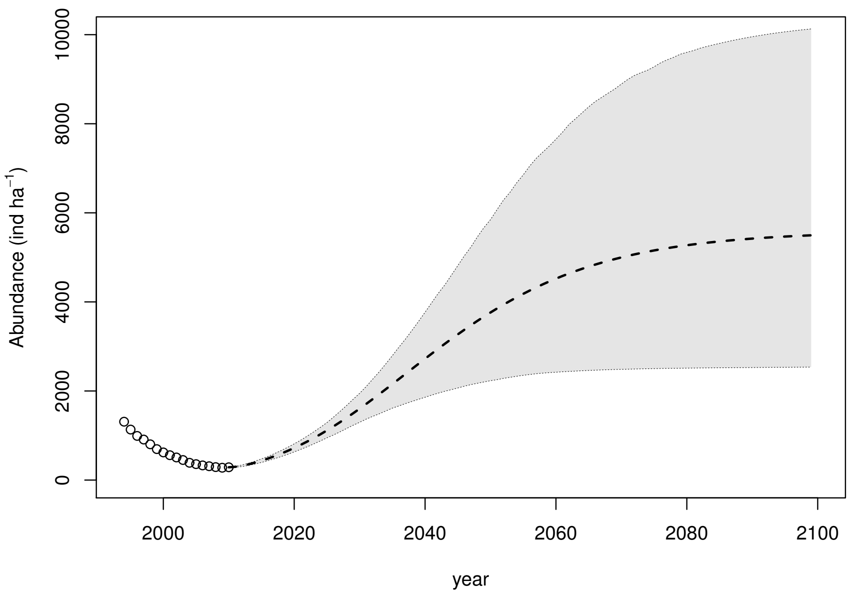

Figure 5.8: Predicted trajectory of abundance in absence of fishing starting from current density level. Results of simulation are reported for zone E

life cycle. I cannot exclude that, given that I am using data of highly depleted population to estimate larval survival, the obtained low lifetime reproductive rate could reflect an ongoing Allee effect, in which the fertilization success is a limiting factor for successful reproduction as spawning adults are further than 1 to 3 m apart (Babcock and Keesing, 1999). The wide posterior distribution of b reflects the fact that it is difficult to accurately estimate the natural carrying capacity in undisturbed conditions by using data of a highly depleted population. The carrying capacity posterior distribution is in fact quite wide spanning a range between 2283 and 12642 individuals per hectare with a mean of 4489. Historical density values for *H. fulgens* are rare (Rogers Bennett et al. 2002) and it is hard to validate this estimation. Despite the great uncertainty associated with this parameter, the estimated range of carrying capacity mostly overlaps with that reported for other species of abalone (*H. rufescens* and *H. cracherodii*) in marine reserves protected for seventy years (Micheli et al. 2008), i.e. 2500-7500 ind/ha.

The joint combination of the distributions of the two parameters defining the catchability rate showed that catchability does increase with shell size. The confidence interval of the estimate is quite narrow until 200-210 mm, while the uncertainty associated with the estimation of catchability increases substantially for size larger than 210 mm. This is partially due to the fact that there are currently very few individuals over 210 mm (less than 2% of the total abalone observations in Isla Natividad), as the majority of large size individuals were

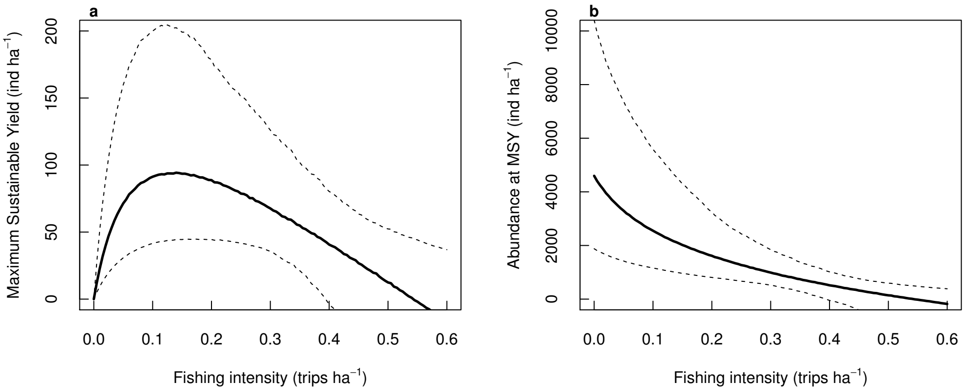

Figure 5.9: Panel a: Sustainable yield (mean and 95%CI) as a function of fishing intensity. Panel b: equilibrium abundances as a function of fishing intensities (mean and 95%CI)

systematically harvested in past and recent times. The estimated harvest rates from 1994 to the present indicate that a large fraction of the population above MLS is removed each year, i.e. more than 30%, and that the fishing pressure is likely contributing to erode green abalone population.

The computation of MSY and effort at MSY suggests that historical effort and related catches in the area have been excessively high, substantially contributing to the observed decline of the abalone population. I estimated that from 1994 to 2008 effort has been at least ten times higher than that that would produce the maximum sustainable yield. Catches have been higher than MSY until 1995 and then declined sharply; in 2011, catches have been less than the 20% of maximum yield. The model suggests that, in order to maximize the long-term yield, a very low fraction of individuals (around 10%) should be removed yearly. This estimate is consistent with fishing mortality rates (not larger than 18-20%) suggested by Shepherd et al. (1998) to maintain sufficient recruitment for green abalone, and with fishing mortality rates around 10% for maximizing yield of slow growing species with similar value of λ (finite rate of population increase) (Sladek Nowlis and Roberts, 1999). To check if the figures of MSY and effort at MSY were reasonably, I also compare them to one of the few example of sustainable abalone fishery in the world, the Australian fishery of *H. laevigata* (Mayfield et al., 2011). The dive fishery of greenlip abalone in South Australia show 40 years of sustainable catch, with stable catch rates around 70 kg per hours of effort and stable abalone densities of 1000-3000 ind/ha. I estimate that, at maximum sustainable yield, green abalone catch rates would be of 627 ind/trip (equivalent to about 65 kg/hr), and abalone densities would be 2000 ind/ha. Therefore, both the emulation of the Australian system and the model would suggest that a recovery of green abalone populations to densities around 2000 ind/ha is necessary to revitalize the fishery of *H. fulgens.*

The model suggest that recovery times for green abalone stocks could be long, in the

