Department of AGRICULTURE FISHERIES & FORESTRY - AUSTRALIA

THE ROLE OF MARINE RESERVES AS FISHERIES MANAGEMENT TOOLS

A REVIEW OF CONCEPTS, EVIDENCE AND INTERNATIONAL EXPERIENCE

BUREAU OF RURAL SCIENCES AUSTRALIA

BRS

Trevor J. Ward
Dennis Heinemann
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AGRICULTURE, FISHERIES AND FORESTRY – AUSTRALIA

A Weight of Opinion

A selection of recent published opinions from marine fisheries managers, scientists and conservationists

"Marine protected areas thus provide the sociological anchor for averting the 'tragedy of the common" and fostering a sense of stewardship for ocean resource and ocean space among the people who most rely on healthy, intact coastal system." (Agardy 1994)

"... possibly high costs relating to exclusion of certain users, the mechanics of boundary delineation, scientific uncertainties relating to identification of ecologically critical areas, lost opportunity and the spill-over of potentially increasing fishing pressure outside the limits of the closed area all necessitate that managers evaluate costs and benefits carefully before using closed areas to complement other forms of fisheries management" (Agardy 2000)

"Reserves will be essential for conservation efforts because they can provide unique protection for critical areas, they can provide a spatial escape for intensely exploited species, and they can potentially act as buffers against some management miscalculations and unforeseen or unusual conditions." (Allison *et al.* 1998)

"To date, most reserve design and site selection have involved little scientific justification." (Allison *et al.* 1998)

"Marine reserves are a critical component of a conservation strategy but must be coupled with other, complementary efforts." (Allison *et al.* 1998)

"...it is not a forgone conclusion that a MPA will adequately protect populations of fish or invertebrates from the effects of exploitation outside its borders, or allow populations to recover from previous exploitation" (Attwood *et al.* 1997b)

"The most compelling reason for implementing a spatial protection approach is that other traditional approaches... habitually fail because they do not effectively control effective fishing effort" (Ault *et al.* 1997b)

"Marine fisheries management is trapped by two assumptions. First, that fishing must be allowed everywhere until demonstrable problems occur. Second, that detailed scientific data on fish stocks can define and then solve these problems in some acceptable way. In fact, there is no convincing factual evidence for either assumption, and the first would prevent the operation of the second, even if the latter was true (no unconfounded controls on which to base valid analysis)" (Ballantine 1995b)

"'No-take' marine reserves offer a new and additional form of fisheries management." (Ballantine 1997)

"The concept of marine reserves is simple: if protected from human interference, nature will take care of itself" (Bohnsack 1993)

"No-take marine reserves are an essential, but underutilized tool in precautionary fishery management" (Bohnsack 1999)

"Overexploitation, stock collapse, and loss of biodiversity are growing problems because of open access fisheries, increased fishing power, habitat damage from fishing, loss of natural refuges, and an inability of traditional methods to effectively control fishing effort and mortality" (Bohnsack 1999)

"Although marine harvest refuges have the potential to contribute an effective tool for fishery management, they should probably be viewed as a supplement for other more conventional management schemes" (Carr & Reed 1993)

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The Bureau of Rural Sciences (BRS), is the scientific bureau within the department of Agriculture, Fisheries and Forestry – Australia (AFFA). It's role is to deliver effective, timely, policy-relevant scientific advice, assessments and tools for decision-making on profitable, competitive and sustainable Australian industries and their supporting communities.

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FOREWORD

Fisheries managers have a number of tools at their disposal to achieve the aims of conservation and management of marine fisheries. Among these tools is the practice of closing areas to extractive activities, and particularly to exploitation by commercial fishers. This practice obviously reduces catches in the short term, but can have longer-term benefits that are not immediately apparent. Recently, the concept of protecting areas of the marine environment with the objective of conserving environmental values has been promoted around Australia, and the benefits of marine protected areas to fish catches are becoming more often discussed.

Input/output control fisheries management regimes require a high level of biological and fishery information, and are difficult and costly to enforce. Alternative management regimes therefore warrant consideration. There appear to be many benefits of managing fisheries through reserves compared with conventional input/output control methods. These benefits may include protection of spawning stocks, supply of recruiting fish, enhancement of catches in adjacent areas, a reduction in the need for biological and behavioural information; and ease of enforcement of statutes and regulations. The pressure to expand the marine reserve system nationwide is poised to intensify into the future, driven by the requirement for multiple use, conservation and fish habitat preservation. Australia's Oceans Policy commits to the creation of marine protected areas, and the Commonwealth is in the process of increasing their area and number. State and territory governments are also developing and implementing their own marine reserve programs.

Despite a lot of enthusiasm about the establishment of marine protected areas, there has been little empirical work undertaken to evaluate their worth in achieving conservation objectives, and less on their effects on adjacent fish stocks. Regardless of the potential benefits of marine protected areas, there is a risk that the goal of achieving sustainable fishing can be undermined if these areas are established as a response only to reducing fishing capacity. The use of marine protected areas as fish refuges may be a simple tool to help resolve a complex problem that requires a number of responses.

This report provides a review of international experience with marine reserves and promotes the understanding necessary to enable areas reserved for fisheries management purposes to be established on scientifically defensible grounds.

P. W. O'Brien

Peter O'Brien
Executive Director

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Trevor Ward is a marine biodiversity specialist and ecological consultant based at the University of Western Australia. His current research interests include the design and implementation of marine protected areas, design of monitoring and performance indicators for sustainable fisheries management, and community-based conservation in small island nations. Trevor was formerly Program Manager for environmental research in CSIRO's Division of Fisheries.

Dennis Heinemann

Dennis Heinemann is a quantitative marine ecologist. He has investigated the ecology of high latitude marine birds, the impacts of oil spills and development on marine bird and mammal populations, the foraging behaviour and ecology of endangered terns, the interactions between fisheries and marine birds, and the ecology of marine fisheries reserves. Currently, Dennis is working in the United States for the National Marine Fisheries Service, studying the conservation and population dynamics of exploited reef fishes.

Nathan Evans

Nathan Evans is an oceans law and environmental policy practitioner. He has worked in the Australian Department of Agriculture, Fisheries and Forestry in both science and policy areas. His interests and expertise are in bycatch policy with particular emphasis on approaches for mitigating fishery interactions with seabirds, sharks, turtles and other species considered at risk. At the time of publication, Nathan had just taken up a research and teaching position in oceans law and policy at the University of the South Pacific, Suva, Fiji.

PREFACE

This document is the report of a joint BRS-CSIRO review of the role of marine reserves as tools in fisheries management. The review was conducted as the basis for development of policy in fisheries management in Australia, but considered the worldwide literature and experience where it was appropriate.

The objectives of the review were:

1. review and assess the effectiveness of marine reserves in Australia, New Zealand and south-east Asia as fisheries management tools and for the conservation of marine resources and biodiversity;
2. identify, describe and make a preliminary evaluation of approaches and models that have been used to identify sites for marine reserves for fisheries management purposes and conservation of marine resources and biodiversity, in Australia and elsewhere;
3. advise as to the potential environmental and social costs and benefits of notional marine protected areas.

Initial funding for the review was provided by the Fisheries Resources Research Fund, and resources to bring the review to completion were provided by Agriculture, Fisheries and Forestry Australia; the Institute for Regional Development, University of Western Australia; and CSIRO Marine Research.

Comments from interested readers are welcome.
Please email comments, questions or updates to:tward@ird.uwa.edu.au

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Callum Roberts, University of York, UK

The report, or portions of this report, has been reviewed by Derek Staples, Geoff Williams and Kerry Truelove (BRS), and Alan Butler, Tony Smith, and Keith Sainsbury (CSIRO), and we acknowledge their support and inputs. Louise Galli (AFFA) provided assistance in compiling parts 5 and 6 of the report. We also acknowledge the support of the Project Steering Committee, established by BRS. Helpful comments on the draft have been provided by Marc Mangel, Neville Barrett, Colin Buxton, Alan Butler, Rod Fujita, Nic Dunlop and Burke Hill.

GLOSSARY OF TERMS

Marine Protected Area

A Marine Protected Area (MPA) is an area of seabed and overlying waters dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means (after ANZECC 1998). MPAs are reserves that may take many forms, and confer different levels of protection for biodiversity depending on the uses permitted and the type and extent of management applied. A Marine Fisheries Sanctuary is a specific form of MPA where all exploitation is prohibited.

Marine Fisheries Sanctuary

A Marine Fisheries Sanctuary (MFS) is an area of seabed and overlying waters that is permanently managed as a 'no-take' reserve as part of an overall fisheries management strategy for a region. Marine Fisheries Sanctuaries are continuously in effect (not periodically open and closed for exploitation) and comprehensive in coverage (cover all living and non-living elements of the ecosystems within their boundaries).

Focal Species/Stock

A stock or species may be of interest in a given discussion for a variety of reasons—perhaps because it is targeted by fisheries, the subject of fisheries management actions, part of the reason for the establishment of a reserve, in need of conservation attention, and/or important to the fishing industry and society. We use the term 'focal' to refer to the stock or species of interest in the given discussion. We avoid the term 'fish' for the simple reason that not all exploited species or species protected by reserves are fish, and constructions such as 'targeted fish and shellfish species' are unnecessarily complex.

Reserve Effect

This phrase refers to a process that typically occurs after the establishment of a reserve in an area previously subject to fishing impacts, in which multiple characteristics of individuals, populations, communities, habitats and ecosystems are altered. For example, reserves typically result in an increase in average age and sizes of individuals, increase in population sizes and densities, enhanced reproductive output, increase in biodiversity, improved habitat complexity, and shifts in ecosystem function. This phenomenon was first referred to as the 'reserve effect', described by Francour (1989, cited in Sasal *et al.* 1996), and the term subsequently has been used consistently in the literature on Mediterranean marine reserves (Francour 1994, Harmelin *et al.* 1995, Macpherson *et al.* 1997, García-Charton & Peréz-Ruzafa 1999, Lamesa & Vacchi 1999), although apparently nowhere else.

Sanctuary Improvement

When the 'reserve effect' results, or is hypothesized to result, in an improvement in identifiable, valued components of a sanctuary (e.g. increased population sizes of fished species, increased biodiversity, or increased habitat complexity), we use the term sanctuary improvement.

Spillover

The net movement of post-settlement individuals from reserves, generally in response to density and habitat differences across reserve boundaries resulting from the reserve effect.

Larval Export

The net movement (export) of eggs and larvae (reproductive propagules) from reserves in response to improved spawning conditions and increased reproductive potential resulting from the reserve effect.

Stability Enhancement

The reduction in variability of the productivity of marine reserves as measured by their rates of spillover and larval export, or their contribution to the number of individuals that are recruited to the fishery.

Fisheries Enhancement

The result and process whereby reserve or sanctuary establishment causes, presumably through the processes of spillover, larval export and stability enhancement, improvements to exploited stocks, the fishers and fisheries that depend on them, and the socio-economic systems affected by those fisheries.

Settlement

We use this term (and sometimes 'larval settlement') to refer to the point in development at which larvae make the transition from the planktonic phase to the juvenile phase, which is usually accompanied by a movement from the pelagic habitat to demersal habitat.

Recruitment

This term refers to the point at which an individual becomes fully established in its juvenile habitat following the process of settlement. Recruitment may occur very shortly after, or effectively at the same time as, settlement. Operationally, in ecological studies, recruitment is defined as the point at which recently settled individuals become detectable and susceptible to specific sampling gear. When the possibility for confusion exists we use the term 'ecological recruitment' to distinguish the type of recruitment defined here from 'recruitment to the fishery' (see below).

Recruitment to the Fishery

In fisheries science, the terms recruitment has a very different meaning, so we use the phrase 'recruitment to the fishery', or 'fisheries recruitment' to specify the fisheries meaning. This concept refers to the point at which an individual reaches the size at which it is subject to capture by a fishery. Recruitment to the fishery may occur long after settlement and ecological recruitment.

Overfishing

Excessive fishing mortality that results in damage to exploited stocks is called overfishing. There are five recognised types of overfishing (Bohnsack & Ault 1996, Attwood *et al.* 1997b).

'Growth overfishing' occurs when the mean size of harvested individuals is less than the mean size that would theoretically result in the optimal yield based on balancing individual growth and mortality rates. This form of overfishing will result in a reduction in the size/age distribution in the exploited population.

'Recruitment overfishing' results when fishing mortality results in a reduction in the population's reproductive potential, which can occur directly if excessive numbers of spawning age/size individuals are caught, or indirectly if so many pre-spawning age/size individuals are caught that recruitment to the spawning population is insufficient to sustain the population, and can lead to population collapse and, at least, local extirpation. In either case, the spawning biomass is insufficient to produce potential recruits to sustain the population.

'Genetic overfishing' occurs when fishing mortality results in genetic changes to the population, such as when the largest and fastest growing individuals are consistently removed from the population.

Overfishing can reduce stocks to the point where fisheries can no longer economically target that species. In this situation, fisheries typically switch their focus to the next most desirable species. 'Serial overfishing' occurs when this process results in the sequential overfishing of a number of species.

In some cases, this level of serial overfishing can escalate to wholesale destruction of marine communities, a process called 'ecosystem overfishing' or 'Malthusian overfishing' (Pauly 1988b, Pauly *et al.* 1989).

CONTENTS

EXECUTIVE SUMMARY

Experience with marine reserves for fisheries management purposes in Australia is limited…

This report reviews the literature and experience in Australia and overseas to determine the extent to which marine reserves have been used to provide effective support for fisheries management. Considerable emphasis has been placed on global experience, because experience with marine reserves for fisheries management purposes in Australia is limited. The focus is on no-take marine reserves (also known as sanctuaries) for fisheries management purposes, and we refer to this form of reserve as a Marine Fisheries Sanctuary (MFS). Our objective is to document potential and realised benefits for fisheries, to identify key gaps in knowledge, and to outline future directions that may be of benefit to fisheries managers as they consider the potential for MFSs in Australia

Fisheries management systems have not always been able to protect fisheries from overfishing…

In general terms, Australia's fisheries are in good shape—few can be classified over-fished. However, many fisheries are fully exploited and overseas experience shows that good fisheries management systems have not always been able to protect fisheries from overfishing. There is a recognised need to adopt a precautionary approach to account for unpredicted dynamics and externalities that may act to destabilise fisheries, with the attendant risk of overfishing. The major imperative for conducting this review is, therefore, to ensure that Australian fisheries are kept at the forefront of ecological experience. This will enable Australian fisheries management systems to adopt the best practices and approaches to fisheries management. The literature that relates to marine reserves used for fisheries management purposes is reviewed to evaluate the potential for reserves to assist fisheries management systems to become more precautionary and more effective in achieving ecologically sustainable fisheries.

Sanctuaries can provide important benefits to marine fisheries…

We find, as have many before us, that there is an overwhelming body of ecological theory and knowledge that suggests that sanctuaries can provide important benefits to marine capture fisheries, provided the reserves are appropriately designed, sited and managed. However, empirical evidence shows that there are very few examples where benefits to a fishery (as opposed to the reserve) have been well studied, and are documented and proven. Most studies have focused on reserve improvement (in the sense that the reserve itself is changed) when, from a fisheries perspective, the key issue is the type and extent of benefits that are derived by the fishery, across such matters as catch, effort, profitability, socio-economic impacts in local communities, and regional development.

A conceptual model is used to identify key elements and processes …

To classify the benefits that sanctuaries may bring to a fishery, a conceptual model was assembled representing the main bio-physical processes involved. The model summarises the main potential benefits to a fishery from a sanctuary, and allowed us to identify many of the issues associated with delivery of these benefits to a fishery. Based on this model and approach, we develop and discuss a set of evaluation criteria that can be used by fisheries and conservation managers to assess the benefits of fisheries sanctuaries. These criteria will permit fisheries managers to assess the performance of MFSs in terms that are meaningful for both fisheries managers and a broad range of stakeholders, and would enable a more active engagement of fisheries managers in the current initiatives on marine protected areas.

Sanctuaries have the greatest potential to enhance fully- or over-exploited populations

Sanctuaries have the potential to provide most benefit to fisheries that are presently either fully or over-exploited. The benefits to be derived from a sanctuary are made possible by two key bio-physical processes: 'spillover'—the export of adults and juveniles of target species to the fishery—and 'larval export'—the distribution of propagules of the target species into settlement areas, from where they will eventually recruit into the fishery. These benefits to a fishery will depend critically on the life history strategy of the target species, and the design of the sanctuary, including its location, size and shape. The third key benefit that we expect to be derived from fisheries sanctuaries is 'enhanced fisheries stability'. Sanctuaries provide the basis for a more precautionary and 'bet-hedging' management strategy for fisheries, and this would reduce variability associated with the interaction of fishing and environmental dynamics. The most effective design for optimal benefits is likely to be a network of sanctuaries with a mixture of large and small individual areas. We identify 7 key Criteria, with a range of optional Indicators, that should be used to assess the performance of MFSs, and in particular to evaluate the fishery benefits as well as broader benefits for biodiversity and regional communities.

Sanctuaries may provide for bet-hedging management strategies

A robust basis for future stakeholder engagement with government and community marine conservation initiatives…

The knowledge needed to design and implement sanctuaries is already available for many Australian fisheries, and such sanctuaries could be designed and implemented now, and, supported by traditional fisheries management tools, would be likely to provide significant fishery benefits. However, given the extremely limited global experience, optimising the performance of sanctuaries and their role in the suite of existing fisheries management tools, and improving the efficiency and effectiveness of the design and implementation process for new sanctuaries, all will require some additional information. These information needs cover 5 areas of fisheries management and 2 areas of ecological knowledge. Better information in these areas will also provide a more robust basis for future engagement of the fishing industry and fisheries managers with government and community marine conservation initiatives:

1) A detailed understanding of the stock-recruitment relationship for the focal species, and what the variation in that relationship in space and time means to achieving fishery benefits from a MFS system;
2) Documented experience about the extent to which MFSs reduce the risk of fisheries collapse caused by environmental stresses, failure of the fisheries management system, or mis-management of the fishery;
3) Documented experiences on the response of fishers to the design and establishment of MFSs intended to assist with the management of their fishery;
4) Empirical measurements of the benefits (such as yield, economic, employment) that are realised by an Australian fishery from the implementation of a network of MFSs, and supporting evidence of the processes responsible for delivering those benefits;
5) Development of explicit procedures and models for identifying which fisheries will benefit from MFSs, and experience with designing and implementing Australian MFSs that are optimised across the range of competing objectives;
6) Knowledge of the processes within sanctuaries in relation to the target species for a fishery, and to their predators, prey or otherwise dependent species;
7) Detailed knowledge of the larval export characteristics of the target species in fully exploited and over-exploited fisheries, and the species dispersal characteristics in relation to local hydrographic and environmental characteristics.

Sanctuaries offer a more precautionary and lower-cost approach to management…

Overall, despite the lack of documented economic successes for fisheries, sanctuaries offer a major opportunity for fully and over-exploited fisheries to adopt a more precautionary and lower-cost approach to management that is highly likely to deliver improved benefits. With careful attention to sanctuary design and management, we expect that MFSs integrated into the existing fisheries management system would provide a net benefit to fisheries that are presently fully or over-exploited. Sanctuaries also offer the added advantages that they stand to make a major contribution to local and regional conservation goals for biodiversity beyond exploited species because they are likely to have a broad range of fishery and non-fishery benefits.

Optimising sanctuary benefits requires balancing many competing interests…

Balancing the many competing interests and objectives, but still achieving strong outcomes for fisheries and fishery management, will require considerable design skills and capacity. To ensure that MFSs are established that have been carefully designed to optimise benefits, in addition to the seven gaps in knowledge outlined above, projects need to be initiated that focus on the development of modeling skills and capacity in fisheries agencies in relation to sanctuary design and implementation. This could be best achieved as part of the demonstration projects discussed above in points 2, 3 and 4.

Systematic design of sanctuaries is needed to achieve maximum benefits for fisheries

The major challenge ahead is to identify specific approaches and design methodologies that will produce reliable marine fisheries sanctuaries to best achieve these benefits in the short to medium term. In order to achieve maximum benefit for implementing MFSs, considerable effort should also be allocated to document and promote this set of benefits, to ensure that experiences across Australia are appropriately recorded and disseminated. The important elements in the MFS implementation process are the systematic design, identification, selection, management and monitoring of the reserves. This will have a high initial cost for the establishment phase, but we expect that the routine fishery-wide management costs will ultimately be lower than at present, certainty and security will be increased, and conflicts reduced because of the existence of demonstrated evidence of sustainability. Implementing networks of sanctuaries for fisheries purposes will provide the capture fisheries sector with an opportunity to further demonstrate its commitment to marine conservation, and to further develop the principles of precautionary management and the practice of ecologically sustainable development within fisheries management systems in Australia.