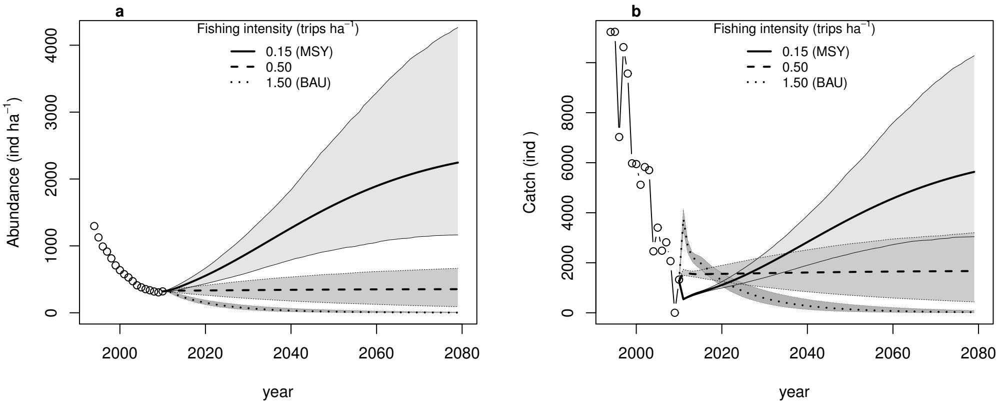

Figure 5.10: Predicted trajectory of green abalone abundance (panel a) and catches (panel b) under different fishery intensity scenarios, including the effort that would guarantee the maximum long-term yield (MSY) and the business as usual (BAU) level of fishing intensity. Trends are shown only for zone E as representative of the other fishing zones

order of 25 years (in absence of fishing) to reach densities that would allow to obtain the yields at MSY, and in the order of more than 50 years to reach the carrying capacity. Such recovery times are consistent with the predictions of about 30 years of Button and Rogers-Bennett (2011) for the pink abalone based on mark-recapture data and body size growth. Fishermen on the island are facing a serious trade off between long and short-term fishery benefits. Exerting historical effort, in fact, although maintaining catches for few years, would ultimately drive the population to a continue decline and to a future closure of the fishery. On the other hand, current levels of abundance are so low that reducing harvest rates to the effort that would guarantee the maximum sustainable yield would result in several years of low catches. Maybe, an intermediate harvesting effort could represent a more desirable option from the fishermen point of view, although it could put the recovery ability of abalone population at risk.

5.4.2 Caveats and limitations

In the present work I tried to explain the observed dynamics of abalone catches in the last two decades only on the basis of historical data on fishing effort and of estimates of abalone natural mortality and fecundity as a function of body size. It is anyway possible that the drop in abalone catches with respect to the first part of the past century may be also ascribed to drivers other than fishing overexploitation, such as subtle ecosystems shifts caused by structural changes in temperature and up-welling frequency and/or intensity. Such changes could either directly reduce reproductive success and increase mortality or, indirectly, make abalone more vulnerable to other stressors such as diseases. Ocean warming is indeed thought to contribute to the decline of Californian abalone through enhancement of infectious disease (L.A. et al., 2005) and possible reduction of kelp forests, the main food source of abalone (Tutschulte and Connell 1988). For *H. fulgens*, however, the effect of increasing water temperature on survivorship, growth or reproduction seems to be limited (L.A. et al., 2005) also when individuals are subjected to the agent of withering syndrome (Moore et al., 2009) . In addition, no long-term historical series of sea surface temperature or upwelling regime dating back to the middle of the past century are available and the analysis of correlation of climatic regime with abalone abundance and survival for the last twenty years is still in process. As a consequence, I could not devise any quantitative data-driven formulation for explicitly introducing climatic variables in the model. Therefore, I deliberately decided to develop a simple size-structured model that does not include environmental variables, as the estimation of unknown parameters presented already its own challenges. Moreover, I are confident that the model developed in this paper represents quite well the observed dynamics at least in the limited time windows of the last twenty years. The analysis of the potential demographic effects of climate variability will be subject to future investigation.

In this work, I suppose that density-dependence in abalone populations occurs only in the survival from eggs to post-larvae and that the Beverton-Holt function is appropriate to describe this compensatory mechanism. Several models conducted on other broadcast spawners also suggest the existence of an upper limit on settlement density or early survival determined by the amount of available habitat (Botsford et al., 1999; Sladek Nowlis and Roberts, 1999). For abalone, coralline habitat for settlers can be a limiting factor for recruitment (McShane, 1992). Density-dependence from larvae to settlers has been observed in laboratory for *H. rubra* and *H. tubercolata* (Daume et al., 2004; G. et al., 2010). In addition, compensatory processes have been shown to extend also in the post-settlement phase (McShane, 1991; Daume et al., 2004). However, there are alternative ways of incorporating density dependence in marine population: mortality, fecundity and growth can be all modeled as density-dependent processes (see Bardos et al. 2006). More experimental studies about density-dependence mechanisms in abalone populations would be desired to clarify the most likely level at which this compensatory mechanism acts. I considered that the population dynamic in each fishing zone is independent from the others; that is, I assume six 6 closed populations with no connectivity through larval dispersion. In abalones, larvae float for only 3-5 days (max 15 days) before settling (Guzmán del Próo, 1992). Given the short larval duration, some authors propose that larval dispersion is limited to tens to hundreds meters, and that the presence of extensive kelp beds and small-scale topographic eddles further contributes to attenuate the larval flux (Prince et al., 1988). However, other authors suggest that larvae could be transported for kilometers, at least in exceptional cases, depending on waves, currents and storms (Tegner and Butler, 1985). Nevertheless, given the high uncertainty associated with the scale and magnitude of larval dispersal, I assumed fully self-recruitment populations and ignore the dispersal process in the model estimation.

5.4.3 Generality of the model

Isla Natividad is representative of the community-based fishery management that characterizes the Mexican Baja California abalone fishery, still worth approx. US $ 20,000,000/year. All fishermen cooperatives in the Baja California region share very similar management plans, and, unfortunately, also face the same challenges of fishery sustainability (Morales-Bojórquez E., 2008). In the region, populations of white (*H. sorenseni*) and black (*H. cracherodii*) abalone, once contributing to local catches, are now virtually extinct. Both recent field surveys and outcomes of the model suggest that abundances of remaining populations of *H. fulgens* in the area are currently extremely low, and mass mortalities events in the area, probably linked to hypoxia events, are imposing additional stress on abalones and other benthic invertebrates. A good management of these depleted fisheries is a real challenge, as failure or misleading indications could be fatal for the harvested stock and for people relying on them. Strengthening the knowledge of key vital rates (as larval survival) and of the understanding of the environmental factors that drive the trajectory of exploited populations can help to prevent a total collapse. In addition, is my intention to apply this modeling approach to evaluate additional alternative scenarios for this fishery (including establishment of no-take zones, change in size limits). While these additions will certainly provide more insights on abalone dynamics and management, this analysis clearly suggests that under the present conditions, continue exploitation could potentially drive the species to a complete local extirpation, and therefore drastic, costly decisions need to be taken in order to prevent the total collapse of the population and, possibility, to foster the recovery of the stock.

Chapter 6

Marine reserves as a management tool for the abalone fishery

6.1 Introduction

In this chapter, I examined the potential of marine reserves to foster the recovery of exploited populations and to support the fishery of the marine mollusk abalone *Haliotis* spp. Abalones populations, once supported lucrative fisheries worldwide, have declined in many countries (Sloan and Breen, 1988; Masuda and Tsukamoto, 1998) and there is an urgent need of promoting the recovery of depleted populations. In particular, there is a growing interest in implementing no-take areas to foster abalone recovery. In a number of cases, in fact, marine reserves have been shown to be effective tools to protect abalone populations. Significantly higher densities of abalones inside no-take zones relative to unprotected sites (up to ten times greater) have been detected for *H. kamtschatkana* in a MR in British Columbia, for *H. asinina* in the Sagay Marine Reserve, Philippines and for *H. fulgens* in the San Diego La Jolla Ecological Reserve. In addition, inside marine reserves abalones are generally bigger than outside. Finally, inside marine reserves, abalones are more likely to be found in aggregations relative to exploited sites. As abalone fecundity increases with individual size (Tutschulte, 1976; Litaay and Silva, 2003) and fertilization success is enhanced when abalones are found in aggregation (Button, 2008), combined responses of abalone densities and size structure to protection can augment the reproductive output of protected populations. The enhanced production of larvae could, in turn, sustain recruitment in the surrounding fished areas if larvae are exported beyond the reserve boundaries.

In particular, I developed a spatially explicit, size-based matrix model mimicking the fishery green abalone *Haliotis fulgens* of Isla Natividad, Baja California Sur, Mexico, to examine how different designs of marine reserve implementation affects population abundance and fishery yields. In Baja California (Mexico), the fishery of green abalone (*H. fulgens*) and pink abalone (*H. corrugata*) is still a high lucrative enterprise, worth approximately US $ 20,000,000 per year. In Isla Natividad, which is representative of the community-level abalone fisheries operating in the entire region, fishermen established in 2005 two no-take marine reserves closing around 8% of their fishing grounds with the aim of protecting remaining populations of abalone and hopefully to enhance their fishery yields. In particular, it is crucial for the fishing community to understand i) if larval spillover effect can compensate for the decrease in abalone catches due to the reduction of the fishing grounds; and ii) if yes, after how much time are the benefits likely to occur.

6.2 Evidence of increased reproductive output inside marine reserves of Isla Natividad

[1]

In Isla Natividad, fishermen collected information about the size frequency distribution of the two populations both inside and outside the marine reserves before and after the reserve creation. Histograms of sizes for green abalone show that size distribution in the reserve site after protection appears different with respect to the non-reserve sites, with the smaller and larger classes more represented (Fig. 6.1). A very similar result can be observed for pink abalone, where bigger and smaller individuals appear more represented in the reserve areas after protection with respect to the non-reserve sites (Fig. 6.2).

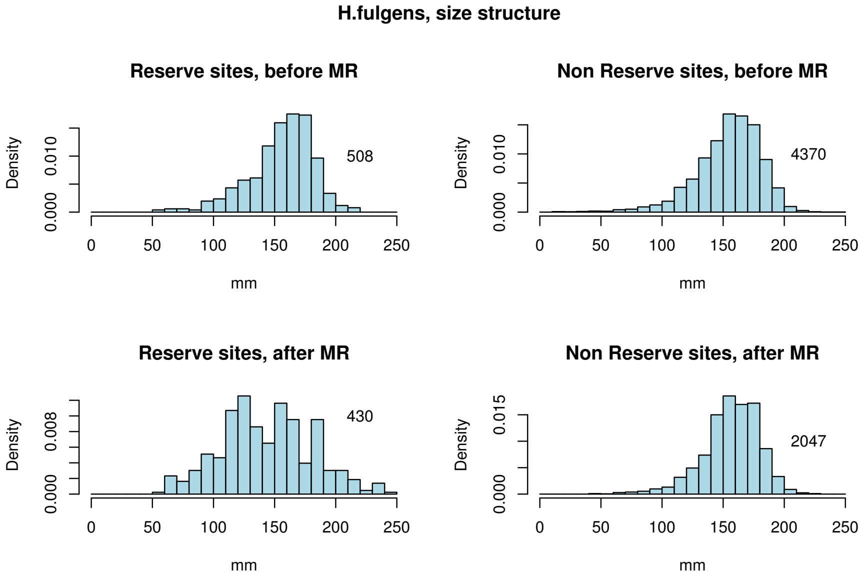

Figure 6.1: Size frequency distribution for *H. fulgens* before and after reserve creation

Although no significant recovery of abundance have been detected so far in the reserve areas, a change in the size distribution can be observed. The presence of bigger individuals can in turn positively affect the reproductive output and hence foster the recovery of the entire population. I tested this hypothesis on *H.corrugata* by calculating and comparing the

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[1] Micheli, F, A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto, G. A. De Leo. Marine reserves enhance population resilience to climatic impacts. *In review*

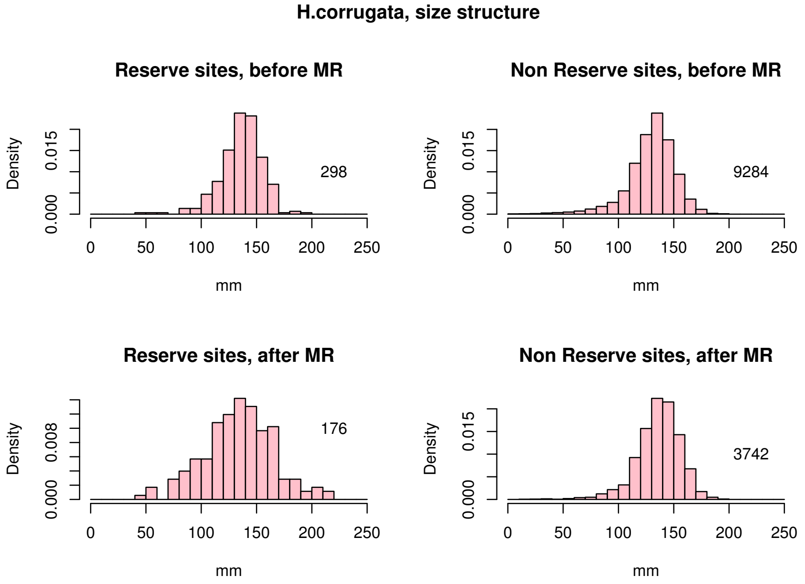

Figure 6.2: Size frequency distribution for *H. corrugata* before and after reserve creation