1. INTRODUCTION AND BACKGROUND

1.1 Marine Reserves

Marine reserves are spatially defined areas of ocean or estuaries where natural populations of marine species are protected, either in part or completely, from exploitation or other detrimental anthropogenic pressures. Typically, reserves are created for the conservation and restoration of high-value species and/or habitats (Kelleher 1996, Attwood *et al.* 1997a, Bohnsack 1998, Dayton *et al.* 2000), with management controls being used to restrict activities that are incompatible with achieving the conservation objectives for the given species or habitats.

Reserves are created for conservation and restoration of high-value species or habitats

Marine reserves can be created for a very broad range of reasons (Allison *et al.* 1998, Agardy 1997), and to benefit many different types of organisms. Marine reserves in Australia exist to protect icon species and habitats (e.g. dugongs and coral reefs), spawning or nursery grounds of commercially harvested species (e.g. seagrass meadows, coral reef flats, and mangroves), areas of importance for recreation or tourism (e.g. coral reefs), and places of cultural heritage value (e.g. historic shipwreck sites, or sites for observation and recreation such as the remains of the former HMAS Swan scuttled in Geographe Bay (WA). Australian reserves vary greatly in size and are controlled under different management legislation and arrangements depending on the primary purpose behind their declaration. In addition to formal reserves, numerous smaller community-managed or-controlled local reserves have been developed, particularly in coastal areas of tropical Australia (Jacoby *et al.* 1997).

Marine reserves contribute to the conservation of biological diversity

Marine reserves primarily dedicated to the conservation of biological diversity are usually known as Marine Protected Areas, or just MPAs (McNeill 1994). Many marine reserves, both formal and informal, make important contributions to the conservation of biological diversity, but if their primary objective is, for example, the preservation of an important shipwreck site, then their contribution to conservation of biological diversity is likely to be coincidental. In these situations, management is not directed specifically to the associated species and habitats that may be found within their boundaries.

MPAs require commitment from government and the local community

Humphrey & Smith (1990) suggested that effective marine conservation requires the integration of 1) threatened-species protection, 2) habitat preservation, 3) mitigation of cumulative anthropogenic impacts on environments, and 4) sustainable resource exploitation; these are objectives which Agardy (1994) suggested could all be met through the use of MPAs. Allison *et al.* (1998) cautioned, however, that while marine reserves are essential to conservation, scientifically sound design and implementation is critical to their success, and that their potential is constrained by the scale of the processes upon which their effectiveness depends (e.g. planktonic dispersal of larvae).

MPAs may be declared for a variety of purposes, but none are guaranteed to attain their objectives. In many countries, particularly those of the tropics, MPAs are declared in order to assist with the sustainable use of living resources, and particularly for local communities that depend on subsistence catches of fish and shellfish (Johannes 1978, Heslinga *et al.* 1984, Savina & White 1986, Alcala 1988, White 1989, Russ & Alcala 1994, Carter & Sedberry 1997, McClanahan *et al.* 1997, Watson *et al.* 1997). However, such reserves, as is the case for all MPAs, are exposed to violation of their management controls (Klima *et al.* 1986, Savina & White 1986, Tegner 1993, Russ & Alcala 1994, McClanahan & Kaunda-Arara 1996, Watson *et al.* 1997, Gribble & Robertson 1998, Guzman & Jacome 1998, Rogers-Bennett *et al.* 2000). The capacity to manage MPAs is often limited, and in addition to the technical difficulties of controlling access, management controls on access and harvesting are sometimes neither implemented nor enforced. This problem is exacerbated where local communities are excluded from directly sharing the benefits of MPAs or cannot be convinced that those benefits will indirectly flow to their community, thus, giving them little incentive to assist in control and management of MPAs to achieve conservation objectives. In such circumstances, MPAs can be easily eroded, and their values lost (Alcala 1988, Russ & Alcala 1994, McClanahan *et al.* 1997, Rogers-Bennett *et al.* 2000). MPAs that are created with little or no commitment from government or the local community to implement the controls identified as necessary for effective management tend to be ineffective in achieving conservation goals (Jones 1994).

Increasingly, scientists are drawing the attention of fisheries managers towards the potential of marine reserves as new tools for fisheries management (see 'Weight of Opinion' box). At the same time, conservation and environment managers have become increasingly concerned that many areas of the global oceans, and particularly near-shore areas and estuaries, are poorly represented in existing MPAs. For example, a recent global analysis has identified that, although there are 1,306 existing MPAs in 18 regions of the world, 81 major new MPAs are required as regional priorities to meet global conservation criteria (Kelleher *et al.* 1995). Much of the global impetus is expressed in international and regional agreements and law (Attwood *et al.* 1997a) including the UN Convention on Law of the Sea, and the International Convention on Biological Diversity (Ward *et al.* 1997). This concern has also resulted in various global programs of action, including the IUCN Marine and Coastal Areas Programme, and the UNESCO Man and the Biosphere Programme. In Australia, marine reserves feature prominently in the National Oceans Policy, the National Strategy for the Conservation of Biological Diversity, and the National Representative System of Marine Protected Areas (NRSMPA).

MPAs are a central element of Australia's Oceans Policy

Australia's Oceans Policy (Commonwealth of Australia 1998), which sets out the basis for achieving sustainable use of Australia's oceans, includes MPAs as a central element of the implementation, together with sustainable uses in non-reserve areas. The National Representative System of Marine Protected Areas (NRSMPA) program, implemented as part of the Oceans Policy, supports the identification, selection and declaration of MPAs that are consistent with national and state-level conservation criteria (ANZECC 1998). In the Great Barrier Reef World Heritage Area, existing zonings are being reviewed to identify a set of representative areas to be dedicated for the highest levels of conservation protection. The Oceans Policy proposes that MPAs and improved implementation of Australia's policy of Ecologically Sustainable Development in off-reserve areas together will be capable of ensuring that conservation objectives can be achieved for Australia's ocean territories while maintaining sustainable uses of our living resources.

The NRSMPA is the combined reserve system of the Commonwealth and the states and territories, and its objective is to establish and manage reserves that contain the range of ecosystems, habitats and species found in Australia's marine jurisdiction (ANZECC 1998). However, at present the NRSMPA system of reserves is very limited—less than 1% of Australia's marine jurisdiction—and the reserves are heavily biased towards shallow water and inshore habitats where human pressures are greatest.

Reserves designed for use in fisheries management can be considered as to be either a subset of MPAs as defined above, or as a distinct, but complementary, form of reserved area that is set aside primarily for resource conservation. Several terms are commonly used to denote reserve areas used for fisheries management purposes (Auster & Malatesta 1995, Allison *et al.* 1998). They include:

- fishery, non-extractive or no-take reserve
- marine protected area, sanctuary or park
- marine, harvest or fishing refugium, and
- conservation zone.

Only occasionally are the terms carefully defined, and rarely are they contrasted with each other. Throughout this review the term 'Marine Fisheries Sanctuary' (MFS) (Plan Development Team 1990) is used to identify no-take reserves specifically created for fisheries management purposes, and it is this form of reserve that is the focus of this report. An MFS is equivalent to a no-take Marine Fisheries Reserve (MFR), a term used by some jurisdictions (Plan Development Team 1990). We have preferred the term 'sanctuary' over 'reserve' because of its more direct everyday language implications, and because we consider that 'sanctuary' is less ambiguous in management terms. For brevity we often used the terms 'marine reserve' or just 'reserve', which may refer specifically to MFSs or more generally to marine reserves, depending on the context.

Marine Fisheries Sanctuaries contribute to broad conservation goals

Many reserves declared for fisheries management purposes (such as fish-habitat reserves) will make important contributions to both fisheries and to the conservation of biological diversity more broadly, even though the conservation of non-commercial species is not their main objective. Such reserves include those dedicated under area-specific fisheries management measures. For example, in Western Australia, these measures include fisheries closures—closed seasons for fishing in specific areas—and formally declared Fish Habitat Protection Areas (Bunting 2001). So, in addition to their contribution to fisheries management, such reserves will have other biological values. In this sense, some forms of fisheries reserves, and particularly Marine Fisheries Sanctuaries as defined here, can make a substantial contribution to broader marine conservation goals beyond just protection for exploited species.

The contribution to the conservation of biological diversity that can be achieved within MFSs and other forms of fisheries reserves, although rarely documented, is recognised by the most widespread classification system for MPAs in international use—the IUCN classification of protected areas (IUCN 1994; Table 1). The IUCN categories for MPAs define a range of reserve types that could be of potential use in fisheries management, including highly protected no-take areas (Category I) and areas designed to foster the long-term sustainable use of natural resources (Category VI). Implicit in the IUCN classification system is the recognition that reserves that are managed for sustainable use can also make an important contribution to conservation goals in a region.

True 'no-take' marine reserves are rare

Although MPAs are widely accepted as an effective tool in marine conservation, most allow the extraction of some natural resources. True no-take marine reserves are rare (Ballantine 1995a, Roberts 1997c), they usually occur as a separate zone within a larger MPA, and their use in fisheries management is controversial (Bohnsack 1996b, Attwood *et al.* 1997a). In British Columbia only 0.01% of coastal habitat is protected in 'no-take' reserves (Wallace 1999), and just 0.001% of U.S. territorial waters are closed to all fishing (Fujita *et al.* 1998b). In the U.K., except for a few small exclusion zones around Naval facilities, there are no 'no-take' reserves (Rogers 1997). In Australia, less than 5% of the Great Barrier Reef World Heritage Area (but about 20% of the coral reefs) is protected within 'no-take' areas, and outside the Great Barrier Reef, probably much less than 1% of Australia's marine jurisdiction is protected in no-take areas. This world-wide rarity of no-take reserves means that conservationists, fisheries managers and marine ecologists have limited experience with them and, therefore, are uncertain about their utility for fisheries management. Amongst other things, this situation creates a strong incentive for the re-evaluation of the impacts of reserve declarations in the past, and where possible on marine systems, fisheries and conservation. It also highlights the need for new research on the impacts of reserve creation on fisheries as well as on conservation.

Table 1. Summary of the IUCN Protected Area Management Categories (IUCN 1994)

Category		Description
I	Strict Nature Reserve	Managed for mainly for science or wilderness protection
II	National Park	Managed mainly for ecosystem protection and recreation
III	Natural Monument	Managed mainly for conservation of specific natural features
IV	Habitat/Species Management Area	Managed mainly for conservation through management intervention
V	Protected Landscape/ Seascape	Managed mainly for landscape/seascape conservation and recreation
VI	Managed Resource Protected Area	Managed mainly for the sustainable use of natural ecosystem

1.2 Fisheries Management and Marine Reserves

Area and seasonal closures to assist with the management of fisheries have long been used in both artisanal fisheries (e.g. Johannes 1978, Heslinga *et al.* 1984, Alcala 1988, Dugan & Davis 1993, Wilson e*t al.* 1994), and modern, industrial fisheries (e.g. Halliday 1988, Walsh *et al.* 1995, McArdle 1997, Rogers 1997, Clarke 1998), for decades if not centuries (Anonymous 1921, as cited in Fogarty *et al.* 2000; Garstang 1900, as cited in Fogarty *et al.* 2000). Many marine fisheries closures and reserves have been established to assist the recovery of severely overfished or collapsed stocks (e.g. references in Jamieson 1993, Attwood *et al.* 1997a); an Australian example is the Tasmanian scallop fishery (Zacharin 1989). In general, however, the most common forms of fisheries closures or reserves in Australia are for the protection of near-shore areas considered to have important nursery, spawning or juvenile recruitment functions and where there are imminent threats (e.g. Bunting 2001).

Reserves have been established to assist the recovery of severely overfished or collapsed stocks

While closures can be effective fisheries management tools, they are rarely the primary tools used to manage a focal species. Most management in commercial fisheries has relied on other forms of input controls or, more often in recent years, on output controls. Controls on input are restrictions on the fishing effort, such as limits on vessel sizes, vessel numbers, or gear characteristics. Closures are considered input controls because they reduce total fishing effort or mortality by restricting access to a portion of the stock. Controls on gear type, as well as specifying configuration (e.g. mesh size), may allow limited use of some gear types, such as traps or recreational line fishing, while excluding other types of gear, such as demersal trawling (a form of closure), as measures to control fishing effort and mortality. Output controls are limitations on the amount of fish permitted to be caught in a fishery, usually imposed as some form of quota either on total catch for the fishery (e.g. total allowable catch, TAC), the catches of individual fishers (e.g. individual transferable quotas, ITQs), or the catch of specimens within a certain category (e.g. a size limit). Thus, traditional fisheries management has been based on managing fishing characteristics (effort and catch) in relation to the target species, rather then aspects of the environment or ecosystems in which target species may live. In principle, the traditional approaches are designed to permit a large enough portion of the stock to escape capture long enough to reproduce sufficiently to ensure adequate recruitment to sustain the population and desired level of fishing. Bohnsack (1998, 1999) drew the contrast between this approach, which attempts indirectly to create a 'numerical refuge' for the spawning population, and the natural or man-made spatial refuges (e.g. MPAs or MFSs) that can provide more certain protection, and, therefore, are more stable or reliable.

Management in commercial fisheries has relied on input or, in recent years, output controls.

Fisheries management based on the traditional approaches has been successful for many decades, but in recent years the over-exploitation and crashes of many fisheries (references in Jamieson 1993, Wilson *et al.* 1994, Ault *et al.* 1997a, Garcia & Newton 1997), the changing nature of fish yields caused by serial over-fishing and 'trophic fish-down' (Pauly *et al.* 1998a), and the losses of biodiversity and environmental damage caused by fishing (e.g. Russ 1991, Alverson *et al.* 1994, Dayton *et al.* 1995, Roberts 1995a, Jennings & Lock 1996, Jennings & Kaiser 1998, Thrush *et al.* 1998, Hall 1999), have alerted fisheries managers and scientists worldwide to the weaknesses of traditional fisheries resource assessment and management systems (Sainsbury 1998). This problem is exacerbated by the fact that the oceans are reaching their productivity capacity, and that many (most in some regions) stocks are now fully or over-exploited resulting in unsustainable levels of exploitation (Jamieson, 1993, Ludwig *et al.* 1993, NMFS 1993, FAO 1994, Botsford *et al.* 1997, Garcia & Newton 1997, Mace 1997, Buckworth 1998), a fact that is often masked by technological improvements (Clark 1996), geographic expansion of fisheries and trophic fish-down (Pauly *et al.* 1998a).

Achieving sustainable exploitation is hampered by seemingly intractable sociological, political and economic problems…

Solving the problem of unsustainable exploitation is difficult because of several seemingly intractable sociological, political and economic problems, such as:

- the increasing need for protein sources in poor countries, driven by exponential world population growth
- the increasing market demand for, and value of, high quality seafood by affluent countries
- the short-term, strictly competitive, and selfish behaviour of some fishers
- the over-capacity and over-capitalisation of industrial fisheries
- the governmental subsidies provided to many fisheries
- the 'ratchet' effect (exploitation is always increased during good periods, but rarely decreased during bad periods)
- the 'shifting baseline' effect (each generation of scientists and managers uses the fisheries conditions and exploitation levels extant at the beginning of their careers as the benchmark against which they assess their actions), and
- the general inability of fisheries management to effectively control and limit fishing effort.

These factors have led to, and are leading to, ever increasing levels of exploitation and over-exploitation in global fisheries (Ludwig *et al.* 1993, Sissenwine & Rosenberg 1993, Pauly 1995, Jackson 1997, Mace 1997, Buckworth 1998, Pitcher & Pauly 1998, Sainsbury 1998, Sumaila 1998, Williams 1998b).

Modern, scientific fisheries management, developed in the 50s (see references in Smith 1998) and based on concepts such as 'surplus production' and 'maximum sustainable yield' (MSY), held great hope for the sustainable exploitation of marine living resources. However, as long ago as the 70's the promises of MSY were thoroughly debunked (Larkin 1977), and since then numerous workers have pointed to these and other problems that have prevented, and will continue to prevent, fisheries scientists and managers from achieving sustainable exploitation using the methods of the 50s (Murawski 1991, Ludwig *et al.* 1993, Apollonio 1994, Wilson *et al.* 1994, Pauly 1995, Roughgarden & Smith 1996, Hilborn 1997, Mace 1997, Jackson 1997, Roberts 1997b, Buckworth 1998, Cochrane *et al.* 1998, Flaaten *et al.* 1998, Johannes 1998a, Lauck *et al.* 1998, Sainsbury 1998, Sumaila 1998, Walters 1998, Mangel 2000a,b; however see Rosenberg *et al.* 1993). In this review we refer to these methods as traditional or classical fisheries management. Some of the more important scientific problems are:

The promises of MSY have been thoroughly debunked

- the difficulty of mathematically representing complex natural systems sufficiently to make accurate stock predictions
- our inadequate understanding of most natural and human systems
- the lack of, and inaccuracies in, data needed to describe and represent those systems for which we have a reasonable understanding
- the use of single-species models and approaches to deal with what are multi-species, multi-dimensional ecosystem problems
- the lack of adequate natural control sites for testing scientific hypotheses (all of the oceans are exploited and subject to the effects of fishing), and
- the many sources of uncertainty and time lags in these systems, some of which are irreducible (i.e. we will never be able to represent or account for it) or so extreme that they mask the patterns of interest.

The crises in marine fisheries and the problems described above have created an imperative to develop innovative, ecosystem-based fisheries management approaches or systems that can reduce the impact of fishing on the environment and better represent and allow for uncertainty in both the biological aspects of a fishery and the socio-economic basis for fisher behaviour (Edyvane 1993, Rosenberg *et al.* 1993, Appollonio 1994, Boehlert 1996, Bohnsack & Ault 1996, Hilborn 1997, Lauck *et al.* 1998, Sharp 1997, Done & Reichelt 1998, Fujita *et al.* 1998a, Pitcher & Pauly 1998, Sainsbury 1998, Walters 1998, Holmlund & Hammer 1999, Agardy 2000). In order to develop management systems that are more conservative, in the sense that they can set realistic levels of optimum yield, and other controls such that major fisheries collapses are avoided, modern fisheries management is increasingly accepting the importance of taking and implementing holistic, ecosystem-based and 'precautionary' approaches (Garcia 1994, FAO 1995, Botsford *et al.* 1997, Hilborn 1997, Mace 1997, Myers & Mertz 1998, Sainsbury 1998, Perry *et al.* 1999).

Modern fisheries management is accepting the importance of holistic, ecosystem-based and 'precautionary' approaches

Precautionary fisheries management involves several components, including the use of risk-averse approaches to the defining of optimum yields, the setting management targets, and in developing control rules (FAO 1995, Roughgarden & Smith 1996). A critical component of the precautionary approach is the implementation of management strategies and actions that minimise the likelihood of producing irreversible impacts such as the extirpation of local populations, permanent community-structure shifts, or species extinctions in the face of pressures from fishing or environmental changes (Agardy 1994, Roy 1996). Where there is uncertainty, history shows that those in control of fisheries will almost always maintain or raise the current level of catch (as catch limits), unless there is convincing evidence that those limits are unsustainable (Ludwig *et al.* 1993, Hilborn 1997). Ballantine (1995b) claimed that an underlying assumption of virtually all fisheries management is that fishing should be allowed everywhere, all the time, unless it can be demonstrated that serious damage is or will be caused by that level of fishing. He argued that this assumption is an historical accident, the validity of which cannot be supported by empirical evidence or theory. He concluded that this view, along with another common, but unsubstantiated, assumption that the intelligent use of scientific information will lead to sustainable management, has been responsible for fisheries collapses becoming the norm and for a nearly complete lack of successful, long-term sustainable management of marine fisheries. Conversely, the precautionary approach, by reversing the burden of proof, would deal with uncertainty and conservation imperatives by calling for the reduction of current catch limits, or the rejection of proposals to raise limits, unless those limits were proven to be sustainable (Ludwig *et al.* 1993, Hilborn 1997).

However, Hilborn (1997) cautioned that effective application of the precautionary approach depends on the situation. While the approach would be appropriate for a developing fishery, if applied to a fully developed fishery it could result in an increased risk of its economic collapse. In the latter situation the approach would be precautionary with respect to biological risk, but not so with respect to socio-economic risk. Although risk-averse management is likely to greatly improve the basis of fisheries management, models and approaches will need to also integrate the socio-economic aspects of fisher behaviour, an area poorly researched or understood (Rosenberg *et al.* 1993).