reproductive potential inside and outside marine reserves. Reproductive output, R, defined as the total number of eggs produced per unit area, was calculated in each year and in reserves and fished areas, using the equation:

$$R = \sum 0.5 f_w n_w \tag{6.1}$$

where 0.5 is the sex ratio, f_w is the fecundity on individuals of weight w and n_w is the mean density (ind m^{-2}) of individuals (estimated through the belt transects) of weight w in the given year (derived from the individuals lengths, see below, which in turn were measured during the timed searches). Fecundity in abalone is known to increase linearly with body mass. The relationship between shell length (mm) and body mass (g) for pink abalone was:

$$w = 1.384 \cdot 10^{-5} L^{3}.50 \tag{6.2}$$

where w is the weight (g) and L is shell length (mm).

I assumed that the number of eggs produced by each female is zero below the size at sexual maturity (103.5 mm, corresponding to 156 g). Above the size at sexual maturity, I assumed a mean number of eggs per gram of female body weight of 2963 [the average between the reported values of 2078 and 3848]:

$$f_w = 2963w \tag{6.3}$$

I bootstrapped the size frequency distributions and density estimates inside and outside the reserves in each year 10,000 times to evaluate the uncertainty in the estimation of reproductive output. The mean and the standard deviation of the reproductive output were computed on the 10,000 bootstrapped replicates. Estimates of reproductive output in the reserves and in fished areas were then compared by using a randomization test performed on the bootstrapped distributions. I used the following procedure: (1) I randomly selected a value θ_i of reproductive output from the bootstrapped distribution obtained for the reserves; (2) I randomly selected a second value θ_k from the bootstrapped distribution obtained for fished areas; (3) I computed the difference between θ_i and θ_k. This procedure was repeated 1,000 times. Significance levels p were computed as the fraction of times the difference between θ_i and θ_k was positive.

Combined responses of abalone densities and size structure to protection enhanced the reproductive output of protected populations. In 2006, when reserves were established, estimated egg production was similar between reserves and fished areas (Fig. 6.3). The difference in egg production between reserves and fished areas increased in each subsequent year of protection. Following the mortality event, estimated reproductive outputs in the reserve were 1.6 and 2.6 times greater than in fished areas in 2009 and 2010, respectively (Fig. 6.3; $p < 0.05$ in both years). Egg production in 2010 was half what estimated in 2006 in fished areas, but increased by 40% in reserves, despite high adult mortality.

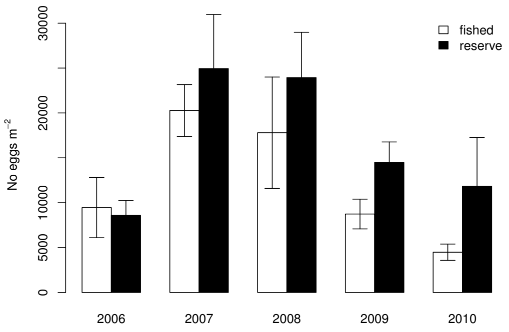

Figure 6.3: Estimated reproductive output (No. eggs produced·m^{-2}· year^{-1}) of pink abalones from reserves and fished areas in 2006-2010. Error bars are bootstrapped standard deviations (SD)

High egg production in reserves resulted in significantly greater juvenile recruitment in reserves compared to fished areas (ANOVA: $p < 0.05$ in 2008; $p < 0.01$ in 2009). In 2008, recruitment rates were, on average, 2.3 times greater in the reserves than in the fished areas (Fig. 6.5a). In 2009, after the mortality event, recruitment rates remained stable in the reserve but were 3.8 times lower, on average, than in 2008 in the fished area, and 9.1 times lower than in the reserve (Fig. 6.5b). Greater recruitment rates were not limited to a single reserve, but were instead documented in both reserves compared to paired fished areas. High recruitment rates were detected at locations inside reserves and within 100s m from the reserve edge, indicative of larval spillover from the reserve to adjacent fished areas (Fig. 6.5b). Recruitment rates at distances greater than 300 m from the reserves edges, except for 1500 m, were significantly lower than within reserves and just outside their edges. Recruitment rates 150, 300 and 1500 m from the reserve edges were highly variable among dates, and not significantly different from recruitment measured within the reserve.

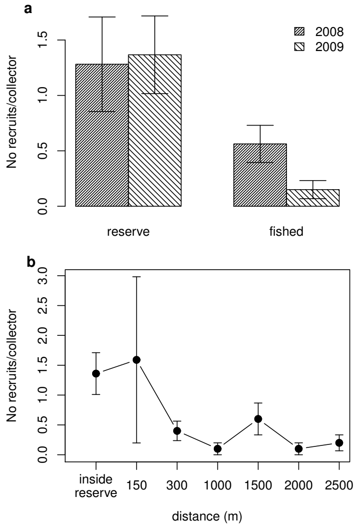

Figure 6.4: Panel a: postlarval recruit abundance (averaged across the recruitment season) within the Punta Prieta reserve and nearby fished area in 2008 and 2009, before and after the mass mortality event of spring 2009; panel b: postlarval recruit abundance (averaged across the recruitment season) within the reserve and at varying distances from the reserve edge

6.3 A modeling approach to assess the efficacy of marine reserves on the abalone fishery of Isla Natividad

6.3.1 Model description

In the model formulation, I assumed that abalones fishing grounds in Isla Natividad extend all around the island perimeter (15 km) extending up to 500 m in the open sea, occupying globally 750 hectares. I represented the fishing grounds as a hypothetical linear array of 150 contiguous patches of 100 m width extending along the coastline. I assumed that all patches are equally suitable for abalone, i.e. that all demographic parameters were the same throughout the fishing grounds. In each patch, abalones grew, survived and reproduced, and-if the patch was fished-individuals also experienced fishing mortality. As abalones are sedentary species, connectivity between patches was driven by the exchange of larvae in the planktonic phase. In each patch, the model followed yearly changes in abalone population separated into eight size/stage categories: two juvenile classes (i.e., below the size at first reproduction of about 75 mm, Shepherd et al. (1991)) (17.5-45, 45-72.5 mm), three classes including unfished adults (72.5-100, 100-127.5, 127.5-155 mm) and three classes including individuals above the minimum landing size (155-182.5, 182.5-210, >210 mm). The boundaries of the first size class were set such that they include the size at one year, approximately between 16 and 50 mm (Guzmán del Próo, 1992).