Reserves are considered to reduce the probability of fisheries collapse by providing for bet-hedging management

Both scientists and managers are increasingly recognising that no-take reserves are potentially key elements of a precautionary approach when faced with the management of over-exploited stocks (Clark 1996, Williams 1998a, Perry *et al.* 1999, Bohnsack 1999). Modelling efforts have suggested the possibility that fisheries may not suffer reduced yields due to sanctuary establishment, and may even experience increase in yields (Mangel 2000b,c). Marine reserves are seen to reduce the probability of fisheries collapse through bet-hedging, a well established technique used in many fields (e.g. business and economics) for coping with uncertainty and lack of knowledge, in order to reduce overall risk (Lauck *et al.* 1998, Sumaila 1998, Bohnsack 1999, Fujita *et al.* 1998b, Fogarty *et al.* 2000), although some researchers have suggested that the benefit will be realised only in large reserves (Clark 1996, Fogarty 1999). Several authors have drawn an analogy between the fishing of marine resources and financial investment (e.g. Roberts 1998a). The ideally managed fishery exclusively exploits the excess production of a stock, which is seen to be equivalent of living off the interest accrued from an investment. However, when management fails to achieve this ideal, fishing results in the excessive exploitation of spawning stock which leads to recruitment overfishing, a situation analogous to using up investment capital. The difficulty with this analogy is that while investment capital can be regenerated from another sector of business activity, fish to replenish stocks cannot normally be regenerated in another sector activity. Rearing of hatchery-bred juveniles to replenish wild stocks is rare (e.g. the Alaskan Salmon fishery) and not cost effective in comparison to maintaining wild stocks at sustainable levels. Marine reserves are a method for protecting and re-building spawning stock, which is seen to be the equivalent of protecting the investment capital and using a portion of the interest to build that capital further (something akin to setting up a re-investment trust fund). Attwood *et al*. (1997b) pointed out that MFSs, because they may deliver economic benefits to fisheries and conservation more broadly, may be received more favourably by the fishing community than MPAs justified as part of a precautionary management strategy designed to mainly benefit conservation of non-exploited species.

No-take reserves should greatly simplify compliance and enforcement

In practice, many fisheries are multi-species fisheries, some involving multiple target species caught simultaneously in a single gear type (e.g. demersal trawling), while some target multiple species sequentially. Also, many fishers are diversified in their operations, moving from one species or fishery to another during the course of a year to maintain their income. In tropical reef systems the fisheries often involve fishers using a variety of gear types to exploit many species (Pauly 1979, Munro & Williams 1985, Appeldoorn 1996, Ault *et al.* 1997a). Roberts & Polunin (1993) pointed out that fisheries controls such as regulating gear characteristics, limiting numbers of operators, closing areas or seasons have been developed mostly for the management of single-species stocks in temperate regions. They question applying this approach to coral-reef fisheries because 1) they are not single-species fisheries, 2) the data required to determine the most appropriate controls to use are usually not available (Plan Development Team 1990), and 3) compliance and enforcement becomes much more complex because of the variety of species and fishing practices involved. In theory, the use of multi-species, rather than single-species, models would improve the basis of management, but such efforts are conceptually and practically very demanding, there is little guarantee of success, and few fisheries are managed in this way (Polunin 1990, Appeldoorn 1996, Botsford *et al.* 1997, Hall 1998, Rothschild *et al.* 1997, Walters *et al.* 1998). Indeed, Lauck *et al.* (1998) suggested that the goal is not realistically attainable given the gap between current understanding, and data availability, and the requirements of multi-species models. Marine reserves have been advocated as an alternative that would not suffer these problems (e.g. Roberts & Polunin 1991, Attwood & Bennett 1995). No-take reserves would protect all species, are believed to require significantly less data, and should greatly simplify compliance and enforcement.

In the past, many marine reserves or closures created for fisheries purposes have been established after target populations have been reduced to densities at which commercial exploitation is no longer viable (references in Jamieson 1993, Attwood *et al.* 1997a, Murawski *et al.* 2000), or where their fisheries are under threat (Halliday 1988, Armstrong *et al.* 1993, McNeill 1994, Piet & Rijnsdorp 1998, Murawski *et al.* 2000). Such use of reserves is for recovery of stocks from a crisis. Recently, however, there has been growing general interest in using marine reserves to provide broader support for conventional fisheries management (Wallis 1971, Davis & Dodrill 1980, Plan Development Team 1990, Davis 1989, Roberts & Polunin 1991, Bohnsack 1993, Dugan & Davis 1993, Roberts & Polunin 1993, Agardy 1994, Bohnsack 1994, Rowley 1994, Ballantine 1995a, b, Roberts *et al.* 1995, Shackell & Lien 1995, Bohnsack 1996a, Roberts 1997c, Allison *et al.* 1998, Bohnsack 1998, Gribble & Robertson 1998, Lauck *et al.* 1998, Pitcher & Pauly 1998, Roberts 1998a, Russ & Alcala 1998a, b, Dayton *et al.* 2000, Mangel 2000b, c). In addition, some scientists and managers have advocated or discussed the use of marine reserves to improve the management of specific stocks of fishes or invertebrates (e.g. Davis & Dodrill 1980, Plan Development Team 1990, Davis 1989, Shepherd & Brown 1993, Rogers-Bennett *et al.* 1995, Defeo 1996). In part, the interest of fisheries managers is focusing on formal reserves because it has now been recognised that much of the earlier success of traditional fisheries management resulted from the existence of *de facto* marine reserves (natural refugia)—grounds that were untrawlable, or areas that were otherwise too distant or inaccessible to fishing (Beverton & Holt 1957, Klima *et al.* 1986, Davis 1989, Dugan & Davis 1993, Jamieson 1993, Lozano-Alverez *et al.* 1993, Walters *et al.* 1993, Ault *et al.* 1997b, Bohnsack 1996a, Walters & Maguire 1996, Fonteneau 1997, Bohnsack 1998, Levy 1998, Walters 1998, Dayton *et al.* 2000, McClanahan *et al.* in press). Advances in navigation, fishing technology and knowledge, over capitalisation, and increasing market demand have opened these areas to fishing and effectively eliminated their former *de facto* marine sanctuary status. It is likely that the loss of such natural refugia has contributed to the collapse of some stocks (Tegner *et al.* 1996, Walters & Maguire 1996).

The loss of natural refugia has contributed to the collapse of some stocks

As the global fishing industry considers how to develop and implement precautionary approaches to fishing, marine fisheries reserves are increasingly being promoted as an important component of precautionary management, because they may be able to act as insurance to help protect against stock collapses (Edyvane 1993, Pollard 1993, Agardy 1994, Clark 1996, Lauck *et al.* 1998, Williams 1998a, Perry *et al.* 1999, Bohnsack 1999, Agardy 2000, Fogarty *et al.* 2000). Besides being a source of mortality, fishing has many effects on an exploited stock, including altering the normal size/age structure, disrupting reproductive behaviour, selecting for less productive genotypes, and reducing genetic diversity, all of which may render populations more susceptible to catastrophic events (Dugan & Davis 1993, Attwood *et al.* 1997b, McManus & Meñez 1997). Persistent fishing can also erode the sustainability of stocks by destroying or degrading habitat, and altering community structure. Marine reserves are considered to have a possible role in addressing all of these pressures (e.g. Auster & Shackell 1997, Attwood *et al.* 1997b, Bohnsack 1998, Roberts 1998a), and to help in rebuilding collapsed fisheries (Bohnsack 1996a).

Modelling suggests that sanctuaries can help to provide a long term solution to fisheries management problems

Most proposals for the use of MFSs to achieve sustainable use of fisheries suggest protecting a small proportion of the area occupied by a stock and continuing to allow fishing on the remainder. The results of modelling studies have led several authors to suggest that protecting something like 20% of a population's range may be sufficient to achieve long-term sustainability, although several studies have suggested higher levels of protection may be required. For example, Clark (1996) suggested that sustainability will not be achieved unless more than 50% is protected, and Pollard (1993) concluded that the 'only long term solution' to overfishing may be in complete protection 'of very large areas of the marine and estuarine environment'. A recent manuscript (Bohnsack *et al.* manuscript) attempts to provide biological, fisheries, ecosystem and managerial rationale for protecting 20–30% of fishing habitats. The wide range of predicted values stems from

How much area should be protected is one of the most important questions facing fisheries & conservation scientists.

the fact that the problem is complex and dependent on processes occurring inside sanctuaries, in fished areas elsewhere, on exchanges occurring between the two, on the response of fisheries to sanctuary establishment, and on the biological characteristics of the focal species (Mangel 1998, Fogarty *et al.* 2000). Walters (1998) used an analysis of cases of successful management of marine resources to propose boldly that sustainability will require that most of the marine environment be afforded protected status, with only a small proportion available for exploitation. This is a management approach that so far has only been employed for severely overfished or collapsed stocks (Williams 1998a). However, Sumaila (1998) countered that protecting such large proportions of a resource does not make sense from an economic perspective, and could lead to an unacceptable lag period until the fishery enhancement effect fully compensates for the loss of access. Furthermore, concentrating existing fishing effort into a much smaller area could result in a much larger rate of damage to the environment (Parrish 1999b). How much area should be protected, or how large sanctuaries or sanctuary networks should be, is one of the most important questions facing fisheries and conservation scientists.

1.3 'No-take' Marine Reserves

The convergent interests of marine fisheries managers and conservation managers on the use of closed areas to help achieve similar sets of objectives is a recent phenomenon, although some conservation biologists, marine ecologists and fisheries scientists have argued in this direction for many years (e.g. Ballantine 1989, Alcala & Russ 1990, Polunin 1990, Bohnsack 1993, Roberts & Polunin 1993). The notion of no-take reserves has evolved to cover the various forms of area protection where all exploitation is prohibited. In concept, no-take reserves are closely similar to protected areas that would be classified as Category I in the IUCN classification system (IUCN 1994). In this review, Marine Fisheries Sanctuaries (defined as 'no-take' reserves—see Glossary) are considered to have the following characteristics:

- spatial bounding—areas of the seabed and water column that are defined in spatial terms, with fixed boundaries
- temporal continuity—in place continuously and not lifted periodically or occasionally, or applied in any discontinuous manner through time
- permanence—not easily revoked or altered, except in very exceptional circumstances or where alterations are occasionally required to enhance the reserve's ability to meet its objectives, and then through a comprehensive public review process, and
- comprehensiveness—covers all living and non-living resources, including exploited species, non-exploited species, habitats, ecosystems, water quality and substrata.

Artisanal fishers have used seasonal and permanent closures of fishing grounds for centuries to conserve stocks of the marine species upon which they depend for food (Johannes 1978, and references therein). Also, seasonal and temporary, but rarely permanent, closures have always been a part of the industrial fisheries manager's toolbox. However, it was not until

Seasonal and permanent closures have been used for centuries to conserve stocks

the 1950s that fisheries scientists began to recognise that permanent protection from fishing had the potential to contribute to traditional fisheries management (e.g. Beverton & Holt 1957). More recently, Gary Davis and Angel Alcala (Florida and the Philippines, respectively) were the first two researchers to test this idea in the field, and to discuss the range of potential benefits that no-take reserves could provide to heavily exploited populations (Davis 1977, Davis & Dodrill 1980, Alcala 1980, 1981, Davis 1981). Later in the 80s and throughout the 90s, what is now a long list of potential benefits, and a considerable body of research regarding the use of marine reserves for conservation, fisheries management, and the fishing industry has emerged from the efforts of numerous workers, most notably:

- Neville Barrett, Johann Bell, Graham Edgar, David Pollard, Gary Russ, and Scoresby Shepherd, (Australia)
- William Ballantine and Robert Rowley (New Zealand)
- Angel Alcala (Philippines)
- Simon Jennings, Nicholas Polunin and Callum Roberts (England)
- Colin Attwood, Bruce Bennett and Colin Buxton (South Africa)
- Tim Lauck (Canada)
- Juan Castilla and Carlos Moreno (Chile)
- Timothy McClanahan (Kenya)
- Enric Sala (Spain), and
- Tundi Agardy, Gary Allison, Peter Auster, James Bohnsack, Lou Botsford, Mark Carr, Paul Dayton, Gary Davis, Jennifer Dugan, Jane Lubchenco, Marc Mangel, Daniel Reed, Joshua Sladek Nowlis (United States).

An extensive and well-organised list of potential benefits is provided in Bohnsack 1998. Below we describe those benefits of most importance to this review. Briefly, some core reserve benefits that have been proposed for exploited species and the fisheries exploiting them include:

- increased abundance and spawning biomass
- increased mean age and size
- improved reproductive potential
- enhanced settlement and recruitment
- protection of genetic diversity
- protection of a critical supply of reproductive stock
- maintenance or enhancement of yields in adjacent fished areas
- reduced variability and uncertainty in fisheries yields, and
- increased likelihood of sustainable exploitation.

For conservation and biodiversity the potential benefits include:

- habitat protection
- increased biodiversity, and
- protection of ecosystem structure, function and integrity.

Sanctuaries provide sites for reference studies of natural populations

Science, fisheries management, the fishing industry and public are also seen to benefit because reserves have the potential to:

- provide reference sites where scientific knowledge and understanding of natural populations of target and non-target species can be improved
- simplify management regulations and compliance monitoring
- reduce data requirements for management
- protect against management failure
- reduce conflict amongst users, and
- improve opportunities for education and tourism.

Reserves potentially export fish to fished areas

A central, widely recognised principle behind the creation of no-take reserves of value for fisheries management is that they will provide permanently closed areas that will export reproductive propagules to surrounding areas that are fished (usually called 'larval export'). Except for pelagic, migratory or highly mobile species, or species with very short-distance larval dispersal, this effect is believed to have the potential to enhance and sustain fisheries. Reserves also have the potential to improve fisheries by providing the conditions necessary for population growth that results in the emigration of juvenile or adult individuals from reserve to fished areas. This effect (often called 'spillover') is believed to be unimportant for highly sedentary species, to operate only locally, and to be much less important than larval export, but, nonetheless, may be of significant benefit in some situations. Both processes are dependent on reserves providing protection from fishing mortality and the disruptive and destructive effects of fishing. In time that protection is expected to result in increased population size and reproductive potential in the reserve, which then are the ultimate sources of levels of spillover and larval export sufficient to enhance and sustain surrounding fisheries. For management based on no-take marine reserves to be most effective, marine areas need to be carefully selected to ensure that they will have the greatest potential for building populations, providing reproductive refugia, and delivering the benefits of spillover and larval export to fisheries. Below we will discuss the variety of reserve factors (e.g. size, location, habitat diversity) that influence and determine the effectiveness of no-take reserves at enhancing fisheries and conserving marine ecosystems.

Reserves export reproductive propagules to surrounding areas that are fished

The increasing pressure on the world's fish stocks, the numbers of stocks that are overfished or have collapsed, the loss of natural refugia, the increasing rate of failure of traditional management systems, the local and international perceptions that fisheries are contributing to broad-scale degradation of the ocean, and the intensifying pressure for the establishment of marine conservation reserves are all leading to mounting pressure on the world's fisheries managers to improve the effectiveness of management (Rosenberg *et al.* 1993, Safina 1995, Sutton 1997). Marine reserves, because they have the potential to replace the lost refugia and, to an extent, reverse the effects of overfishing on marine environments and populations, are seen as central to the improvements that are necessary to achieve the goal of sustainable fisheries management and marine conservation.

Sanctuaries are considered to be an actively adaptive approach to integrated management

The over-exploitation of fisheries is expressed as effects on the target stocks and their environment, but also in social, economic and cultural consequences for the people dependent on fishing for income or food. The management of marine fisheries is well recognised as a highly complex problem (Rosenberg *et al.* 1993). Many scientists argue that inclusion of marine reserves within management strategies will make fisheries management easier, more effective and less risky (Dugan & Davis 1993, Roberts & Polunin 1993, Bohnsack & Ault 1996, Roberts 1997b, Bohnsack 1998, Botsford *et al.* 1999, Mangel 2000b, Bohnsack *et al.* manuscript). Also, in the face of ineffective classical management strategies, the many possible benefits that no-take marine reserves potentially bring to both fisheries and conservation management is widely advocated as sufficient evidence in itself of the need for broad-scale introduction of no-take reserves as part of an actively adaptive approach to the integrated management of marine ecosystems and resources (Bohnsack 1998, Fogarty *et al.* 2000).

Despite the overwhelming opinion, there are few documented examples of fishery benefits

Despite the mounting levels of opinion amongst scientists that reserves can make a positive contribution to fisheries management (see the preface Box), there appear to be few well documented examples of fisheries that have been shown to benefit from the introduction of reserves. The experiences often cited in support of reserves are limited to either the recovery of stocks from a highly depleted state, using temporary closures of various forms, or involve mainly subsistence-scale tropical reef fisheries. Experiences in neither of these categories can be related directly to the world's commercial capture fisheries, and there is little documented evidence that in a well managed fishery, no-take reserves offer additional advantages to a fishery over and above those offered by better classical management techniques. Indeed, a few fisheries scientists argue that classical management tools, augmented with modern risk management procedures, can overcome the fisheries-management problems experienced in the past (Rosenberg *et al.* 1993, Mace 1997). In contrast, a growing number of fisheries scientists are discussing and/or advocating a paradigm shift in the way marine fisheries are managed (e.g. Botsford *et al.* 1997, Sharp 1997, Sutton 1997, Johannes 1998a, Pauly *et al.* 1998b, Pitcher & Pauly 1998, Sainsbury 1998, Walters 1998, Williams 1998b, Fogarty *et al.* 2000).

Ecosystem and precautionary approaches, and the use of no-take reserves, are key elements of the developing new fisheries-management paradigm. Like most new ideas, marine fisheries sanctuaries have not been immediately embraced by fisheries scientists, managers or fishers as the panaceas they have appeared to be in the advocacy literature. Indeed, proposals for no-take reserves usually meet opposition, sometimes intense, from a variety of stakeholders (Roberts & Polunin 1993, Gubbay 1995, Ballatine 1996b, Bohnsack 1997, Williams 1998a). Roberts (1997c) pointed out that 'no-take' reserves that are incorporated within larger multi-use MPA proposals often create the greatest difficulty in achieving acceptance of the proposal. There usually is very little controversy about whether the reserve will serve conservation of biodiversity and the environment. So, in many ways, the crux of the issue is whether the establishment of a marine reserve will have a negative or positive impact on fisheries and those dependent on fisheries for their livelihood. Fishers rightly point to the obvious loss of a portion of their fishing grounds, and the potential subsequent loss in yield and profit that may result (Munro & Polunin 1997). On the other hand, MFS and MPA proponents point to the myriad environmental improvements the reserve will almost certainly bring, and to the potential, if the reserve is designed intelligently, to actually enhance medium- and long-term yields to the fishery (Munro & Polunin 1997). Ballantine (1995b) argued that the loss of fishing grounds and effect on displaced fishers is an 'invented problem', because it only looks at one aspect of a multi-dimensional problem. His argument suggests that the key question is not what is the immediate impact on fishers, but rather what are the long-term benefits to fisheries and other stakeholders including the public interest. For these reasons, and because MFSs have a limited history in Australia (Barrett & Edgar 1998), it is important to critically examine the potential benefits and costs of no-take reserves to fisheries and the environment. To this end, in this review we specifically consider the:

Proposals for 'no-take' reserves usually meet opposition

- types of benefits that have been proposed in support of arguments to use 'no-take' reserves (MFSs) as a fisheries management tool
- conceptual ways in which such benefits might be delivered to fisheries
- empirical evidence that exists to provide support for the delivery of such benefits to a fishery, or the existence of the component processes, and
- criteria by which the tangible benefits of MFSs might be evaluated in the future.

2. METHODS AND APPROACH

This section discusses an approach to evaluating the literature and experience with marine reserves.

There is a vast global information base on the topic of marine reserves, and the potential role that they may play in fisheries management. The literature spans the formal journal literature, the published reports of government agencies, and the unpublished reports and internal documents of agencies and research institutions. Many marine fisheries and conservation scientists have direct experience of efforts to protect and manage areas. And there are many *de facto* reserves and refuges that exist both within fishing grounds and near installations where public access is prohibited (such as near defence facilities). Further, the literature is rapidly expanding, with a number of major initiatives under way in 2001 that are expected to lead to a substantial increase in technical interest and knowledge (such as the special issue of the Ecological Society of America's journal Ecological Applications devoted to marine protected areas).

The approach taken in this review was to consider the Australian and global literature and experience with marine reserves to assess what evidence existed that would support the contention that marine reserves benefit fisheries, and to identify what processes might have been operating to create and deliver those benefits. The review takes a broad view of global experience, without a specific focus on Australian literature, because of the limited experience with reserves for fisheries management in Australia.

To conduct this review we assembled a three-part strategy to try to ensure a comprehensive coverage of the subject material:

1. assemble and review in detail the peer-reviewed scientific literature on marine reserves for fisheries purposes;
2. make personal contact with researchers to find unpublished or obscure reports and/or data of importance (the 'grey' literature);
3. make personal contact with leading researchers to document the most current trends in thinking and analysis, and what initiatives are in the planning stages. This included attendance at a major international symposium, and personal interviews with selected researchers.

This review is structured in the following way:

1. We consider the nature of biological processes that operate in and around reserves that might potentially bring benefits to a fishery;
2. We develop a conceptual model for how these processes interact and how such benefits might potentially be delivered into a fishery;
3. Consider the existing data and experience on benefits that have been demonstrated for reserves-fisheries interactions, or the component processes;
4. Briefly consider approaches used in the literature for building of models to assist with the design or evaluation of reserves, or to predict/assess benefits;

5. Develop a set of evaluation criteria for assessing the evidence for fishery benefits that stand to be delivered from no-take reserves;
6. Draw from this a synthesis and conclusions about the demonstrated impact of reserves on fisheries;
7. Discuss some future directions to guide research, and development of reserves that will provide benefits to Australian fisheries

3. POTENTIAL BENEFITS OF MARINE SANCTUARIES FOR FISHERIES

This section details the potential benefits of marine sanctuaries for fisheries management purposes.

Marine reserves, protected areas or sanctuaries may be established for very general purposes such as preserving biodiversity, or highly specific reasons such as the conservation of a particular valued species or habitat. In the case of no-take marine reserves, advocates of their use in the management of marine fisheries point to a diverse array of potential benefits. They argue that benefits from no-take reserves can flow to:

- exploited species
- the environment
- fisheries
- management agencies
- the public, and/or
- associated sectors of the socio-economic system.

Of primary interest is the question of what role MFSs, as refugia for exploited species, can play in delivering benefits to marine fish stocks, fisheries, and the fisheries and social systems that depend on them (Hockey & Branch 1997). Recent reviews and commentaries have listed a large number of potential benefits that may, or have been shown to, result from the establishment and effective management of no-take marine reserves. Most of the proposed benefits are supported by logical or theoretical arguments based on our scientific knowledge and understanding of marine ecosystems and fisheries. In some cases, those arguments are supported by field studies or modelling studies. In this section we will describe most of the potential benefits that have been identified in the literature.

Underlying and connecting the various potential benefits are physical, ecological, fisheries, economic or social elements, dimensions or processes of the system. Our description of potential benefits is organised to reflect their functional relationships, and we classify them by:

- spatial dimension (inside versus outside the reserve)
- temporal dimension (short-, medium- or long-term)
- causal dimension (direct or indirect effect)
- system (exploited stock, general environment, fishery, etc.), and
- biological component (population, reproduction, genetics).

The full list of potential fishery benefits is provided in Tables 2, 3 and 4. The list was constructed primarily from the lists and discussions provided in the following references: Plan Development Team 1990, Roberts & Polunin 1991, Buxton 1992, Carr & Reed 1993, Agardy 1994, Bohnsack 1994, Rowley 1994, Novaczek 1995, Roberts *et al.* 1995, Shackell & Lein 1995, Auster & Shackell 1997, Hockey & Branch 1997, Roberts 1997c, Bohnsack 1998, and Roberts 1998a, although most papers in the literature mention at least the main benefits. This section describes the benefits using these papers as sources without citing them for each benefit. Benefits are described from the perspective of the targeted species/stocks, the fisheries exploiting those species/stocks, or the agencies responsible for managing those stocks/species and regulating those fisheries. Discussion of support for many of these potential benefits is provided in Sections 3.2-3.7. Section 5 reviews the empirical evidence that relates to the potential benefits discussed here in Section 3.

3.1 Benefits Inside Sanctuaries (Table 2)

3.1.1 Fishing Mortality

Rates of direct fishing mortality (capture of targeted species and size/age classes) can be intense, sometimes reaching several times natural mortality rates (e.g. Plan Development Team, 1990, after Ralston 1987), resulting in the over-exploitation or collapse of numerous stocks in recent years (e.g. Roberts 1997b). The fundamental, and intended, change brought about by the establishment of no-take reserves is the elimination, or at least substantial reduction, of direct fishing mortality within the reserves. Fisheries management controls are designed to control fishing mortality in order to ensure a sustainable, optimal or maximal yield of targeted stocks, depending on the approach taken. The no-take fisheries reserve (MFS) represents another method, in addition to the classical input/effort and output/catch controls, for regulating the overall rate of mortality on a stock by reducing that rate to zero on a portion of the fishing grounds. The MFS is usually not intended to be an alternative to traditional controls, as is often assumed, but rather as an additional control to be integrated with the others (Carr & Reed 1993, Roberts 1997b, Allison *et al.* 1998, Bohnsack *et al.* manuscript).

The capture of targeted size/age classes of focal species is only one form of mortality that occurs as a result of fishing activities. Other sources of mortality are the:

- bycatch of illegal-sized individuals by the fisheries targeting that species
- bycatch of the focal species by fisheries not targeting that species
- incidental mortality directly due to fishing gear (e.g. trawl nets) and practices (e.g. using explosives), and
- incidental mortality indirectly through damage and destruction of habitat or removal of prey species essential to the survival of the focal species (Hall 1999).

Of the total world fisheries catch, roughly one-third is bycatch and discards, of which the largest contribution comes from shrimp fisheries (Alverson *et al.* 1994). Marine fisheries sanctuaries are expected to benefit focal species by providing refugia from these other types of mortality. Because bycatch can significantly contribute to population declines (e.g. Dayton *et al.* 1995), and can have a large impact on species whose juveniles are vulnerable to being caught by other fisheries (e.g. the bycatch of juvenile fish by prawn trawling), sanctuaries established in habitats of the juveniles are expected to be very beneficial to the impacted species (e.g. Auster & Shackell 1997, Walsh *et al.* 1995). Likewise, the protection of spawning grounds or sites may be critical to maintaining stocks of some species (e.g. groupers; Johannes 1998b, Beets & Friedlander 1999). These are direct benefits that occur immediately on sanctuary establishment.

Table 2. Potential fishery benefits of marine fisheries sanctuaries that occur primarily within a sanctuary.

FISHING MORTALITY (direct short-term benefits; realised immediately)
• Eliminate mortality to targeted species and size/age classes
• Eliminate bycatch mortality
• Eliminate incidental mortality directly caused by fishing gear/practices
• Eliminate indirect mortality caused by the damage/destruction of habitats caused by fishing gear/practices
• Eliminate indirect mortality caused by fishing mortality of prey species
POPULATION SIZE (direct short- to medium-term benefits)
• Increase abundance, density and/or biomass of the focal species
• Increase abundance and/or density spawning individuals, or spawning biomass, of the focal species
POPULATION STRUCTURE (direct short- to medium-term benefits)
• Increase mean size/age of individuals of the targeted species
• Restore/maintain 'natural' size/age structure in reserve populations
REPRODUCTION (direct short- to medium-term benefits)
• Increase potential and actual reproductive output
• Protect portion of the stock's spawning biomass
• Enhance settlement/recruitment
HABITAT 'QUALITY' (secondary medium- to long-term benefits)
• Protect and allows recovery of 'natural' habitat characteristics
• Increase biodiversity
• Protect against loss of keystone species, and cascading or indirect effects of fishing on community structure
• Re-establish 'natural' community composition, trophic structure, food webs, and ecosystem processes
• Improve amenities and resources for other non-fisheries sectors of society

3.1.2 Population Size

Sanctuary establishment is expected to result in an increase in the number of individuals and, therefore, an increase in density and biomass, of the population within the reserve. This change is a direct result of the change in fishing mortality, and is expected to occur in the short- to medium-term depending on the processes responsible. Severely overfished stocks have been observed to show orders-of-magnitude increases in biomass following reserve establishment or in comparison to areas outside reserves (see Halpern in press, Section 3.3). The potential for increases in the biomass of spawning size/age classes, a change commonly observed in studies of marine reserves, is a particularly important benefit of marine fisheries sanctuaries.

3.1.3 Population Structure

In addition to changes in population size/density/biomass, there are expected to be changes to the population structure of focal species inside sanctuaries. A direct result of the elimination of fishing mortality will be that individuals are expected to live longer and grow larger. Thus, populations within reserves are expected to show increases in the number/density of larger sizes, and older age classes in the short- to mid-term. An especially important benefit of the 'maturing of the population' is considered to be an increase in the numbers/density/biomass of reproductively active individuals, thus increasing the reproductive potential of the sanctuary (see below).

Fishing mortality typically is selective with respect to the size and age of individuals in the targeted species (e.g. Jennings & Lock 1996). In the short- to medium-term, this process removes individuals of specific sizes/ages from the population disproportionately to their abundance in the population. Thus, the natural size/age structure of the population is altered, usually so that, compared to unexploited populations, the numbers of large/old individuals are reduced, sometimes severely, relative to the numbers of small/young individuals (e.g. Rice & Gislason 1996). The elimination of the exploitation causing the alteration of natural size/age structure is expected to result in changes in the populations in reserves moving them 'back' toward their 'natural' or 'normal' size/age structure, which is expected to enhance the reproductive output of reserves. This change will result directly from the cessation of fishing mortality, but it will probably be realised in the medium-term.

3.1.4 Reproduction

Fishing mortality frequently is greatest in the largest size classes, which are responsible for the majority of the population's reproductive potential (e.g. Trippel *et al.* 1997). A direct result of the changes at the individual and population levels described above, is that on a per-area basis relative to area outside sanctuaries, or before sanctuary establishment, reproduction is expected to be much higher in sanctuaries. With increased numbers of individuals, which are older, larger and more densely packed, reserves are expected to have more spawning activity, increased fertilisation success for species with external fertilisation, and a greater production of eggs and larvae. Sanctuaries are considered to increase spawning biomass, as described above, and, thereby, to provide protection to a portion of a stock's spawning individuals. This is hypothesised to be a key to the ultimate success of sanctuaries as a means to enhance fisheries (see below). Further, because of improvements in the quality of habitats in sanctuaries that are expected to occur in the absence of the immediate effects of fishing (see below), rates of larval settlement and 'ecological' recruitment are expected to improve, an indirect effect expected in the medium-term.

3.1.5 Habitat Quality

Many fishing practices and gear types are destructive to habitats (e.g. trawling, drive netting, or use of poisons and explosives) (e.g. Jennings & Kaiser 1998), reducing properties such as structural complexity and biodiversity (e.g. Gray 1997). In areas where destructive fishing has altered/damaged habitats, the establishment of marine sanctuaries is expected to result in the improvement of the health of habitats required by the focal species for their survival and reproduction. [We are aware of the difficulty in rigorously defining the term 'habitat health', but it is used in this literature, and we simply take it here to refer to those habitat components required by, or critically important to, the organisms in question.] In many species, one or more age classes may depend on particular habitats (e.g. nursery or spawning habitats), or on particular, traditional spawning sites (e.g. sites used year after year by many tropical reef fishes). Aggregations of individuals in these habitats or sites may be especially vulnerable to targeted or incidental fisheries mortality (e.g. Penn *et al.* 1997, Johannes 1998b, Beets & Friedlander 1999). Sanctuaries established on, or including such habitats, will benefit populations within, and potentially far beyond, the boundaries of the sanctuary.

Eliminating the destruction of essential habitat will benefit focal species in the manner just described, and further, should lead to the general improvement of habitat quality within the sanctuary. It is expected that habitat complexity will increase, that the 'natural' balance or interplay of ecological elements and processes will be re-established, and that habitats and ecosystem in general will become more stable. [Again, here we are following usage in the literature, although we are aware of the debate concerning the usefulness of the concept of 'ecosystem stability'; we take it to refer to features such as resistance to natural and anthropogenic pressures and the capacity for self-maintenance within the domain of stability, or the role played by key species in organizing ecosystem structure and function. This is not to infer that 'natural' ecosystems are stable and predictable, but they may be more resilient to pressures within a domain of stability, and more resistant to sudden changes to alternative states (Holling 1973, 1996)].

Most importantly, biodiversity is expected to increase within sanctuaries, specifically with respect to the suite of species subject to exploitation, and generally at the genetic, population, species, community and habitat levels (Bohnsack 1996a and references therein). Shifts in diversity and species composition that have occurred through exploitation and the destructive impacts of fishing are expected to be reversed. The restoration of a 'natural state or balance' to reserve habitats is expected to be especially dramatic where keystone species have been subject to heavy exploitation (e.g. McClanahan 1995).

3.2 Benefits Outside Sanctuaries (Table 3)

3.2.1 Spillover

Because of the population changes occurring within sanctuaries (greater density and biomass), and the differences in habitat quality between areas inside and outside reserves, it is expected that there will be a net movement of juvenile and adult individuals out of sanctuaries. This process is referred to in the literature as 'spillover', and to clearly contrast it with 'larval export' (see below), we consider it to be the net movement of post-settlement individuals (juveniles and adults) out of sanctuaries, regardless of whether they were produced within the sanctuary, or were produced outside and settled inside. We will carefully define the term and fully describe the process (something that hasn't been done in the literature) later in Section 4.4. Few studies have examined the process of spillover, although there is abundant evidence of the type of contrasts between inside and outside reserves that are expected to produce spillover (see Section 3.3).

For the most part, spillover is not expected to have a beneficial affect on fisheries outside sanctuaries except close to their boundaries. This is primarily because fishers are expected, and commonly have been observed, to respond to the establishment of marine reserves by concentrating fishing effort close to boundaries. Therefore, most spillover individuals are expected to be caught adjacent to sanctuaries. Because the size of individuals emigrating from sanctuaries is expected to be larger, on the average, than those that settled in fished areas outside sanctuaries, spillover is considered to be able to create the availability of a high-value resource to commercial fisheries and/or the opportunity for the development of recreational trophy fisheries (Bohnsack 1996b).

Table 3. Potential fishery benefits of marine fisheries sanctuaries that occur primarily outside a sanctuary.

SPILLOVER (direct medium-term benefits)
• Result in net emigration of juveniles and adults from reserves
• Increase catches of larger, more valuable individuals near reserves
• Increase abundance of trophy-sized fish near reserves
LARVAL EXPORT (direct medium-term benefits)
• Result in net export of eggs and/or larvae to fished areas
• Enhance recruitment to fisheries (i.e. fished stocks) outside reserves
FISHERIES (indirect medium to long-term benefits)
• Increased catches, fisheries yields, profits
• Decreased variability in catches, fisheries yields, profits
• Reduce conflict between fisheries/fishers
• Reduce conflict between different users
• Maintain diversity of fishing opportunities
• Sustain fisheries for vulnerable species
• Increase likelihood that existing fishing effort levels are sustainable
• Increase long-term stability of fisheries

3.2.2 Larval Export

If the enhanced reproductive output expected for marine sanctuaries is realized, then it is expected that there will be a net movement of eggs and larvae out of sanctuaries, a process that is often referred to in the literature as 'larval export'. In other words, if we view the population structure as an array of sources and sinks with respect to reproductive output or potential recruits, then properly designed sanctuaries are expected to be sources of reproduction, and they have the potential to be very important sources. It is expected that well designed MFSs will enhance fisheries stocks, because the net larval export will result in increased settlement, ecological recruitment, and subsequent fisheries recruitment.

3.2.3 Fisheries

Advocates of marine reserves argue that the processes of spillover, and especially larval export, from well-designed sanctuaries will increase fisheries recruitment, and thereby produce higher fisheries catches and yields over time. It is expected that such enhancement will at least compensate for the loss of catch due to the reduction in fished area, and probably result in higher catches and yields than under traditional management controls (i.e. before sanctuary establishment). This effect is expected to be most pronounced for those species that have been overfished and have the life-history characteristics that would most enable them to benefit from the creation of a spatial refuge from fishing. Those benefits should be realized in higher fishing profits to individual operators, which should have flow-on effects to the industry in general, and, possibly, to associated sectors of the socio-economic system and the public. Increased yield and profit could result directly from increased availability of fish, from an increase in the size and quality of available fish, or from a decrease in the variability in catches across areas or years.

Irrespective of whether fishery yields are increased, it is expected that marine sanctuaries will increase the diversity of fishing opportunities available to the industry and public. For example, species that have been overfished are often those that are the most desirable and valuable. In the overfished state, they are generally available in only small quantities, and the most valuable, large individuals may not be available at all. In extreme cases, the stock may be economically extinct, and, therefore, completely unavailable to the market. MFSs may enable the sustainable harvest of stocks, which could not exist otherwise, except perhaps at very low catch levels. In addition, a very similar process may create stable recreational fisheries for species that are sought by trophy fishers (Bohnsack 1996b), or fishers supplying high value, specialty markets.

In the long-term, it is expected that year-to-year variation in catch and yield, and the probability of population collapse, should decrease (Lauck *et al.* 1998). A more predictable stock size is expected to translate into economically more viable fisheries, and to avoid the boom and bust cycles so typical of many ineffectively managed fisheries.

A range of indirect benefits to fisheries that have relatively little to do with catch and yield are also expected to be realized as benefits from sanctuaries. A major problem with the multitude of input and output controls currently imposed on marine fisheries, is that it is very difficult to equitably balance the impact of existing and new regulations on different sectors of the industry. It has been argued that MFSs will minimize this problem, because, ideally, all fisheries and fishers will be similarly affected in losing access to a portion of the fishing grounds. Of course, equitably re-establishing and redistributing rights to fishing in the non-reserved areas may create conflicts, but in general, the establishment of MFSs is expected to reduce conflicts between different fishery sectors (Bohnsack 1993).

Conflicts can occur when one fishery imposes a heavy incidental or bycatch mortality on the juveniles of the species targeted by another fishery (Alverson *et al.* 1994), or when there are gear incompatibilities (e.g. pot and trawl fisheries; Somerton & June 1984, Polunin 1990, Armstrong *et al.* 1993). Well-designed sanctuaries are expected to reduce this type of conflict between fisheries. This argument relies on the assumption that all sectors/fisheries made equal use of the sanctuary area prior to its establishment, which would often not be the case. In situations in which a sanctuary is established in a location that is critical to one fishery but marginal to another, the former would be likely to feel most disadvantaged, at least in the short-term. In addition, it is considered that MFSs are more likely to consistently reduce conflict between fishers targeting the same species, but in different ways or as part of different fisheries (e.g. trawl versus line gears, or commercial versus recreational fisheries). The likelihood that the use of MFSs as a fisheries management tool will create more equitable allocation of fishing rights may be increased if the fisheries enhancement effect allows a general relaxation of other fishing controls overall. It should be noted, however, that it is possible for reserve establishment to have the opposite effect by increasing the overlap of effects of fisheries on each other because if they are forced into a smaller area with increased competition for resources, or interactions of gear types. In this situation, equitable allocation of resource use rights becomes crucial.

A more easily defended benefit is the expectation that conflicts between fisheries and non-consumptive users will be reduced (Polunin 1990). For example, recreational and commercial fishing on coral reefs can remove many of the species and most of the individuals of greatest interest to non-consumptive users of the resource, such as divers and snorkellers, leading to conflicts with the tourism industry. The establishment of MFSs may create a win-win situation, in that tourists will have relatively pristine areas to visit and fisheries will experience some or all the benefits described above, and conflict between the two industries will be reduced or eliminated.

3.3 Overall Benefits (Table 4)

3.3.1 Stock

Modelling research has suggested that relatively modest amounts of fishing grounds, if completely protected from fishing, could act as significant reproductive sources for the stock as a whole and result in higher levels of stock available to fisheries than under traditional input/output controls. This phenomenon would be most pronounced for those stocks that have been overfished. If sanctuaries produce a higher rate of recruitment to the fishery, then it has been suggested that stocks may be able to sustain a higher level of fishing mortality. Of course, the purpose of establishing sanctuaries could be subverted if the extra productivity were to be immediately exploited, thus keeping overfished stock at depressed levels. It is expected that a major benefit of sanctuaries will be to use the improved productivity to allow stocks to recover from overfishing.

In addition, creating sources of high and predictable reproductive output is expected to provide an important protection to stocks vulnerable to overfishing, such as species with highly localized and dense spawning aggregations (e.g. orange roughy, Koslow *et al.* 1997; most groupers, Thresher 1984, Shapiro 1987; and many other tropical reef fishes, Domeier & Colin 1997). This function should extend to reducing the probability of stock collapse under the pressures of intense fishing mortality, large-scale environmental changes (e.g. global warming), and the high environmental variability and uncertainty that species in some environments experience. Because sanctuaries would act as predictable sources of recruits subject only to environmental variability, it is expected that stock recovery after a collapse or severe decline would be more likely and rapid. All of this together, suggests that large variations in stock levels, a major problem with the current management of many stocks, could be minimised. Of course, natural processes and variability would continue to create variation in recruitment levels, but such phenomenon would not be as severely affected by fishing pressure.