Each size category contributed to future population through the following rules. First, adult individuals above the size at sexual maturity contributed to larvae production with size-dependent per capita fecundity ϕ_i. In abalones, the number of eggs produced by a mature female is known to increase linearly with individual weight (Tutschulte, 1976; Litaay and Silva, 2003). Accordingly, I assumed that the number of eggs produced by a mature green abalone female was a linear function of body mass with a mean fecundity of 2.67 million eggs at 172 mm length (727 g) after Tutschulte (1976) and Shepherd et al. (1998). Then, I computed the fraction of sexually mature individuals θ_i in size class i by using an s-shaped curve fitted on the experimental data of Shepherd et al. (1998) on sexual maturity as a function of individual size (see section 5.2.2). Finally, mean fecundities ϕ_i were computed as the product of the number of eggs produced by a mature female with the proportion of fecund individuals θ_i and the factor 0.5 to account for a 1:1 sex ratio.

Larvae produced in each patch were partially retained in the source patch and partially exported to contiguous patches. Available studies suggest that abalone larvae, that spend 3-5 days (max 15 days) in the water column before attaching to the substratum, are mostly retained in areas close to parental reefs, because of the short larval duration and because extensive kelp beds and small-scale topographic eddles significantly attenuate the larval flux. Therefore, the majority of studies indicate that abalone larval dispersal distance is limited to ten to hundreds meters (McShane, 1991), although dispersion could reach several kilometers in concomitance with strong currents or storms (Tegner and Butler, 1985). In Isla Natividad, an experimental study on abalone larvae spillover suggests dispersal distance of 300 m (Micheli et al., submitted). Here, I assumed that abalone larvae produced in each patch had a probability to be dispersed at distance x from the center of the patch described by a Gaussian curve of the form:

$$p(x) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{x^2}{2\sigma^2}} \tag{6.4}$$

in which the parameter σ was set so that the 95% of larvae are likely to be retained between -300 m and 300 m from the source. The fraction of larvae f produced in a patch that were dispersed n patch far from the source could be hence computed as:

$$f(n) = 100 \int_{2n-1}^{2n+1} p(x)\, \mathrm{d}x. \tag{6.5}$$

with $f(0)$ representing the fraction of larvae that were retained in the source patch.

Of the total larvae arriving on a patch, only a fraction successfully settled and metamorphosed. Several models conducted on marine broadcast spawners suggest the existence of an upper limit on settlement density or early survival determined by the amount of available habitatr (Botsford et al., 1999, Sladek-Nowlis et al., 1999). For abalone, coralline algae, the preferred substrate by settlers, can be a limiting factor for recruitment (McShane 1992). Density-dependence from larvae to settlers has been observed in the laboratory for *H. rubra* and *H. tubercolata* (McShane, 1992). In addition, compensatory processes have been shown to extend also in the post-settlement phase (McShane, 1991; Daume et al., 2004). Here, I assumed a Beverton-Holt function to describe the dependence of successful settlers S in the first size class on the total number of larvae L reaching each patch:

$$S = \frac{a}{1 + bL} \tag{6.6}$$

Parameter a, representing fertilization success (50%, Babcock and Keesing 1999), survival in the larval stage (10^{-3}, Bardos 2006) and post-settlement survival during the first year of life (assumed around 1%), was set equal to $5 \cdot 10^{-6}$, so as to provide a finite rate of population increase λ at low density equal to 1.2, a plausible value for a slow growing species such as abalone. Parameter b was set to 10^{-9} so that abalones reach in absence of harvesting a carrying capacity around 7000 ind/ha.

After reproduction occurred, individuals in each size class i survived to the following year with survival rate s_i. In abalone, natural survival rates have been shown to be strongly size-dependent, with smaller individuals having lower survival probabilities than larger individuals (Rossetto et al.). Accordingly, stage-specific survival rates were calculated from mean body mass (computed from mean stage length using the length-weight relationship reported in Shepherd et al. 1998) using the empirical allometric relationship between instantaneous mortality rates and body mass reported for green abalone in natural environment (Rossetto et al.).

After survival, individuals either remained in the same size class with probability $g_{i,i}$ or grew to the following ones j with probability $g_{i,j}$. To estimate the growth elements $g_{i,j}$, a maximum-likelihood estimation of a probabilistic Gompertz model for non-negative growth (Bardos 2005) was performed on length-increment data available for *H. fulgens* (see section 5.2.2).

If the patch was fished, individuals above the minimum landing size (i.e., belonging to the sixth, seventh and eighth class) experienced fishing mortality. Harvesting activity was represented using the parameter h, equal to the proportion of individuals caught per year, which is related to fishing mortality F by the equation:

$$h = 1 - e^{-F} \tag{6.7}$$

I used the model to explore the combination of different levels of harvest rates h (from 0 to 1), percentage of fishing grounds closed (0% (no reserve), 10%, 30% and 50%) and size of reserve (100 m or 1500 m) on short-term (25 years) and long-term (i.e. at equilibrium) abalone abundance and fishery yields.

6.3.2 Results

The combination of percentage of fishing grounds closed (10%, 30% and 50%) and size of reserve (100 m or 1500 m) originated six scenarios of reserve spatial arrangement (Table 6.1). An example of a 30% reserve configuration achieved with single no-take areas of 100 m or of 1500 m is depicted in Figure 6.5.

The establishment of marine reserves had an immediate effect in enhancing abalone population abundance both in the long-term (Figures 6.6 and 6.7) and in the short-term (Figures

Table 6.1: Scenarios of reserve spatial arrangement analyzed in this study

% protection	N. of small reserves (100 m)	N. of large reserves (1500 m)
10%	15	1
30%	45	3
50%	75	5

6.8 and 6.9). The positive effect that marine reserves exerted on population abundance relative to the non-reserve scenario was more intense at high harvest rates than at low harvest rates (Figures 6.6 and 6.7). In addition, at a given harvest rate and at given percentage protection, abalone population abundance stabilized at higher values when small reserves (100 m width) rather than big reserves (1500 m) were implemented.

At the equilibrium, in absence of reserves, the model produced standard yield-effort curves (Figures 6.6 and 6.7): equilibrium catches steeply increased with increasing harvest rates, peaked at the maximum sustainable yield (MSY), than sharply declined at higher harvest rates. For abalone, the model suggested that the maximum long-term yield are obtained at a harvest rate of 22% (hereafter referred to as h_{MSY}, harvest rate at MSY).