Table 4. Potential fishery benefits of marine fisheries sanctuaries that are not restricted to areas inside or outside a sanctuary.

POPULATION (direct medium- to long-term benefits)
• Increase size of stock available to fisheries
• Possibly permit increased fishing mortality
• Have greater success than traditional controls at maintaining sustainable fisheries
• Reduce overfishing of vulnerable species
• Protect species vulnerable to overfishing
• Protect from incidental mortality on spawning or nursery grounds
• Protect/buffer against stock collapse, or serious decline, from overfishing
• Protect/buffer from natural recruitment failure
• Improve probability and rate of recovery after serious decline or collapse
• Reduce variance in stock size and, therefore, in fisheries yield
• Improve prospect of long-term sustainability of stocks
• Improve predictability of recruitment under environmental uncertainty
• Reduce impacts of variation/extremes in natural conditions on stocks/fisheries
GENETIC STRUCTURE (indirect, mostly long-term benefits)
• Protect genetic diversity of focal species
• Reduce risk of loss of genetic information from gene pool
• Reduce effects of fishing selection
• Select for beneficial behavioural changes
ECOSYSTEM (secondary, mostly long-term benefits)
• Reduce risk of disruption of ecosystem structure and function
MANAGEMENT (tertiary, short- to long-term benefits)
• Simplify regulations making compliance enforcement easier
• Avoid difficulties of observing and enforcing size and gear regulations
• Allow violations to be more easily detected
• Reduce need for data collection to support management
• Provide resource protection without detailed stock/system data
• Protect against management failure (precautionary approach)
• Provide a basis for rebuilding stock (bet-hedging strategy)
• Provide areas for study of natural/anthropogenic processes in absence of fishing mortality/effects
• Provide sites with minimal disturbance for study of effects of fishing, natural/anthropogenic environmental pressures, and/or harvest strategies

3.3.2 Genetic Structure

When stocks are reduced to low levels through overfishing, the effects of environmental extremes (e.g. epidemics, El Nino or climate change), or a combination of the two, genetic information may be lost through random processes (known as genetic drift) as stocks pass through low-population bottlenecks (Smith 1994, Bergh & Getz 1989). This is a particular concern with respect to rare alleles and alleles that may be critical for responses to extreme environmental stresses. Thus, reserves are seen as potentially providing protection to the gene pool by creating a refuge that will rarely, if ever, go through low-population bottlenecks. Of course, this protection would probably not be realized in small reserves or systems naturally subject to very high levels of environmental variability. It is well understood that only very small migration rates are necessary for this genetic reserve effect to be beneficial to the focal species as a whole, not just to the populations in reserves (Hubbell 1997), and most exploited marine species have pelagic larvae and, therefore, very high rates of gene flow (Shulman 1998).

Because most fisheries are size selective, either because of regulations, gear/practice characteristics, or the relative distribution of fishing effort in relation to that of different size/age classes, fishing mortality can act as a strong artificial selective pressure on target species (Policansky 1993). The reduction of the average size of individuals in species subject to intense fishing is widespread and, although many such changes could also be due to environmental effects, a few studies have shown that these changes have a genetic component (Jennings *et al.* 1999). In addition, fishing selection may affect other characteristics, such as growth rates, size/age at maturity and reproductive rates (Policansky & Magnuson 1998). This process may lead to the non-random loss of genetic information. Marine reserves, by protecting a portion of the focal populations from this selective pressure, are expected to reduce the tendency for populations to be susceptible to this pressure, and possibly reverse it in some cases. Finally, because marine reserves act as refugia from fishing pressure, it is possible that selection will occur for characteristics that may enhance the effectiveness of reserves as sources of reproductive output, e.g. selection for reduced aggressiveness or restricted movement of adult individuals (Nuhfer & Alexander 1994, Boehlert 1996).

3.3.3 Ecosystem

Extreme fishing pressure on widely abundant and important species can cause severe disruptions of the state and functioning of ecosystems. The loss of top-level predators from a community may 'release' other species from predation, resulting in an increase in their abundance (reviews in Jennings & Kaiser 1998, and in Hall 1999). The removal of 'keystone' species can have cascading effects within its ecological community (Steneck 1998), and potentially result in regime shifts in community composition (e.g. McClanahan 1995, Estes *et al.* 1998). With protection from fishing it is expected that further impacts of these types will be avoided, and changes caused by past fishing may be reversed, within reserves. It is also possible that changes within sanctuaries will have a beneficial effect on ecosystems beyond the boundaries of those sanctuaries.

3.3.4 Management

Fisheries management plays an integral part in determining the health of exploited stocks, and therefore, ultimately in the economic viability of the fisheries. Changes in fisheries management brought about by the inclusion of MFSs in the management toolbox will therefore have impacts on fisheries. Determining the nature of those impacts can be difficult. A benefit to management will not always result in a benefit to fisheries or other stakeholders. Nonetheless, several potentially important benefits to management, which may, in turn, produce benefits to fisheries, have been identified in the literature.

First, as described above, it is expected that to the extent that MFSs are used in lieu of other controls, fisheries regulation will be simplified. Particularly, with respect to the sanctuaries themselves, it is expected that enforcing compliance with the control, namely not fishing within the sanctuary, will be much easier than typically is the case with most other controls. For example, many input controls involve very detailed specifications or limitations of the gear that can be used or fishing practices that may be employed, and detecting non-compliance can be difficult, time-consuming, and expensive. Alternatively, ensuring compliance with no-take regulations may be accomplished simply by monitoring fishing activity with radar or a Vessel Monitoring System (VMS: provides for automatic and remote logging of vessel positions). Nonetheless, entry alone into a reserve would not be sufficient to represent a violation (because usually the rights of innocent passage of vessels are not restricted), leaving the difficulty of interpreting radar or VMS data to determine if fishing activity had occurred.

Often, the effective application of traditional controls, especially output controls, relies on detailed knowledge of stock dynamics and fisheries behaviour. That knowledge is built, and relies, on large data sets describing the stock, catch and covariates. Inadequacies and uncertainties in such data sets, as well as in their use and interpretation, have often been cited as contributing to fisheries management failures (e.g. Botsford *et al.* 1997, Ludwig *et al.* 1993, Walters 1998). It has been argued that the implementation of marine reserves as a management control does not require such data and knowledge. Against this view, however, it has been argued that achieving the potential benefits of marine reserves requires their configuration (e.g. size, shape, location and number) to be right, if not optimal (Fogarty 1999), and to achieve this requires a substantial investment in design optimisation and verification. However, reserve proponents have claimed that some resource protection and benefits to fisheries can be realized even if reserves are not optimally configured. If this is true, then reserves could greatly reduce the need to obtain system data and knowledge, which can be very expensive, and provide some protection against the kind of management failures mentioned above (Johannes 1998a). In this sense, MFSs are seen to represent a precautionary approach to the management of exploited marine species (Clark 1996, Lauck *et al.* 1998, Bohnsack 1999).

Earlier we described how marine reserves are expected to enhance the likelihood and rate of stock recovery after a serious decline or collapse. This provides management agencies with the opportunity to implement bet-hedging strategies by imposing different controls on different segments of the stock (no-take inside sanctuaries, and traditional input/output controls outside), with the intention being that if controls outside the sanctuaries fail to function as intended the protected portion of the population inside the reserves will prevent collapse of the stock, or at least ensure a timely recovery (Lauck *et al.* 1998).

Increasingly, it is being recognised that a major difficulty facing fisheries scientists and managers striving to improve their effectiveness is the lack of areas that are free from the effects of fishing. For example, proper assessment of the affects of habitat destruction by gear on the focal species, other exploited species, or unexploited components of the ecosystem depends on the comparison of fished with unfished areas, and/or areas before and after the onset of fishing. Because almost all of the marine environment is open to fishing, and because the evolution of fishing technology has eliminated most 'natural' refuges available to exploited species (Bohnsack 1998), it can be very difficult, if not impossible, to now make these comparisons. Over time, as natural conditions re-establish themselves in marine sanctuaries, it is expected that the sanctuaries will provide crucial reference sites needed for such observational or experimental studies. Stock-assessment models require estimates of natural mortality rates (i.e. mortality in the absence of fishing). A serious vulnerability of such models is that natural mortality rates often cannot be obtained for the reasons just described, and they have to be derived from aggregate mortality rates. Because fishing mortality would be eliminated in MFSs, they may provide crucial reference areas where natural mortality rates could be estimated and monitored, which could lead to improved stock-assessment model predictions, and therefore better management of exploited stocks (Bohnsack 1999). In addition, MFSs may act as reference sites where other important parameters of natural fish populations can be estimated in order to improve stock assessments. Such parameters could include estimates of size at age, fecundity, growth rate, and natural population structure. Accurate estimates of many genetic and population parameters for 'virgin' or pre-exploitation populations are becoming increasingly difficult to obtain because of the 'sliding baseline' phenomenon—reference conditions are restricted to only recent experience and data, ignoring the likelihood that historic conditions and non-fished populations may be very different from those currently observable (Pauly 1995, Moreno *et al.* 1986, MacDiarmid & Breen 1993). Reserves are considered to be able to provide important fisheries-independent data that could improve fishery models (Bohnsack 1998) and to help determine better restoration targets for over-fished stocks by assisting to establish the 'natural' characteristics of their populations (Dayton *et al.* 1998).

More generally, fisheries management is expected to benefit because MFSs will provide areas not directly influenced by the effect of fishing, and these areas could then be used:

- for studies of natural population, community or ecosystem processes
- in the investigation and monitoring of patterns of variation in natural populations,
- as reference areas to compare with areas subject to anthropogenic pressures, and
- for conducting experiments designed to evaluate different harvesting strategies with respect to their resource sustainability (Davis 1981, Agardy 1994, Arcese & Sinclair 1997, Murray *et al.* 1998, Dayton *et al.* 2000).

All of these benefits would be expected to improve fisheries management, and therefore, indirectly the stocks and fisheries themselves.

Beyond this, most authors have listed and discussed a suite of potential benefits that extend beyond stocks, ecosystems, fisheries and management agencies (see Bohnsack 1998 for extensive list), examples of which are:

- provides opportunities for basic research and education
- creates sites for non-exploitative recreation activities and ecotourism
- enhances wilderness and aesthetic experiences, and
- stabilises the economy.

These benefits may feed back to enhance fisheries indirectly, but we do not analyse these potential benefits any further here.

The benefits described in this section are wide-ranging and potentially very important to the success of marine sanctuaries and fisheries. Support for the benefits from empirical studies, modelling analyses and theoretical treatments varies from strong (e.g. size and abundance increases in reserves), to moderate (e.g. increased reproductive potential), to weak or non-existent (e.g. reduced variance in yield) (Bohnsack 1998). Later we review evidence from empirical studies (see Section 5). We find, as have numerous other researchers, that direct support for reserve improvement is reasonable, but there is virtually no empirical support for the key benefits beyond what happens in reserves—spillover, larval export, production stability and fisheries enhancement outside reserves. Assuming the existence of the first three processes, modellers have extensively explored the conditions under which fisheries enhancement could occur, but their models have not evolved to the stage where they can make testable hypotheses about actual systems. Thus, to a large extent, convincing stakeholders of the potential of marine reserves to enhance fisheries depends on theoretical or logical arguments based on our basic knowledge of marine ecology. Most authors have offered at least a minimal logical/theoretical argument to justify a claimed or proposed benefit of no-take marine reserves, and some have gone to great lengths to examine the processes and conditions necessary for a benefit to be realised (e.g. Plan Development Team 1990, Roberts & Polunin 1991, Carr & Reed 1993, Rowley 1994). In some cases the links between different processes have been identified and discussed, and various modelling efforts have numerically investigated the relationships between some of the most important processes. In Section 4 we provide a single conceptual model that attempts to identify and connect the processes that are necessary for the establishment of a marine fisheries sanctuary that will provide enhancement of fisheries.

4. A CONCEPTUAL MODEL FOR MARINE FISHERIES SANCTUARIES

In this section we present a conceptual model for how benefits from sanctuaries may be delivered to fisheries. The model is presented graphically in Figure 1, and its components and links are described in this section of the text.

Empirical studies have shown that ‘sanctuary improvement’ is a nearly universal effect, although it does not apply to all species and it is difficult to predict which ecosystem components will be affected and to what degree they will be affected. Modelling has shown that there is great potential for sanctuaries to enhance fisheries, but this research has not evolved to the stage of producing models that can be used to predict the behaviour of real systems. Support for the claim that sanctuaries enhance fisheries is based primarily on theory, logic and strategic models, rather than empirical research or management experience (Attwood *et al.* 1997b). Here we construct a conceptual model that attempts to trace potential chains of cause-and-effect from the inception of a sanctuary through to impacts on fisheries and associated human institutions. Our focus is on the chain, rather than the individual links, those being the components and processes of the biological, ecological and human systems. Numerous authors have analysed and reviewed the evidence for individual links (e.g. larval dispersal) and the relationships between various links (e.g. reproduction and habitat quality). We will cite and briefly summarise their work, while trying to illustrate how it fits into the relationship between sanctuaries and fisheries.

The establishment of a sanctuary is believed to initiate a series of changes that cascade through the sanctuary’s ecosystem. The cascade may extend to areas beyond the reserve, and ultimately affect the fisheries and communities that depend on the resources of the sanctuary. Some changes may occur immediately, but others may occur in the short-term (<5 years), medium-term (5–15 years), or long-term (decades). Most changes that occur within such sanctuaries are expected to be beneficial to the organisms and environment of the reserve, and, assuming the sanctuaries are properly designed and managed, the benefits have the potential to extend to fisheries that operate outside the sanctuary.

Describing the full extent of potential changes is not possible due to the complexity of natural systems. We present a simple conceptual model that describes some of the primary and secondary mechanisms through which those changes could affect ecological components of reserves, exploited populations, and the human systems dependent on those resources (Figure 1). Overall, the model can be seen as occupying three realms:

- the ecological, biological and physical processes occurring within the reserve,
- the ecological, biological and physical processes occurring outside the reserve and on the fishing grounds, and
- the human processes associated with the fisheries and linked sectors of society.

Because of differences in knowledge about the effects reserves have on other systems, we will discuss the first realm (inside reserves) in the greatest detail, identify and discuss just the major elements of the second realm (outside reserves), and only briefly identify some of the important factors of the third realm (human systems).

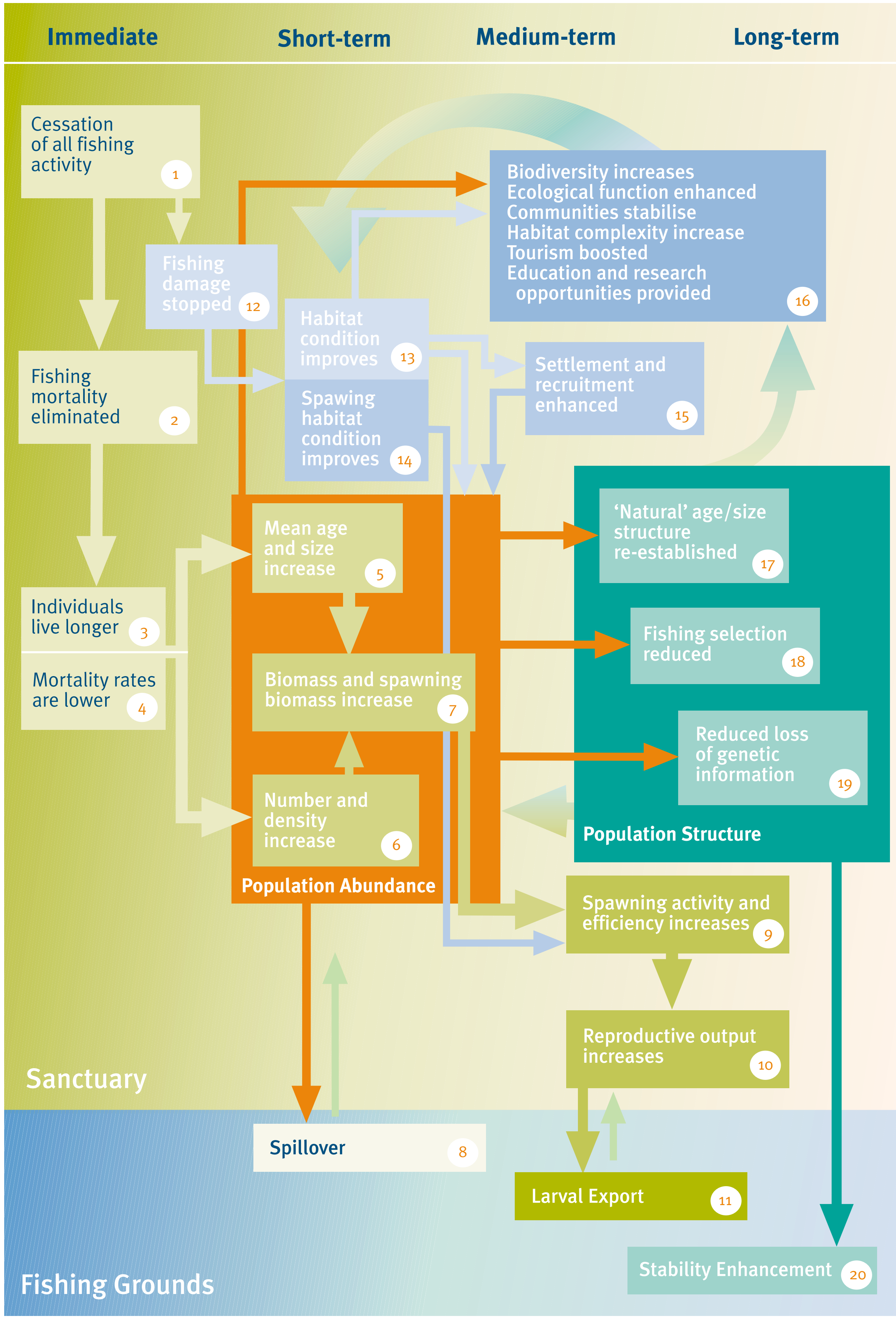
The model presented in Figure 1 shows the changes occurring inside a sanctuary as a result of its establishment, what we call 'sanctuary improvement', and the three processes primarily responsible for transferring those changes to areas outside the sanctuary. This model reflects, on one hand, basic ecological knowledge of marine systems and the effects of fishing on those systems, and, on the other, an hypothesis about how they will respond to sanctuary establishment. The model was constructed not to show all the effects reserve establishment could have, but rather to illustrate how a sanctuary could deliver benefits to fisheries operating outside the sanctuary. The model will apply to any exploited species, but will be most applicable to species with planktonic dispersal phases and to those populations that have been overfished.

The process of delivering benefits to fisheries must begin, paradoxically, with the cessation of fishing in the area designated to be the sanctuary.

Figure 1.

Conceptual model showing the pathways by which the establishment of a MFS could lead to environmental enhancement within the reserve and potentially to enhancement outside the sanctuary through the processes of spillover, larval export and stability enhancement. The large upper box represents a sanctuary, and the lower box represents the fished areas outside the reserve. Each text box within the sanctuary box represents an event, state or effect within the hypothesised cause-effect pathways; numbers are referenced in the text. The size of arrows roughly indicates the hypothesized importance of that pathway to the potential for fisheries enhancement. Very roughly, the time frame within which these events/states/processes might be expected to occur, following sanctuary establishment, increases from 'Immediate' on the left to 'Long-term' on the right. Text boxes 5–7 are grouped together to indicate that they are the processes involved in increases in population abundance, the most obvious manifestation of the process of sanctuary improvement (see text). Text boxes 17–19 are grouped because they are the processes responsible for the long-term changes to sanctuary populations, which along with the short-term abundance changes, are responsible for the improvements in population stability and resilience. The large blue and green arrows indicate poorly defined or understood pathways. For example, improvements to population structure have been hypothesised to feedback to improve population abundance, but the mechanisms have not been clearly identified. Similarly, it is believed that the general improvements to the ecosystem and human institutions will in some ways contribute specifically to sanctuary improvement at the population, community and habitat levels.

Figure 1.



4.1 Cessation of fishing

4.1.1 Model Expectation

The cascade of changes initiated by sanctuary establishment would begin with the cessation of fishing activity within the sanctuary (Figure 1—Box 1), usually the immediate objective of a no-take marine fisheries sanctuary. That event should have two immediate manifestations within the reserve. First, fishing mortality to target species would be eliminated (Box 2), and second, further damage to the environment and other species from fishing activities would cease (Box 12).

These manifestations would, of course, be dependent on compliance with no-take regulations (Fogarty *et al.* 2000). Modelling has shown that relatively low levels of illegal or unintended fishing in sanctuaries can eliminate the potential for those sanctuaries to deliver fisheries benefits, and experience has shown that poaching can be a cause of MFS failures (Tegner 1993, Attwood *et al.* 1997b, Gribble & Robertson 1998, Guzman & Jacome 1998, Murray *et al.* 1999b, Rogers-Bennett *et al.* 2000; however, see Jennings *et al.* 1996).

4.1.2 Effects of Fishing

Eliminating fishing mortality is critical to sanctuary success because fishing can have large impacts on exploited populations, either directly on those populations or indirectly through impacts on marine ecosystems (see reviews by Plan Development Team 1990, Russ 1991, Jennings & Lock 1996, Jennings & Kaiser 1998, Goñi 1998, Hall 1999). Populations that are overexploited:

- can be driven to extremely low densities
- older, more fecund size classes can be nearly eliminated, and
- normal behavioral patterns can be severely disrupted;

all of which can greatly reduce the reproductive potential of those populations (e.g. Pauly 1979, Davis 1981, Alcala 1988, Halliday 1988, Koslow *et al.* 1988, Jamieson 1993, Rowley 1994, Sebens 1994, Roberts 1995a, Hutchings 1996, Sluka *et al.* 1996b, Zabala *et al.* 1997, Shumway 1999, Stephens & Sutherland 1999, Roberts & Hawkins 2000).

Although many of the most notorious fisheries collapses were precipitated by intense fishing pressure (e.g. the collapse of the Atlantic cod stocks, Hutchings 1996; Australian gemfish, Rowling 1997; or Alaskan crab and shrimp populations, Orensanz *et al.* 1998), for some species, population declines have been caused by relatively low exploitation levels (Shepherd & Brown 1993, Munro & Polunin 1997, Roberts 1997b, 1997c, McClanahan *et al.* in press). Pauly (1997) suggested that large, long-lived predatory species with annual mortality rates on the order of 10-20% cannot sustain exploitation rates greater than 10% (a low fishing mortality rate) without being in danger of suffering recruitment overfishing. In such species a relatively small number of very large, fecund individuals are responsible for most of a population's reproductive output, and those individuals would be removed very quickly by anything more than very low fishing pressure. Conversely, some fisheries seem to defy logic by being able to sustain extremely high fishing mortality rates (e.g. F>5.0, Jamieson 1993).

Over time, the effects of fishing may significantly reduce the resilience of exploited populations by reducing their numbers, changing their population and genetic structure, and altering their communities and habitats, thus making them more vulnerable to collapse and extinction (Attwood *et al.* 1997b, McManus & Meñez 1997). However, not all species are affected by fishing in the same way. A species' life-history characteristics have a great deal to do with how it responds to fishing pressure (Adams 1980, Jennings *et al.* 1998, Tegner & Dayton 1999, Fogarty *et al.* 2000). Many, if not most, of the species that are most desired and valued by fisheries are 'K-selected' species. These species share a common suite of life-history characteristics; some of the more important are:

- slow somatic grow rates
- delayed maturation
- large adult size
- low natural mortality rates
- long life span
- show a strong site attachment
- low reproductive rates
- sporadic recruitment, and
- small population sizes.

This suite of characteristics is associated with the following impacts or effects:

- rapid population decline in response to fishing pressure, and slow recovery when that pressure is eased (Adams 1980, Roberts & Polunin 1991, Jennings *et al.* 1998, Russ & Alcala 1998b)
- greater vulnerability to overfishing (e.g. Adams 1980, Brander 1981, Thorpe *et al.* 1981, Munro & Williams 1985, Russ & Alcala 1989, Plan Development Team 1990, Roberts & Polunin 1991, Jamieson 1993, Tegner 1993, Dye *et al.* 1994, Dayton *et al.* 1995, Trippel 1995, Adams *et al.* 1997, Koslow *et al.* 1997, Roberts 1997b, Jennings *et al.* 1998, Russ & Alcala 1998b, Pitcher & Pauly 1998, Jennings *et al.* 1999), and
- an increased probability of the local extirpation of populations or even extinction of species (Russ 1991, Dayton *et al.* 1995, Roberts & Hawkins 1999).

Many of these species and their fisheries possess other characteristics that are thought to exacerbate their vulnerability to these impacts (Jamieson 1993, Roberts 1995b, Adam *et al.* 1997):

- aggregative behavior
- sedentarity
- territoriality
- sequential hermaphroditism
- living in shallow waters
- lack of natural refugia

- restricted geographic range
- ready availability to human population centres
- easily caught
- high commercial value and market demand
- mobile fisheries, and open markets.

Species with suites of characteristics like those above have been driven to economic extinction by fishing pressure in many places around the world (e.g. see references in Roberts & Polunin 1991, Jamieson 1993, Roberts 1995a), a process that may proceed quite rapidly (Roberts & Polunin 1991, Conrad 1997, Rowling 1997, Jennings *et al.* 1998). For example, the discovery by commercial fishers of large, pre-spawning, migratory aggregations of the highly valued gemfish (*Rexea solandri*) along the continental shelf break of south-eastern Australia, was followed by their intense exploitation, which lead to the stock's collapse just a few years later (Rowling 1997).

Most marine species of fish and invertebrates have what is known as an open population structure—recruitment to local populations is not dependent on (and is decoupled from) reproduction in that population by a planktonic dispersal phase (Caley *et al.* 1996). The existence of the open population structure, among other characteristics (e.g. high levels of fecundity), of marine organisms has led to the view that their populations should be highly resilient to environmental and anthropogenic pressures. As a result, the possibility that anthropogenic pressures could cause the extinction of a marine species has long been thought to be extremely low (Carlton 1993, Culotta 1994, Huntsman 1994, Tegner *et al.* 1996, Roberts & Hawkins 1999), especially as the result of overfishing (Jamieson 1993). Fogarty *et al.* 2000 point out that several marine mammalian and avian species have been driven to extinction by human exploitation, and recent work has uncovered several examples of near extinctions, or what have been termed crypto-, functional or economic extinctions (see references in Culotta 1994, Roberts & Hawkins 1999, and Dayton *et al.* 2000), some of which clearly have been significantly contributed to, if not caused by, overfishing (e.g. white abalone in Southern California, Davis *et al.* 1996, 1998; barndoor skate in the north Atlantic, Casey & Myers 1998).

The overfishing of stocks is not restricted to 'K-selected' species. In some cases, 'r-selected' species may be highly valued, perhaps because they are abundant and, therefore, targeted by fisheries. The high potential for population growth certainly makes these species less susceptible, but not immune, to overfishing. In some circumstances, the loss of the most desirable species from a system (usually large top predators) is followed by the fishing-out of less valuable, usually lower-trophic-level species (Munro & Williams 1985, Lock 1986, Russ & Alcala 1989, Dugan & Davis 1993, Ault *et al.* 1997a, Orensanz *et al.* 1998, Pauly *et al.* 1998a), a process that has been termed 'serial overfishing' and 'fishing down the food web'. The impacts of overfishing lower-trophic-level species can be catastrophic, as illustrated by the well-known collapses of sardine and anchovy populations in the Pacific Ocean (see Botsford *et al.* 1997).

4.1.3 Sanctuary Effects

Populations protected within marine sanctuaries and, therefore, released from the impacts of fishing pressure, should revert to being structured by natural mortality rather than fishing mortality (Bohnsack 1992). This release typically results in population increases (Stephenson & Kornfield 1990, Myers *et al.* 1995, Halpern in press). In these circumstances, the status and condition of once exploited populations that are now within sanctuaries will markedly improve, a process dependent on a suite of processes described below. While marine reserves should contribute to the improvement and recovery of most over-exploited populations, Roberts and colleagues have argued that they may be the best, perhaps the only, management tool that can prevent the elimination of the 'K-selected' species that are vulnerable to overfishing (Roberts & Polunin 1991, 1993, Roberts *et al.* 1995).

4.2 Decreased mortality and increased longevity

4.2.1 Model Expectation

The cessation of fishing mortality within sanctuaries (Box 2) should result in individuals of targeted species living longer than they would in a fishing regime (Box 3), and in overall mortality rates decreasing within sanctuaries (Box 4). Increased longevity within sanctuaries will immediately result in increased average age of individuals, and because in most exploited populations a large proportion of individuals are smaller than the size at which their growth would stop or slow to negligible levels, it will also result in increases in mean size of individuals (Box 5).

4.2.2 Effects of Fishing

Most fishing targets the larger individuals within a population (Roberts & Polunin 1991, Russ 1991). Under intense fishing pressure mature individuals are removed quickly (e.g. Borisov 1978, Davis & Dodrill 1980, 1989, Rice *et al.* 1989, Plan Development Team 1990, Jamieson 1993, Trippel *et al.* 1997). In addition, faster growing individuals tend to suffer a higher mortality rate because they recruit to the fishery sooner (e.g. Parma & Deriso 1990, Russ 1991, Rice & Gislason 1996), thus a fishery selects for slow-growing individuals (Bergh & Getz 1989). Both impacts result in an immediate and continuing reduction in the mean age and size of individuals in the population (see references in Roberts & Polunin 1991, Buxton 1992). Fishing that is intense enough to remove individuals before they have a chance to grow to the optimal size for harvesting is termed 'growth overfishing', a common phenomenon in marine fisheries. Russ (1991) cites numerous examples of growth overfishing in coral reef fishes. Overfishing may also produce a selective pressure on the population, 'permanently' reducing size over many generations (see Section 4.9). For example, Trippel *et al.* (1997) cited data showing a decline in 'age-at-maturity' and 'size-at-maturity' for several groundfish species subject to fishing pressure in the Northwest Atlantic.

Several compensatory processes may operate in fisheries to reduce the impact of these trends. First, the bycatch of juveniles, which are younger and usually smaller than mature individuals, will tend to increase the average size and age of individuals in fished populations. Second, larvae in the planktonic stage and immediately after settlement typically experience high rates of natural predation (Sale & Ferrell 1988, Carr & Hixon 1995, Roberts 1996, Caley 1998, McCormick 1998, Caselle 1999), a process that favours faster growing individuals because of their shorter period of vulnerability (Shepherd & Cushing 1980, Houde 1987, Miller *et al.* 1988), and this therefore counteracts the tendency for fishing mortality to select against fast-growing individuals. Third, the loss of larger individuals could result in a density-dependent increase in the growth rates of younger individuals, perhaps due to a decrease in the intensity of intraspecific competition, which would result in a 'size-at-age' increase (Russ 1991).

In extreme cases, the removal of mature individuals can reduce a population's reproductive potential, so that the number of propagules produced, and therefore recruits, becomes a factor limiting population growth (examples in Russ 1991). This is a process referred to as 'recruitment overfishing'. It can result in the elimination of whole age classes, thus increasing variation in recruitment and potentially leading to occurrences of years with little or no catch, and the concomitant impacts on fishers (Pauly 1987, Palumbi manuscript). Extreme recruitment overfishing can lead to the catastrophic, long-term collapse of stocks, as has happened recently with North Atlantic populations of cod and other groundfish (Hutchings 1995, 1996, Roughgarden & Smith 1996, Myers *et al.* 1995, Roy 1996, Sinclair and Murawski 1997, Myers 1997b, Fogarty & Murawski 1998, Shelton & Healey 1999). Although there has been considerable debate regarding the causes and contributing factors behind the groundfish population collapses, it is generally agreed that overfishing was at least a major factor. Even if an environmental factor played a major role (Hutchings 1996, Hofmann & Powell 1998), it is important to recognize the role played by overfishing. High levels of fishing that are sustainable under normal environmental conditions, may be unsustainable under abnormal conditions (Plan Development Team 1990, Rosenberg *et al.* 1993, Lauck *et al.* 1998), such those as associated with cyclones, ENSO events, or large-scale environmental change, and associated regime shifts in ecosystems and community structure (Francis & Hare 1994, Bakun 1998, Hayward 1997).

4.2.3 Sanctuary Effects

The release from fishing mortality is expected, in most cases, to result in a large increase in the mean age and size of individuals of overfished species within just a few years, and, most importantly, in the proportion of large, fecund individuals in the population (see references in Roberts & Polunin 1991, references and analysis in Halpern in press, and the review of empirical studies in Section 5). The resultant change in a population's age structure is likely to be a key to the success of a marine sanctuary, because older, larger individuals make a much larger contribution to the population's reproductive output than do younger, smaller individuals (Plan Development Team 1990; see Section 3.2).

4.3 Increased numbers and density

4.3.1 Model Expectation

The decline in overall mortality rates should result in the number and density of individuals increasing and, consequently, an increase in population biomass (Box 6), although the latter also will also increase because of the increased mean size of individuals. Considering these changes and those occurring at the individual level (see Section 4.2), it is expected that reserves will be populated by greater densities of individuals that tend to be older and larger than are extant in areas outside sanctuaries. In aggregate, the spawning biomass, and perhaps total biomass, of target species should increase within sanctuaries (Box 7).

Because we are dealing with a fixed area (the sanctuary), we can discuss numbers or densities interchangeably. Changes in numbers will typically produce changes in biomass, but the form of that relationship will depend on other factors (e.g. growth rates). In situations where we do not need to draw the distinction between how sanctuaries could affect numbers/densities versus biomass, we use the terms 'abundance' or 'size'. In other words, phrases such as 'population abundance' or 'population size' will refer to absolute number/density and/or biomass, without having to specify how they will differ.

4.3.2 Effects of Fishing

There is ample evidence that extreme fishing pressure will reduce population abundance (e.g. Koslow *et al.* 1988, Russ & Alcala 1989, Plan Development Team 1990, Russ 1991, Sebens 1994, Roberts 1995a, Hutchings 1996, McManus & Meñez 1997, Goñi 1998, McClanahan & Arthur 2001). As discussed above, this effect may be expressed to different degrees in different age/size classes. Fishing typically reduces the abundance of the most desirable/valuable members of the population—the oldest and largest individuals—which, because they are sexually mature, can have an effect on the populations reproductive potential (see Section 4.5). Alternatively, unintentional fishing mortality, such as that caused by the catch and discarding of under-sized individuals, or the bycatch of juveniles by other fisheries, has the potential to reduce the abundance of immature age classes. This reduction will not have a direct effect on reproductive potential, but may reduce reproductive potential in the long-run if it creates a limiting shortage of recruits to the spawning population. Independent of the age-distribution of fishing mortality, extreme overfishing can lead to local extirpation and even extinction of exploited populations (Roberts & Hawkins 1999).

4.3.3 Sanctuary Effects

It seems logical that establishing a marine sanctuary in an area that has been severely overfished results in abundance increases within that area, and numerous studies comparing populations inside and outside reserves support this expectation (see the evidence presented in Section 5). However, it is possible that populations that have been subjected only to low or moderate levels of fishing could respond to protection with a decrease in abundance in a reserve. A central theoretical and operational premise of the exploitation and management of living resources is that maximum population productivity will occur at intermediate mortality rates. The premise is based on the assumptions that resources (e.g. food, space, shelter, etc.) are limiting and that competition for those resources will limit the abundance of younger age classes. Species that experience very low mortality rates will have relatively high numbers of large, mature individuals, which will competitively limit the number of smaller, younger individuals that can enter the population, when the population is near carrying-capacity. The removal from a population of a number of large individuals 'releases' resources, which enables an even greater number of smaller individuals to enter the population (Plan Development Team 1990). Subject to reduced competition, the smaller individuals are able to achieve faster growth rates, and because most of their non-maintenance energy is used for growth (as opposed to reproduction), a greater population biomass is reached for the given levels of resource availability. Thus, following sanctuary establishment in this scenario, the abundance of large/old reproductive individuals would increase, fewer young, immature individuals would enter the population, and the population size would decrease. However, from the viewpoint of the value of the population to non-extractive human activities and its reproductive potential, such changes in the population structure and shift in biomass distribution may be important benefits to the population as a whole.

The question of how a population will respond to changes in mortality rates is part of a broader question about population regulation. The regulation of populations of marine organisms such as fish and invertebrates has been the subject of considerable debate and controversy in the last decade (e.g. Sissenwine 1984, Keough 1988, Hixon 1998). It is generally agreed that if populations are regulated, they must be subject to density-dependent controls (Murdoch 1994, Turchin 1995). However, there is a lack of general agreement about whether those controls will operate primarily on pre- or post-settlement-phase individuals. Although, the controls may be ineffective or absent during some periods, for some life stages, or in some locations, they must operate on the population as a whole (Chesson 1998). It is apparent that the response of a population to the cessation of fishing mortality will be dependent on its current state, the magnitude of that mortality, other population processes, and, as we shall see later, on interactions with other species. Nonetheless, whether local population sizes are ultimately controlled by recruitment or post-recruitment density-dependent processes, it is reasonable to expect that, at least in cases of overfishing, increases in number, density and/or biomass will occur commonly in response to the cessation of fishing mortality. However, increases in abundance following sanctuary establishment will eventually be constrained by limits imposed by some process or processes, such as insufficient recruitment, excessive predation, or availability of space, food or shelter. Although it may be difficult to predict what that limit will be relative to pristine conditions or to those conditions existing before sanctuary establishment, or which species will respond positively, it is likely that many exploited species will be more abundant inside than outside sanctuaries.

However, the problem may be even more complex than this. Models constructed by Botsford *et al.* (1999) suggest that the effectiveness of marine reserves established to protect red sea urchins in Northern California will depend on the form of the relationship between larval settlement rates and subsequent survival. Parrish (1999b) argued that the effectiveness of marine sanctuaries will dependent on which life stages are subject to density-dependent processes. Post-settlement density dependence would enhance the effectiveness of marine sanctuaries, but density dependence operating on adult growth or reproductive rates could easily reduce their effectiveness (Parrish 1999b, Mangel pers. comm.).

4.4 Spillover

4.4.1 Model Expectation

If population improvements occur within sanctuaries in the absence of fishing (one aspect of 'sanctuary improvement'), then a disparity in density and/or biomass between areas inside and outside reserves will be created. In this situation, 'all other things being equal', the rate of emigration from sanctuaries should be greater than the rate of immigration into sanctuaries, especially if it is driven by density-dependent processes operating inside reserves. The resulting net movement of individuals out of reserves is expected to elevate densities in the vicinity of reserves and increase the availability of stock to fisheries. This process and pattern is typically referred to as 'spillover' (Box 8), the first of three processes that are hypothesised to lead to the enhancement of fisheries operating outside sanctuaries. As well, it can arise in other circumstances and by other processes (see below).

4.4.2 Movement terms

We use the term 'trans-boundary movement' to refer to movements that take an individual across a reserve boundary, without respect to the direction. The terms 'excursion' and 'incursion' are used to refer to directional movements across reserve boundaries.

4.4.3 Spillover elements

There are at least four elements to spillover:

- the movement of individuals out of reserves, relative to movements into reserves, and the causes of those movements
- the effects those movements have on population densities outside reserves
- the recruitment to fisheries of those individuals that have left (i.e. the effect they have on stock size), and
- the degree to which fisheries are enhanced (e.g. increased yields).

Spillover terms

We can think of the excursions as the 'process', the changes to populations and stocks as the 'pattern', and the impacts on fisheries as the 'effect'. In the literature the term spillover is used typically to refer to the 'process', the 'pattern' and, at least the potential for, the 'effect' of spillover. To facilitate discussion of these elements, we will use the term 'excursion' when focussing on the process, and the term 'spillover' when focussing on the process and the pattern and/or effect.

In this section, we consider excursions, their causes and their density effects (i.e. the 'process' and 'pattern' of spillover), and later (Section 4.12) discuss the potential for spillover to enhance fisheries (i.e. the 'effect' of spillover). Discussion of the 'pattern' of spillover will be split with the relationship between the spillover process and changes to population sizes/densities dealt with in this section, and the changes to stock sizes dealt with in Section 4.12.