When a reserve was present and effort was below the h_{MSY} (i.e. the ascending part of the yield-effort curves), the long-term yields with reserves were always below those achievable with traditional management (Figures 6.6 and 6.7). Instead, whenever the fishery was overfished (that is, $h > h_{MSY}$), the effect of reserves on fishery yields strongly depended on individual reserve size. In fact, when small reserves were implemented (Figure 6.6), protection always enhanced fishery yields compared to traditional management, meaning that the overall catches with reserves exceeded those without ones, though protection decreased the amount of fishing area. In particular, protecting about 30% could ensure yields equal or even higher than traditional MSY for most of the harvest rates above the h_{MSY} (Figure 6.6). However, when large reserves were implemented (Figure 6.7), protection enhanced fishery yields only if the fishery was strongly overharvested. Overall catches with reserves exceeded those without ones only if $h > 0.5$. In addition, with large reserves, catches were always lower than those achievable under traditional management. Lastly, protecting at least 50% would produced higher catches than protecting the 30% for $h > 0.5$.

Before reaching the equilibrium yield, marine reserve produced an inital reduction of yields compared with traditional management for every spatial arrangement analyzed (Figures 6.8 and 6.9). The amount of initial catch loss was higher when large proportion of fishing grounds were closed. The duration of such initial fishery loss was strongly affected by the size of individual reserve. For harvest rates higher than h_{MSY}, yields with reserves remained lower than without for about 10 years if reserve size were small and for almost 25 years if reserves were large. In addition, yields with reserve increased more rapidly with small reserves than with large reserves.

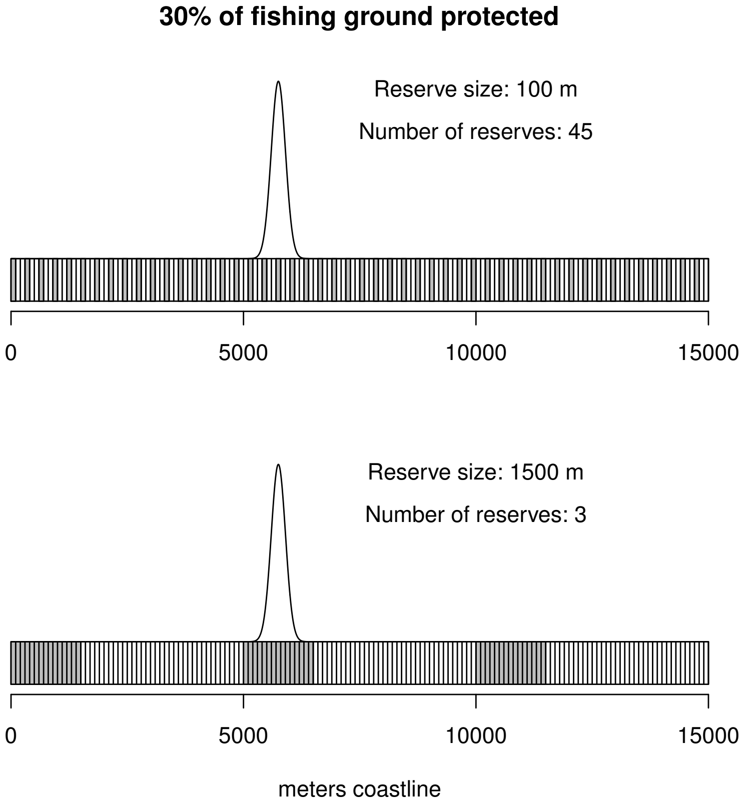

Figure 6.5: Example of two alternative spatial arrangements of marine reserves to achieve an overall protection of 30% of the fishing grounds, with networks of no-take areas of 100 m (upper panel) or of 1500 m (lower panel). The larval dispersal kernel is also depicted

6.3.3 Discussion

The present modeling study produced several key results. First, marine reserves have a positive effect on abalone population persistence, hence providing an effective tool in enhancing abalone population recovery. Conservation benefit are more strong when large proportions of the fishing grounds are protected, and when networks of small reserves rather than large, single reserves are implemented. This result is consistent with most modeling studies on the effect of marine reserves on population recovery (see Gerber et al. (2003) for a review), as well as with experimental studies conducted in existing marine reserves (Roberts et al., 2001; Micheli et al., 2004; Guidetti, 2006).

Second, the establishment of marine reserves is always part of an optimal fishery management strategy whenever the population would otherwise be recruitment overfished. This result is coherent with other modeling studies that highlighted that, for sedentary species, the benefits of marine reserves (relative to traditional managementy strategies) arise only when harvest rates are higher than those that would produced the maximum sustainable yield (Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1999). However, the fact that

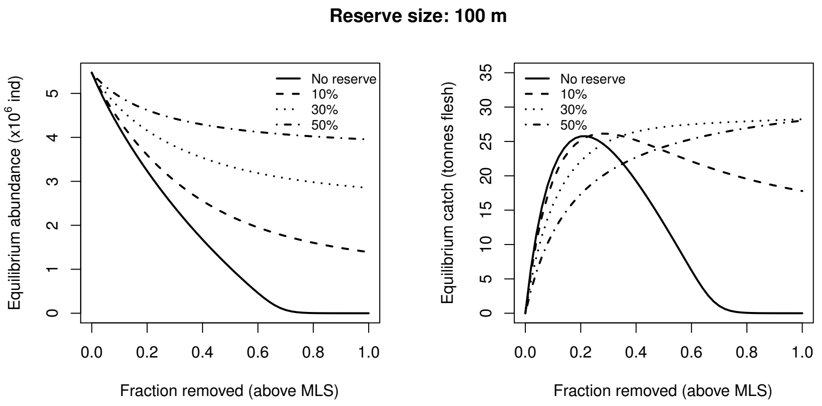

Figure 6.6: Equilibrium abundance (right panel) and catch (left panel) for the whole island at different levels of harvest rate and under different options of percentage closure, achieved with networks of small reserves of 100 m width

reserves increase yield only when a fishery is recruitment overfished should not be taken to mean that they are of little use. Apparently, in fact, effective control of fishing mortality is inadequate in many fisheries worldwide: nowadays, it is estimated that at global scale about half of the stocks (53 %) is fully exploited and another 32% is either overexploited, depleted or recovering from depletion (FAO, 2010). For abalone, the many stock collapses occurred worldwide also suggest that recruitment overfishing is frequent in the management of this marine mollusk, indicating that marine reserves could represent a viable instrument to foster the recovery of the population and of the commercial catches.