4.4.4 Process and Pattern

The process element of spillover is usually described as the net movement rate of individuals out of reserves (net excursion rate) as a result of, or in response to, a density difference or gradient. However, what distinguishes spillover, as defined above, from other excursions, is the population density pattern it produces, and, ultimately, its effect on fisheries. It is not necessary that there be a net excursion rate or that the cause is a density gradient for there to be spillover, although they can play an important role. What is key is that excursions at least result in changes to populations outside sanctuaries and stocks in fished areas. From the point of view of the individual, the key is whether the excursion involves relocation to areas outside sanctuaries and/or exposure to fishing-mortality risk. For example, large numbers of individuals leaving one sanctuary (e.g. a nursery habitat) and settling in another sanctuary (adult habitat) could represent a substantial net excursion rate from the first reserve, but those movements may have little to do with density gradients and would not constitute spillover, unless those individuals were at risk of being caught by fishers while travelling between sanctuaries. In addition, it is important to be clear about the time frame within which spillover is being considered. For example, large, highly mobile, pelagic species will be likely to exhibit high incursion and excursion rates within short time frames, compared to small, site-attached, reef species. However, if the latter species go through a developmental habitat shift then they may exhibit similarly high excursion rates within longer time frames.

The distinction between an excursion and the process and pattern of spillover, may seem academic, given that any excursion from a reserve would seem to alter the sizes of populations and stocks. However, the time-frame of that alteration can vary from a few minutes to the rest of the life-time of the individual, and what the individual does will determine the 'effective' contribution it makes to the population or stock. Very short excursions (e.g. to visit a cleaning station), would result in such a minor, transitory change in external populations/stocks or to the individual's risk of being caught, that they would only technically constitute spillover. More to the point, the magnitude of spillover excursions should be considered to be the product of at least three components—'rate', 'intensity' and 'duration'. The 'rate' is simply the number of individuals making excursions per unit time. The 'intensity' could be measured as the degree to which the individual became integrated into external populations or stocks, or the risk of fishing mortality per unit time. The 'duration' would be the length of time the individual would belong to the external population/stock or would be exposed to the fishing mortality risk.

Excursions from sanctuaries can occur for a variety of functions, such as feeding, spawning or visiting cleaning stations, or under a number of circumstances, such as dispersion in response to high competition or predation, or as part of an ontogenetic habitat shift. As well, excursions can occur on a range of spatial and temporal scales (Williams 1991), and the movement scale may be closely related to the function of the movement. For example, an excursion to visit a cleaning station would usually occur on a very different spatial and temporal scale from the movements associated with a seasonal or annual spawning migration. In addition, several other factors have the potential to influence trans-boundary movements (Kramer & Chapman 1999), most of which can show density-dependent variation. Some of the most important are listed below.

Species characteristics:

- size
- mobility
- habitat requirements
- population characteristics
- sex ratio
- social interaction rates
- densities inside and outside reserves

Community characteristics:

- competitive interaction rates and intensities
- predation rates
- availability of prey or food resources

Habitat characteristics:

- suitability inside and outside reserves
- availability of spatial resources, such as spawning sites, territories, and sheltering sites
- patch distribution outside reserves.

Roberts & Hawkins (2000) suggest that the following six key factors will determine the spillover rate from no-take marine fisheries reserves:

- reserve protection (determines degree of sanctuary improvement)
- reserve age (determines strength of density-dependent forces)
- fishing pressure outside reserves (contributes to density gradients across reserve boundaries)
- organism mobility (determines potential dispersal distances)
- boundary length (proportional to the number of individuals that could leave the reserve), and
- boundary porosity (related to suitability of surrounding habitats for dispersal and settlement).

We will identify four situations or scenarios that can lead to potential spillover, describe the associated spatial and temporal scales, and discuss the factors influencing the excursion rate and the effect it has on areas outside sanctuaries.

4.4.5 Relocation movements

This scenario applies to site-attached species, and probably is the one that most authors discuss first when they describe spillover. Benthic, and some mid-water species, in many habitats are site-attached, meaning that they occupy territories or well defined home ranges permanently or for long periods of time (Kramer & Chapman 1999 and references therein), the classic examples being numerous fish and invertebrate species living on coral reefs (e.g. Ehrlich 1975, Sale 1980b). Kramer & Chapman (1999) pointed out that the traditional view that relocations should be uncommon in strongly site-attached species is changing as evidence to the contrary accumulates (see references therein). Some of the most compelling evidence comes from numerous artificial-reef studies that have recorded rapid colonization of new artificial habitat by post-settlement individuals (Cliff 1983, Bohnsack 1989, Bohnsack *et al.* 1994, Cummings 1994, Golani & Diamant 1999). Relocations occur when these individuals leave their home site, make a one-way movement and permanently re-establish themselves at another site (Robertson 1988, Kramer & Chapman 1999), which may be in the same habitat patch, an adjacent patch or a far-distant patch (Williams 1991). We recognize two types of relocations. First, relocations by individuals may occur in response to density-dependent processes, such as high levels of competition, predation or disturbance, and/or low resource levels. Such processes may be extreme on an absolute scale (i.e. individuals move to escape from a poor environment), or on a relative scale (i.e. individuals relocate to take advantage of a better environment). We might term these 'pasture relocations'—leaving a pasture because it is 'brown' (and, hopefully, finding one that is less 'brown') or moving to another because it is 'greener'. Second, many species undertake ontogenetic shifts in resource use that typically involve a relocation to another habitat (references in Carr & Reed 1993, Roberts 1996, and Robertson 1998); we will call these 'ontogenetic relocations'.

How are excursions associated with 'pasture relocations' affected by the factors listed in the dot-points above? We consider a simple scenario in which a sanctuary is established in an area of uniform fishing pressure, population density and habitat, with the latter two having been negatively impacted by fishing. If we assume that there is always some level of pasture relocation going on in the population, then there would be nominal rates of excursion and incursions. Because these movements result in resettlement they have the potential to change population sizes, and, therefore, we can refer to the excursions as spillover. At first, we would have no reason to expect that the rates of the excursions and incursions would be different on the average. Therefore, the net trans-boundary movement rate would be zero and there would be no net spillover. Because every excursion would be balanced by an incursion, on the average, the excursions would have no affect on population densities outside reserves. However, several factors could alter this idealised scenario over time. First, we can reasonably assume that densities would increase within the sanctuary due to the process of 'sanctuary improvement' (see above). Second, if we assume that fishing pressure outside the sanctuary remained a significant source of mortality for the population, then we would expect to see a density difference established between inside and outside the reserve. This pattern alone, assuming the random diffusion of individuals, or something approximating such a process, would be enough to constitute the process of spillover, as more individuals would move out of the sanctuary and resettle outside, on the average, than would do the reverse (Bennett & Attwood 1991, Rakitin & Kramer 1996, Kramer & Chapman 1999).

We would expect this simple random-diffusion process to be enhanced once densities inside sanctuaries reached levels at which density-dependent processes affecting movement probabilities become appreciable (Kramer & Chapman 1999). At high densities we would expect a shortage of resources such as territories, shelters, mates, breeding sites, and/or food to result in an increase in competitive interactions. In addition we would expect that predator numbers would increase in response to greater prey numbers and general improvements to the environment. Both processes would increase mortality rates and reduce the quality of the habitat, which would induce more individuals to relocate. The relationship between density and the relocation rate would depend on the species, communities and habitats involved. Ault & Johnson (1998) suggested that a common response to resource competition or predation is emigration to areas with lower competitive or predation pressure. It is possible that density-dependent pressure would be sufficient to induce individuals to relocate, but it is reasonable to expect that the available alternatives for relocation would also affect the process. It is this view that results in the emphasis given to net spillover by many authors. Assuming that areas outside sanctuaries are more suitable (e.g. more resources, fewer predators), relocation could be seen to be a response to high densities inside sanctuaries and the density difference between areas inside and outside sanctuaries. Again, movements would be expected to occur in both directions, but because of the density gradient and associated suitability differences, the excursion rate would be greater than the incursion rate, creating a net spillover rate.

Two important factors, habitat quality and predation risk, could affect this process strongly. First, the assumption that areas outside sanctuaries would be more suitable may not be tenable. Although it is most likely that there would lower densities of competitors and predators, given the focal-species density difference, that does not guarantee that the areas outside a sanctuary would be more suitable. The suitability of areas surrounding reserves for the settlement of relocating individuals will depend on the inherent quality of habitats. For example, a sanctuary established on a set of coral reefs would provide ideal habitat, at least in time, for a range of coral-reef species. If the sanctuary was surrounded by non-reef habitat, there would not be suitable habitat for relocating coral-reef species to settle near to the reserve, thus forcing those individuals to travel long distances to find suitable habitat. Even if inherently suitable habitat was located close to a sanctuary, it may have been degraded by fishing impacts, thus lowering its suitability. The avoidance of low-suitability habitats outside sanctuaries could lead to lower rates of spillover than would be expected given differences in the densities of the focal species (Roberts & Polunin 1991, Rowley 1994, Kramer & Chapman 1999). Second, the processes of movement and resettlement themselves are likely to expose relocating individuals to increased predation risk, the largest component of which may often be fishing mortality. If individuals have to cross habitats of significantly higher predation risk than they experience within sanctuaries, or if settlement outside the sanctuary exposes them to higher predation risk than it would within the reserve, then the likelihood of relocation would be even lower than expected given the differences in habitat quality and focal-species density (Kramer & Chapman 1999). A similar phenomenon could occur if the nearest suitable relocation habitat patches were a long way from a sanctuary, thus creating a large energetic cost to relocation or a significant total predation risk, even in the situation where there was only a slightly higher instantaneous predation risk.

When applied to non-territorial species, this balance of factors is commonly represented with the use of frequency-dependent 'ideal free distribution' models (Fretwell & Lucas 1970). In these models individuals select or choose the habitat patch with the highest quality. The quality of a patch is determined by all those factors affecting the expected fitness for that individual, which, in turn, is determined primarily by its expected survivorship and reproductive capacity in that patch. These expectations are assumed to be a function of the interaction between the individual's phenotype and environmental factors such as: habitat quality, predation risk, food availability, density of competitors (especially conspecifics) and potential mates. If we consider a hypothetical situation in which there are two patch types that differ in their 'intrinsic quality', one high and the other low, the model predicts that at first all individuals introduced to this environment would choose to settle in the high-quality patches. However, as individuals enter the environment they alter the quality of patches they occupy. Increases in density within a patch will reduce its 'realised quality' through several processes, such as reducing the availability of essential resources and creating competition for those resources, increasing cannibalism rates, attracting more predators or parasites, increasing disease infection rates due to crowding, or degrading the habitat. Thus, as the density of individuals in the preferred patch type increases, its realised quality decreases until eventually it reaches that of the 'low quality' patch type. At that point individuals would enter both patches or move between patches in such a manner that the quality, i.e. fitness expectation, remained roughly equal. Thus, the choice of patches is dependent on the frequency distribution of individuals in the patch types, which controls the realised patch quality or suitability through within-patch density-dependent processes.

We can see the parallel between this model and a situation in which an environment has fished areas and protected sanctuary areas—high ('inside') and low ('outside') quality patch types, respectively. The patch types differ in quality, assuming they do not differ intrinsically, because of 1) the destructive effects of fishing reduce habitat quality outside the reserve, and 2) mortality rates are greater outside reserve areas due to fishing. Thus, much like the model above we would expect individuals to settle inside reserves in preference to outside, until such time that densities had built up to the point that outside areas would be just as attractive. This suggests the establishment of an equilibrial state (a prediction of simple 'ideal free-distribution' models) in which the movements between patches are equal. Therefore, at equilibrium there would be no net spillover, assuming that an individuals' impact on patch suitability was the same in both patches. Furthermore, the model predicts that as the system progresses toward equilibrium there would be a net incursion rate as individuals move from the low quality to high quality patch, or what we might term 'spillin' (note, we do not need to draw the distinction between 'potential spillin' and 'realised spillin' because it can only affect population densities inside reserves; affecting stock sizes or fisheries has no meaning inside reserves).

The ‘ideal free distribution’ model does not seem to be able to account for the process of spillover without the inclusion of additional factors. The most important missing factor is the ongoing effect of fishing on populations outside sanctuaries. If we assume that 1) there are habitats reasonably close to sanctuaries that are intrinsically suitable, 2) those habitats have not been too severely damaged by fishing, 3) fishing has not removed necessary food resources, 4) individuals that have left sanctuaries are replaced by recruitment from within the reserve, and 5) fishing mortality keeps focal-species densities low; then we would expect to see a steady-state net spillover rate in response to density-dependent pressures within sanctuaries.

The first assumption is not unreasonable as many reserves are established within a matrix of similar, suitable habitat. The second and third assumptions will hold for some situations but not others. The fourth assumption is required to avoid the situation in which an excursion is balanced by an incursion, as predicted by the model. In that situation, there would be no net change in densities outside the sanctuaries and, therefore, no spillover. This assumption is not unreasonable given that we expect sanctuaries to trend towards high productivity, recruitment, and growth rates. The fifth assumption is logical because we were considering the situation in which fishing pressure had been strong. The evidence suggests that individuals that leave sanctuaries may be removed rapidly by fishers who learn very quickly to concentrate their efforts in the immediate vicinity of sanctuary boundaries—an activity known as ‘fishing the line’ (Davis & Dodrill 1989, MacDiarmid & Breen 1993, McClanahan & Kaunda-Arara 1996, Piet & Rijnsdorp 1998, Roberts 1998a, Walls 1998, Johnson *et al.* 1999, Fogarty *et al.* 2000, Roberts & Hawkins 2000, McClanahan & Mangi 2000). Thus, it is possible that a frequency-dependent habitat selection process as represented by ‘ideal free distribution’ models, coupled with the effects of fishing mortality outside sanctuaries, may explain the process and effect of spillover in the case of ‘pasture relocations’.

We can expect the rate of spillover to vary among species, depending on their mobility and innate propensity to relocate. In general, the balance of density-dependent pressures within sanctuaries and the attractiveness of areas outside sanctuaries will be different for different species. Species that are highly vulnerable to predation while travelling between patches may have very low relocation rates, even when experiencing intense density-dependent pressures and/or higher quality habitats are available nearby. The calculation for territorial species must include the additional cost of acquiring a territory in the new patch, a process that can involve energetic costs and the risk of injury. On the other hand, the saturation of sanctuary areas with territories at high population sizes could force juveniles to relocate to other areas to acquire territories, thus increasing the spillover rate beyond what it would be for a non-territorial species (Paddack & Estes 2000). Species with low mobility may have lower spillover rates because relatively long-distance movements are energetically costly, risky and/or dependent on certain substrate types.

Spillover should be considered on an age-/size-specific basis. As described earlier, spillover is usually defined in terms of a net excursion rate. An implicit assumption of such definitions is that the net spillover applies to a given species or population and that the measure of spillover is numbers of individuals. This view is simplistic because it implicitly describes the movement of a homogeneous pool of individuals. In fact, during the process of sanctuary improvement, those individuals emigrating from sanctuaries may be very different than those immigrating into sanctuaries. The emphasis on the net excursion rate of all individuals can be misleading. For example, imagine a situation in which there is a high excursion rate of pre-fisheries-recruitment juveniles from a ‘saturated’ reserve in search of territories, and a low incursion rate of large, mature individuals attracted to the reserve because of its undamaged habitats and absence of fishing pressure. Clearly, there would be a net excursion rate, but it is not obvious that it would constitute spillover. There would be elevated population densities in fished areas, but there actually would be a decrease in stock size (i.e. numbers of individuals that have recruited to the fishery). Even if the juveniles were large enough to have recruited to the fishery, it is possible that their value would be less than the relatively small number of large, high value individuals that were lost to the fishery (i.e. stock biomass would have declined). Indeed, spillover is expected to be a benefit to fisheries in some situations (e.g. severe overfishing), precisely because sanctuaries have the potential to produce a relatively steady supply to adjacent fisheries of large, high quality individuals, which usually cannot be caught in fished areas away from sanctuaries (Plan Development Team 1990, Bohnsack 1996b, Johnson *et al.* 1999; Section 4.12). Thus, spillover in its fullest meaning may be best thought of as the movement of individuals from sanctuaries to fished areas that increases the availability of stock-at-age to fisheries.

Spillover will be influenced by the dispersal distance of individuals undertaking a ‘pasture relocation’. For a given environmental situation (e.g. density gradient and habitat suitability distribution), dispersal distance should vary with the size and mobility of the species/individuals in question. Highly sedentary species such as gastropods are likely to have much shorter dispersal distances than mid-water fishes, for example. For species with equivalent mobility, dispersal distance is likely to be proportional to body size or home-range/territory size; note that body size is highly correlated with home-range or territory size (Kramer & Chapman 1999). In general, the area over which sanctuaries produce a spillover pattern or ‘density halo’ will be a function of the habitat distribution, fishing intensity, species mobility and size, and the size of the individuals that are dispersing.

The interaction between dispersal distance and the size and shape of a sanctuary is also believed to influence spillover rate (Roberts & Polunin 1991, Rowley 1994, Munro & Polunin 1997). For a species with a dispersal distance that is a small fraction of the sanctuary diameter, it would be only those individuals very near the boundary that would have the potential to relocate outside the reserve, and thus constitute spillover. Conversely, for a highly mobile species, or one with a large home-range/territory size relative to reserve size, individuals over a much larger portion of the reserve would be potential spillover dispersers. Thus, spillover rates for highly sedentary species would be expected to vary very little with sanctuary size over a broad range of sanctuary sizes (Rowley 1994, Bohnsack 1996a), but would increase sharply for highly mobile species as reserve size decreased below a threshold related to their home range size (Rowley 1994, Auster & Malatesta 1995, Kramer & Chapman 1999). For any given species, the larger the perimeter-to-area ratio, as a result of a complex shape, the larger the proportion of individuals that would leave the sanctuary as a result of relocation dispersal (Plan Development Team 1990, Rowley 1994). However, Roberts & Hawkins (2000) pointed out that sanctuaries with large interiors would provide better protection and, therefore, achieve a faster rate and higher degree of sanctuary improvement, which, in time, would tend to increase spillover rates. Finally, spillover rates would also be affected by the interaction between shape and the distribution of surrounding habitats. A long, linear sanctuary on a fringing reef would be likely to have substantially different spillover characteristics compared to a large patch reef within a matrix of other such reefs (Munro & Polunin 1997). Similarly, spillover characteristics will be influenced by the location of the sanctuary in relation to suitable habitat patches, or the interface between suitable and unsuitable habitat (Roberts 2000, Roberts & Hawkins 2000).

As described above, the spillover of targeted size/age classes would be expected to be influenced by density-dependent processes, which would increase in importance as sanctuary improvement progressed. Therefore, it is reasonable to expect that spillover characteristics would change over time as a sanctuary develops. The time it would take before density-dependent processes would cause a significant increase in the spillover rate would depend on factors affecting the growth rates of individuals, recruitment rates, the rate of increase in population density, and habitat differences inside and outside sanctuaries. It could occur within months or be delayed for years as populations and habitats recover from overfishing. Russ & Alcala (1996b) provided several simple models for change in fish density over time in sanctuary and non-sanctuary areas. They considered the possibility of linear or exponential population growth rates both within and outside a sanctuary, which, in combination provided four models. Data from their system (Sumilon and Apo Island Reserves, Philippines) supported a model showing a linear increase within the reserve and an increase outside the reserve that only became apparent years later. These results are consistent with the assumption that spillover would be driven by density-dependent processes within the reserve that would not become important until densities had built up to near carrying-capacity levels.

Many species show ontogenetic shifts in resource use associated with changes in habitat or diet (see Roberts 1996, Auster & Shackell 1997, Robertson 1998, and references therein). Classic examples are the many reef species that settle as larvae in coastal habitats such as seagrass beds or mangroves, and later as juveniles migrate to reefs where they complete development and spend their adult lives, although there is some question about the prevalence of this pattern (Parrish 1989, Williams 1991, Roberts 1996). These movements constitute the second type of relocation dispersal—we term these 'ontogentic relocations'. 'Ontogenetic relocations' have the potential to produce much higher spillover rates than is the case for 'pasture relocations'. Because these movements are driven by the developmental process of individuals, they may not be as strongly related to density-dependent processes. We suggest that the excursion rate will be most strongly influenced by the recruitment rate to the sanctuary and suitability of habitats for the survival and development of juveniles. Juveniles will leave the nursery habitat when they have reached the appropriate stage of development, although it is possible that the timing may be affected by density-dependent processes. The excursion rate should be a function of the number of juveniles in the sanctuary, and, therefore, influenced by the number of recruits settling in the sanctuary, their growth rates and survival rates. As will be discussed later, recruitment rates will depend on the condition of populations in other areas, the placement of reserves, the quality of reserve habitats, and the predation rates on newly settled larvae. Although the recruitment of coral-reef fishes was once thought to be a largely density-independent process, it is now recognized that the influences of habitat quality and predation on settling and newly settled recruits can be a density-dependent process in some circumstances. Furthermore, it is likely that in many situations the survival and development of juveniles is density dependent. Thus, it is quite possible that the excursion rate from reserves established on nursery grounds will be influenced by the relative importance of increases in predator densities and habitat improvements, both of which would result from the process of 'reserve improvement'. Population improvements are likely to proceed more rapidly than habitat improvements (Roberts & Hawkins 2000). Therefore, it is possible that excursion rates would actually decline for a period of time after sanctuary establishment as predator densities increased, the decline would then slow and eventually increase as habitat quality increases became important. Nonetheless, sanctuaries established on nursery habitats are expected to have very high rates of spillover as a result of ontogenetic relocations (Rowley 1994, Kramer & Chapman 1999).