Importantly, the magnitude of the fishery benefits of marine reserves for abalone depended strongly on the size of the reserves relative to its larval dispersal distance. In the present study, the establishment of marine reserves can ensure fishery yields equal or higher than traditional maximum sustainable yield (MSY) only when small reserves were implemented (Figures 6.6). In the case of large reserves, instead, implementing marine reserves resulted always in a suboptimal choice (Figure 6.7). In addition, the size of individual reserves also significantly affect the time after which the fishery benefits are likely to occur: the positive effect of protection on fishery yield was expected to occurr earlier with small reserves ($\approx$ 10 years) than with large ones ($\approx$ 25 years). The importance of reserve size in affecting fishery yields is likely due to the fact that, in the case of abalone, with assumed larval dispersal of about 600 m, the size of marine reserves strongly influences the degree by which the enhanced larval production inside the reserve contributes to recruitment rates in adjacent fished areas. In the case of small reserves, in fact, a significant fraction (75%) of larvae produced inside the protected zones are exported in the surrounding fished areas. In this case, reproductive individuals protected inside the reserves ensure succesfull recruitment also in all the outside fishing zones, also when harvesting pressure in the fished areas is intense. In the presence of large, isolated reserves, instead, a significant portion of larvae produced inside the no-take areas is retained in the reserve (Fig. 6.5). Therefore, recruitment in the

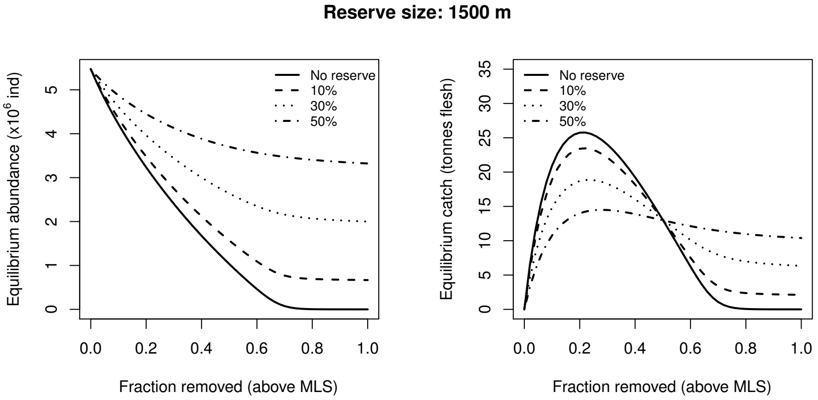

Figure 6.7: Equilibrium abundance (right panel) and catch (left panel) for the whole island at different levels of harvest rate and under different options of percentage closure, achieved with networks of large reserves of 1500 m width

fished areas depended mostly on the local abalone abundance and benefit from protection only near reserve boundaries (Fig. 6.5).

The results agree with previous findings that, for sedentary species with poor larval dispersal, the fishery goal is best achieved by many small reserves covering a large fraction of the coast, alternating with areas of intense fishing (Neubert, 2003). In the present model, the establishment of many, small, equally-spaced marine reserves approximates a 'mixed-larval pool' scenario, in which all larvae produced in the coastline enter a common larval pool and are redistributed equally among adult populations (Gerber et al., 2003). Under these conditions, several models indicate that the maximum yield is the same whether one manages by reserves or specyfing fishing mortality rate (Sladek-Nowlis and Roberts 1999).

Although networks of small reserves are theoretically better than single large reserves for achieving fishery management goals, in many cases a practical implementation of such spatial management could be impossible. For example, it clearly appears from Figure 6.5 that chosing larger reserves could be much more practical than closing many small areas. Nevertheless, in the case of the abalone fishery at Isla Natividad, where historical, exlusive fishing rights exist and where the management of the fishery is carried out by the fishermen community itself, a trade-off between the theoretical optimum and the practical implementation could be more easily found than in open-access, unregulated fisheries. In Isla Natividad, the results of the model could be translated in the local protection of one third of abalone aggregations found during the fishing dives.

Results of the present model are clearly sensitive to the assumptions about larval dispersal ability of abalone. The dispersal distance is a critical variable that is difficult to measure in natural environment and is therefore affected by great uncertainty. Additional studies on the larval dispersal ability of marine organisms can help to ameliorate the confidence in the quantitative results of the population dynamic simulations.

Along the Californian coast, the implementation of networks of small marine reserves

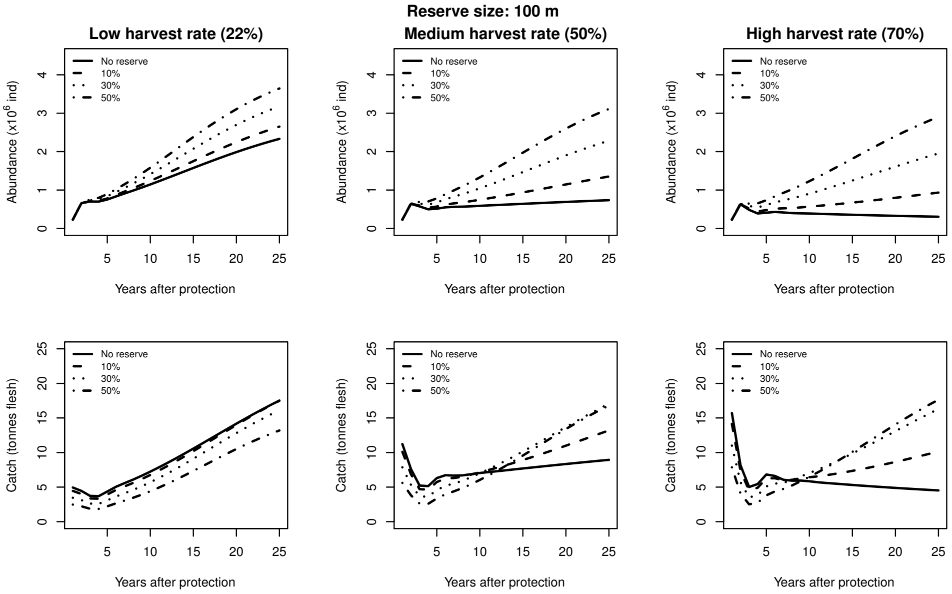

Figure 6.8: Trajectories of abundance (upper panels) and catch (lower panels) for selected harvest rates and under different options of percentage closure in the first 25 years after reserve establishment, with reserve size equal to 100 m

could be beneficial not only for *Haliotis* spp., but also for lesser-known long-lived marine invertebrates, such as wavy turban snails, urchins and crabs, that are expected to become increasingly important fisheries in California (Rogers-Bennett et al. 2007). For example, conservation and management of red sea urchins distributed along the Californian coast may also benefit from the establishment of opportunately spaced multiple reserves (Botsford et al. 1999). Management guidance derived for this system may also help to devise sustainable fishing strategies for many invertebrate fisheries that are rapidly expanding worldwide with limited stock and ecosystem impact assessments, and for which enhanced management attention is needed to avoid negative consequences for ocean ecosystems and associated fisheries and human communities (Anderson et al., 2011).

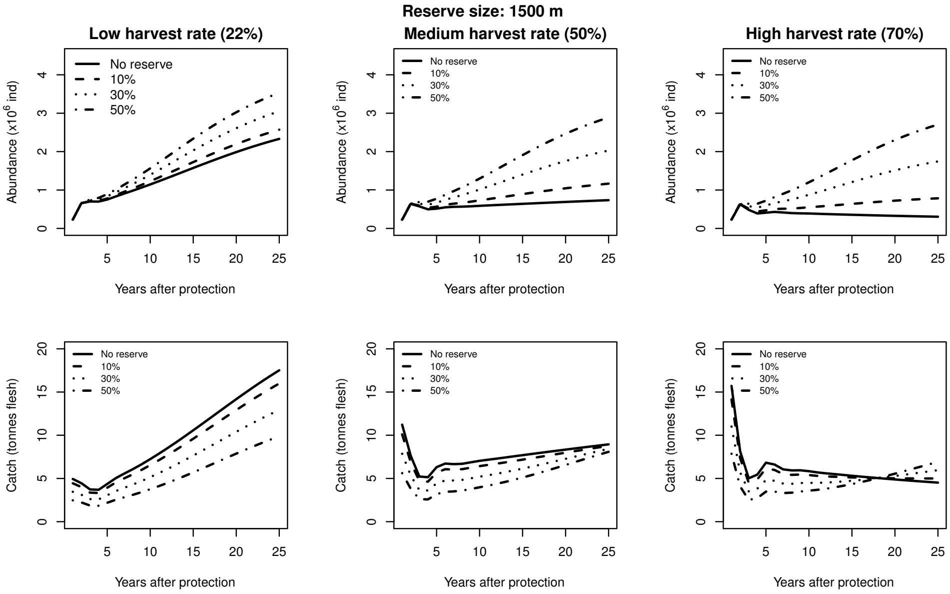

Figure 6.9: Trajectories of abundance (upper panels) and catch (lower panels) for selected harvest rates and under different options of percentage closure in the first 25 years after reserve establishment, with reserve size equal to 1500 m

Chapter 7

Conclusions

Widespread decline of exploited marine populations and associated fisheries requires achieving a better understanding of their potential responses to alternative management strategies. A critical step forward in this direction is to develop demographic models able to reproduce the observed dynamics of exploited populations, then use these empirically-validated models to examine population trajectories under different management scenarios.

Abalone (*Haliotis* spp.) stocks have declined worldwide and attempts to recover depleted populations have generally failed. Thus, there is a critical need to understand current population status, and timeframes and strategies for recovery. In my work of thesis, I tried to contribute to a better comprehension of the population dynamic of this marine mollusk, to ameliorate the management of the abalone fishery and to support the decisions of the fishing community that directly depends on it for its livelihood. This case study is representative of many fishing communities that rely on the exploitation of threatened species, therefore, I hope that the results and the proposed solutions presented in this thesis could be of inspiration for other systems that face similar challenges.

During the three years of doctorate, I visited the fishing community of Isla Natividad several times. I believe this experience has been highy profitable. The interaction with the fishermen communities helped me to understand the importance of the sustainable harvesting of our natural resources and how human prosperity is intimately linked to the safeguard of our planet. Fishermen also found independent interlocutors to support them in the management of a so vulnerable resource. On the island, I collected and analyzed a big amount of fishermen data, that would otherwise be not analyzed by fishermen themselves. The analysis allowed to clarify the population trends and the recent decline of the exploited stock.

To construct the demographic model for abalone, I conducted a thorough review of existing literature on the life history traits of *Haliotis*. First, this review has resulted in a published work on the allometric scaling of mortality rates of abalone (see Chapter 4). Besides providing general insights on the mechanisms of the scaling of this vital rate, this review helped to summarize a big amount of previous scientific works on abalone mortality rates. These estimates can be used for a sound and reliable calibration of abalone demographic models.

In Chapter 5, I presented a comprehensive analysis of current and future trends of abalone populations and associated fisheries in Baja California, carried out through a fine-calibrated size-based matrix model of *Haliotis fulgens*. This work has been novel and of wide interest for several reasons. First, this was the first time that a model of abalone dynamics had been derived by tightly calibrating its demographic and management parameters on fishery independent data and on historical time series of catch and effort. In addition, in this study I provided a robust estimate of a number of relevant demographic and management parameters for abalone, such as first-year survival, density-dependent stock-recruitment relationship and catchability coefficients. Thanks to this analysis I was able to show that the focal abalone population of Isla de Natividad is highly depleted and to quantitatively support the hypothesis that historical and recent harvesting rates likely played a critical role in causing the dramatic decline of the population. In conclusion, this analysis provided ample evidence that *Haliotis* species are highly vulnerable to overfishing and that future persistence of abalone fisheries will critically depend on the communities ability of facing the challenges of trading off between the short-term fishery goals and the long term conservation objectives.

In the last Chapter, I showed that marine reserves can be a useful tool not only for abalone conservation, but also for sustainable management of its fishery. Firts, marine reserves are an effective tool in enhancing abalone population recovery. In addition, the establishment of marine reserves can be part of the optimal fishery management strategy, especially whenever the population would otherwise be recruitment overfished. Importantly, I highlighted that the fishery goal would be best achieved by many small reserves covering a large fraction of the coast, alternating with areas of intense fishing. In Isla Natividad, the results of this simulation model could be practically translated in the local protection of one third of abalone aggregations found during the fishing dives.

Although I am confident that my work provided new perspectives in abalone demography and some useful tools for developing sound fishery management policies, I am convinced that a lot of work on modelling abalone population dynamic still needs to be done. Strengthening the knowledge of key vital rates (as larval survival) and of the understanding of the environmental factors that drive the trajectory of exploited populations can help to prevent a total collapse. More experimental studies about density-dependence mechanisms in abalone populations would be desired to clarify the most likely level at which this compensatory mechanism acts.The analysis of the potential demographic effects of climate variability is also needed. Then, I am convinced that the next challenge for scientists involved in abalone population dynamics will consist in strengthening cooperation with different research fields in order to find quantitative ways of expressing new insights and integrate them in more exhaustive studies of population dynamics.

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