The extent of spillover of this type will depend on the distribution of habitats. In some cases, nursery and adult habitats may be adjacent to each other, but in others they may be 10's or 100's of kilometres apart (Parrish 1989). Under certain circumstances ontogenetic relocations will not create spillover, such as when both habitats are within a single sanctuary. Similarly, spillover may be reduced if both habitats are in separate sanctuaries. In this situation, individuals will be leaving a sanctuary area and relocating to another sanctuary area. The potential for a spillover effect is transient, and dependent on the vulnerability of the individuals to being caught by fishers while in transit. It is conceivable that the move could be made during a period when there was no fishing effort (e.g. at night), in which case there would be no risk and, therefore, no spillover despite a net excursion rate from the first sanctuary. It is more likely, however, that because of responses of fishers to spillover that these individuals will experience considerable risk, assuming that they are large enough to be targeted.

4.4.6 Cyclic movements

The second scenario we consider is that of regular movements out of and back into sanctuaries that do not involve relocation. Some species will exhibit occasional or cyclical movements among habitat patches for the purposes of cleaning, feeding, or reproduction (e.g. references in Hobson 1973, Parrish 1989, Hutchings 1996, and Roberts 1996). Return-trip movements will differ in their degree of regularity, varying from highly regular (e.g. feeding excursions timed to tidal, diel, lunar or seasonal cycles; e.g. Hobson 1973, Ogden & Quinn 1984, Williams 1991, Holland *et al.* 1993, 1996, Hutchings 1996, Roberts 1996) to sporadic or random (e.g. excursions made to exploit ephemeral feeding opportunities, Kramer & Chapman 1999; or to visit cleaning stations, Samoilys 1997). These movements will vary in duration from minutes (e.g. cleaning station visits), to hours (e.g. tidal feeding), to days or weeks in the case of migratory movements associated with reproduction.

As with relocations, we would expect these movements to be influenced by environmental factors. In many cases, excursions for the purposes of feeding or reproduction may be obligatory because of specific habitat requirements or the use of traditional spawning sites. In other cases, density-dependent pressures may increase the likelihood of individuals making these types of movements. High densities within sanctuaries may be associated with increased parasite loads, thus requiring more frequent visits to cleaning stations, and, perhaps, visits to more distant stations to 'avoid long queues'. Food resources may be less available at high densities, which would create the incentive for individuals to forage beyond their normal home range. However, the excursion rate associated with spawning may be greatest at low densities, as individuals have to search more widely for mates or spawning aggregations. Of course, as before, the distribution of habitats around reserves will influence an individual's tendency to make habitat-dependent excursions.

We would also expect these movements to be influenced by the intensity of fishing outside sanctuaries. As with all types of excursions, intense fishing pressure will restrict the tendency of individuals to leave reserves, assuming that they are capable of detecting and responding to fishing-mortality risk. In addition, effects of fishing on habitats will have an influence on this type of spillover. Reductions in food/prey resource levels or damage to the habitat characteristics necessary for spawning will act as a disincentive to individuals that might otherwise make excursions.

Again, body size will affect the rate and extent of spillover, at least with respect to feeding excursions. The increased energy demands of large species/individuals will require longer foraging excursions to meet demands, on the average. In addition, predation rates may be inversely related to size, thus making the risk of long excursions less for large individuals, although the opposite is likely to be true with respect to fishing mortality. The interaction between body size and sanctuary size will also influence spillover. The likelihood that an individual's feeding or spawning movements will result in an excursion from the reserve would be expected to decrease with sanctuary size. In large sanctuaries, it would be only those individuals living near the boundaries that would be likely to make excursions. In addition, the shape or perimeter-to-area ratio of the sanctuary will affect the excursion rate. The absolute number of individuals making an excursion would increase with the length of its perimeter, but the proportion of reserve individuals making excursions would increase as a function of the increasing perimeter-to-area ratio.

It is important to ask whether cyclic movements will produce spillover. Such movements would not represent a net movement when integrated over periods longer than a single cycle and, therefore, they might not appear to create a potential for spillover. However, during each trip there is the potential that the individual 1) will contribute to the dynamics of populations/stocks outside sanctuaries, and 2) will be exposed to the risk of being caught by fishers. Therefore, cyclic movements have the potential to produce substantial levels of spillover.

4.4.7 Overlap movements

The third scenario arises because fine-scale, short-term movements by individuals whose home ranges or territories straddle sanctuary boundaries will result in part of their time being spent outside the sanctuaries (Kramer & Chapman 1999). For a given individual, the probability that its home range or territory straddles a reserve boundary would increase with its home-range/territory size, which is strongly correlated with body size (e.g. Sale 1978, Goeden 1978, Larson 1980, Leum & Choat 1980, Jones 1984, Samoilys 1997, DeMartini 1998, Kramer & Chapman 1999), or with increasing perimeter-to-area ratio, but would decrease with increasing sanctuary size. As sanctuary size and perimeter length increases or home-range/territory size decreases, the number of home ranges or territories straddling boundaries will increase, and therefore the number of individuals spending part of their time outside the sanctuary will increase. The spatial extent of this form of spillover would be relatively quite small. Nonetheless, the spillover rate could be high under certain circumstances. If fishing intensity was high right up to sanctuary boundaries, then we could expect individuals straddling the boundaries to be removed rapidly. Assuming that sanctuary productivity and densities were high, individuals lost at the boundaries would be replaced from the interior, thus maintaining the spillover. The strength of this effect (interior replacement) would increase with sanctuary size and the size-to-perimeter ratio. In small sanctuaries, it is possible that the removal of boundary individuals could have a negative affect on sanctuary improvements, draining the reserve of a significant portion of its productivity.

4.4.8 Migratory movements

Highly mobile species such as pelagic, nomadic or migratory species, may not be expected to stay in sanctuaries long enough to build up their numbers, and, thus, would receive little or no protection (Parrish 1999b). Their distributions are not expected to be related to sanctuaries and, therefore, spillover is not an issue for these species. Barrett & Edgar (1998) suggested that this may apply to many soft-bottom fishes as well. Although, they may spend time in sanctuaries and cross sanctuary boundaries, the excursion rate would not be directly dependent on the sanctuary. This is not to argue that sanctuaries do not have the potential to benefit highly mobile species (however, see arguments in Roberts 1998a, Roberts & Hawkins 2000), but it would be likely to occur through other mechanisms. For example, Roberts has argued that migratory species may benefit maximally from sanctuaries established at sites where they are at greatest risk of being caught by fishers (e.g. geographic bottlenecks or spawning aggregations). Populations protected in this manner would be expected to maintain larger sizes, and, therefore, the numbers of individuals passing through the sanctuary would be greater than if the reserve did not exist. Although, this does not strictly constitute spillover, as defined above, it would have a similar effect on fisheries, which would be expected to take advantage of the higher densities close to the sanctuary and concentrate their fishing effort along sanctuary boundaries. Because the most important function of the sanctuary in this scenario is protection of the stock for part of its annual cycle, it may be the size of the reserve that is critical to its success and, therefore, to its 'spillover' rate. In some cases, habitat quality may also be of importance, such as when the sanctuary is sited on a spawning ground.

4.4.9 Sanctuary effect

We see that the amount of spillover arises from several processes and is dependent on a variety of species or individual-specific and environmental factors (Holland *et al.* 1993, Rowley 1994, Holland *et al.* 1996, Zeller 1997, Kramer & Chapman 1999). In general, we can expect that species that occupy well defined territories or home ranges (see references in Kramer & Chapman 1999), and do not stray beyond their boundaries, or have very limited mobility (e.g. gastropods) will show the lowest degree of spillover. Spillover is expected also to be a relatively unimportant process for mid-water and pelagic species, especially those that are migratory or nomadic. Species of intermediate mobility may generate the greatest amount of spillover—showing enough site attachment and spending enough time within sanctuaries to benefit from reserve protection but moving far enough at some times or life stage(s) to have a high probability of leaving the sanctuary (e.g. Davis & Dodrill 1989, Kramer & Chapman 1999, Parrish 1999b, McClanahan & Mangi 2000). In general, the rate and extent of spillover will increase with body size and home-range or territory size. Environmental factors, such as the intensity of density-dependent processes operating inside sanctuaries, damage to resources and habitats caused by fishing outside sanctuaries, and the size and shape of sanctuaries will all have a strong influence on spillover.

Despite the potential importance of spillover, at least locally, very few studies have attempted to detect or measure the rate of spillover from reserves (Russ & Alcala 1989, Attwood & Bennett 1994, Rakitin & Kramer 1996, Kramer & Chapman 1999, McClanahan & Mangi 2000; see review in Section 5).

As described, spillover is expected to result from, and be enhanced by, sanctuary improvement, at least in some situations. However, it has the potential to feed back on the process of sanctuary improvement. Spillover will tend to reduce the build-up of densities within reserves, perhaps as part of density-dependent processes controlling population size within the reserve (Kramer & Chapman 1999). In certain circumstances this effect could be strongly accentuated. For example, high fishing pressure on a large, high-mobility species focussed along the boundaries of a sanctuary, could effectively remove most spillover individuals and reduce densities well inside of the sanctuary (Kramer & Chapman 1999). This situation could prevent the build-up of such species in sanctuaries and, by removing those individuals with the greatest reproductive output, eliminate the potential for the sanctuary to enhance fisheries through larval export (see below; Rakitin & Kramer 1996).

4.5 Increased reproductive output

4.5.1 Model Expectation

The general process of 'sanctuary improvement' should result in increased numbers/density of reproductive individuals, and an increase in the average size of those individuals (see above). Further, sanctuary improvement should promote or result in an increased reproductive activity, increased reproductive output by larger individuals, and increased reproductive efficiency (Figure 1—Box 9), as discussed below, all of which should contribute to an increase in the reproductive output of the sanctuary on a per-area or per-individual basis (Box 10).

4.5.2 Effects of Fishing

Fishing pressure can impair the reproductive performance of individuals and the reproductive potential of populations in a number of ways. Because reproduction does not occur until individuals have reached a certain age, size and/or condition, overfishing can severely reduce the size of the spawning population either by removing mature individuals and/or reducing the number of individuals recruiting to the spawning population. In extreme cases the size of the spawning stock is reduced to the point at which recruits become limiting to population growth ('recruitment overfishing').

Fishing mortality can alter the characteristics of the spawning population. For example, Grimes *et al.* (1988) found that during a period of rapid growth of a tilefish fishery, which resulted in a 50% reduction in population size, males spawned at significantly smaller sizes and younger ages. Reduction in 'age-at-maturity' and 'size-at-maturity' is a common feature of heavily exploited fish stocks (Trippel *et al.* 1997). To some extent, this and other compensatory effects (e.g. increase in size-specific fecundity), which are expected to operate in populations subject to density-dependent control, will limit the reduction in reproductive potential caused by overfishing (Trippel *et al.* 1997, Mangel pers. comm.). For example, orange roughy increased in mean fecundity by 20% when population size was reduced by 50% (Koslow *et al.* 1995).

In many species (e.g. groupers, labrids and scarids), individuals undergo a sexual transformation at some point during development (sequential hermaphrodism). The point of transformation may be determined by relative size of individuals and/or the sex ratio in the population (Ross 1990). In severely overfished populations significant numbers of individuals may be caught before they recruit to reproductive stages of the population, or before they have a chance to undergo a sex change. The removal of large individuals may have a much larger effect on productivity in protandrous species (males become females) than in protogynous species (females become males) (Carr *et al.* in press). If transformation is relatively fixed and dependent on size or age (endogenous control), then over-fishing of larger individuals (older age classes) could produce a significant shortage of one sex and highly skewed sex ratios (Roberts & Polunin 1991, Russ 1991, Roberts 1995b, references in Jennings & Kaiser 1998), which may inhibit normal reproductive behavior and limit the reproductive potential of the population (Rowley 1994, Shumway 1999). On the other hand, if transformation is socially dependent (exogenous control), as may be the case in groupers (Shapiro *et al.* 1994), then removal of the larger sex (males in this case) would induce transformation of females, thus acting to compensate the effect of fishing on the sex ratio (Russ 1991, Ferreira & Russ 1995, Sluka *et al.* 1996b, Sluka & Sullivan 1998) and stabilise reproductive potential. Nonetheless, intense fishing still can produce dramatic changes in the sex ratios of these species (e.g. Beets & Friedlander 1999). These changes in the availability of one sex have the potential to lead to gamete limitation (e.g. sperm limitation in groupers, Sluka *et al.* 1996b, Sluka & Sullivan 1998) and, therefore, to recruitment overfishing and population collapse (e.g. Caribbean grouper, Roberts & Polunin 1993).

The allocation of non-maintenance resources in individuals typically shifts from growth to reproduction as they age (Edwards 1984). In the case of species with indeterminate growth, size and fecundity increases continuously as the individual grows older, although at a decreasing rate (i.e. growth and fecundity asymptote). The reproductive output of many species increases disproportionately as size increases (Plan Development Team 1990, Roberts and Polunin 1991, MacDiarmid & Breen 1993, Rowley 1994), which means that the proportional contribution of larger (older) individuals to the reproductive output of the population is greater than their proportional contribution to the population's spawning biomass. For example, the per-unit-mass fecundity of a large (12.5 kg) red snapper (*Lutjanus campechanus*) is 18.7 times greater than that of a small individual (1.1 kg, 11.4 times smaller) (Plan Development Team 1990). Roberts & Polunin (1991) provide several similar examples of fish species in which fecundity scales to a power of body length. In addition, it appears that larger individuals spawn more often and for longer periods of time (Roberts & Hawkins 2000). Therefore, the removal of mature individuals can have an effect on reproductive output that is disproportional to the biomass of those individuals.

Reproductive activity also can be related to population density. A disproportionate reduction in reproductive performance at low population sizes or densities is known as the 'Allee Effect' (Allee 1931); strictly speaking it is the per-capita rate of increase in the population that is reduced (Courchamp *et al.* 1999). The reduction in performance can result from reduced reproductive activity and/or efficiency at a given level of activity. At low population densities, spawning activity may be disproportionately low, perhaps because encounter rates are too low (mates may be difficult to find), densities are too low for sufficient social interaction to occur, or sex ratios are too skewed. Thus, reduction in population size by overfishing may put the population into a density- or demographic-state where recovery is unlikely. Above the Allee Effect threshold spawning activity would be expected to increase and reach its maximum potential at intermediate densities, but then decline at very high densities due to inhibitory social or species interactions. In many species, reproduction is partially or wholly dependent on the formation of spawning aggregations, making those species highly susceptible to fishing (Hutching 1995, Roberts & Hawkins 2000), especially given that fishers are highly skilled at targeting such aggregations (Johannes 1998b, Parrish 1999a, Dayton *et al.* 2000).

For species with external fertilisation, the density of reproductive individuals or density of spawning aggregations may be the most critical factor determining whether and how much reproduction occurs (Denny & Shibata 1989, Levitan 1995, McShane 1995, Styan 1998; however, see Yund 2000). Because dispersion of gametes occurs in a three-dimensional environment, fertilisation rates in broadcast spawners should, all other factors aside, decline disproportionately as the density of spawning aggregations decreases and the average distance between individuals increases. Several empirical studies, mostly of invertebrates, have found fertilization success, or related variables, to be dependent on density of gametes and/or spawners (e.g. Pennington 1985, Prince *et al.* 1988, Levitan 1991, Levitan *et al.* 1992, Trippel & Neilson 1992, Shepherd & Brown 1993, Andre & Lindegarth 1995, Levitan & Petersen 1995, Babcock & Keesing 1999). Not all studies have detected this pattern (e.g. Petersen *et al.* 1992, and Robertson 1996), and Yund (2000) pointed out that fertilisation rates are generally higher than expected. Reproductive failure due to poor fertilisation success resulting from low spawning densities may be responsible for recruitment failure, and possible population declines, in overfished free-spawning species (e.g. Shepherd & Partington 1995).

Fishing activity may create a source of disturbance and stress for fish, producing behavioral effects in individuals that lower their reproductive output (Roberts & Hawkins 2000). Atlantic cod stressed in the lab to simulate the affects of trawling disturbance were found to initiate fewer courtships, to have abnormal courtship behaviour, and to produce more abnormal larvae (Morgan *et al.* 1999).

Finally, habitat quality may decline in response to fishing (e.g. Collie *et al.* 1997). Given the well established relationships between habitat and community characteristics, e.g. structural complexity and species-diversity (see references in Russ 1991, Roberts 1996, Jones & Syms 1998), it is not surprising that habitat degradation may have detrimental impacts on reproduction (Hutchings 1995, Shackell & Lien 1995); see Section 4.7 for further discussion.

4.5.3 Sanctuary Effects

With the establishment of a sanctuary in an area that has been subject to significant fishing pressure, we would expect to see the process of sanctuary improvement taking place, which would lead to a reversal of most of the fishing effects described above. Reproductive output would be expected to increase on a per-area or per-individual basis because of increases in the mean size of mature individuals, increases in age/size-at-maturity, increases in the amount of spawning activity, increases in fertilization efficiency at higher spawning densities, improvement in sex ratios, reduction or elimination of Allee Effects, and spawning habitat improvements (Dugan & Davis 1993, Quinn *et al.* 1993, Rowley 1994, Dayton *et al.* 2000). It is possible that these changes also could result in an increased reproductive output per unit time per individual. Total reproductive output would increase due to these effects and the increased number of spawning individuals in the sanctuary (Edgar & Barrett 1999). Dugan & Davis (1993) argued that no-take reserves may be more effective than traditional fisheries controls at protecting spawning biomass, and, therefore, stabilising fisheries yields by preventing recruitment overfishing. Further, they argued that this effect will be critical in the face of natural sources of variability (e.g. poor recruitment years), catastrophic events (e.g. large-scale climate fluctuations), or human impacts (e.g. management errors). Dayton *et al.* (2000) argued that, for many species, spawning aggregations are essential to reproduction and, therefore, the potential for reserves to enhance fisheries relying on such species is dependent on spawning sites or habitats being included within reserves (Rowley 1994, Johannes 1998b). These effects would be most certain to occur in the short- to medium-term in areas where populations had been overfished. It is possible that if fishing pressure had not been intense, or as recovery continues, that density-dependent processes would limit increases in the mean size and reproductive output of individuals within a sanctuary (Mangel pers. comm.). The increase in reproductive output in no-take reserves is responsible for the second major process that is hypothesized to lead to fisheries enhancement—'larval export'.

4.6 Larval export

4.6.1 Model Expectation

Most marine fish and invertebrates have a planktonic dispersal phase. Marine sanctuaries will be exposed to ocean currents of various types operating on various scales, which will result in the export of at least some of the gametes, fertilised eggs and/or larvae produced within the sanctuary to areas outside the sanctuary. This process, which has been called 'larval export' (Figure 1—Box 11), although it technically refers to the net export of larvae, spores, eggs and/or gametes, is believed to have the potential to increase the size of larval pools, the numbers of recruits to stocks and enhance fisheries. In this section, we examine the process of 'larval export' as defined here, and leave the consideration of the fate of exported larvae and their potential to enhance populations and fisheries to later (Section 4.13).

The term 'larval export' has neither been carefully defined in the literature, nor clearly contrasted with 'spillover'. First, we note that the term has usually been used to refer to the net movement of eggs and larvae from sanctuaries to fished areas, and has often included the processes that would be responsible for those larvae contributing to fisheries enhancement. In the interests of clarity, we use the term simply to refer to the movement of reproductive propagules from reserves to areas outside reserves. Second, we suggest the use of settlement as the event that allows for a clear conceptual separation of the processes of spillover and larval export. In our view, 'larval export' should cover the largely passive movement of pre-settlement reproductive propagules or individuals from reserves, in contrast to 'spillover', which is the largely directed movement of post-settlement individuals from reserves. In those cases where the process of settlement cannot be determined, or is not applicable, then a developmental transition, such as the transition from the larval to juvenile stage, could be used to classify emigration as being 'larval export' or 'spillover'.

4.6.2 Sanctuary Effects

As described in the previous section, MFSs have the potential to produce substantial quantities of reproductive propagules. Whether, those propagules are exported from the sanctuaries will depend on a variety of factors (Rowley 1994, Tilney *et al.* 1996). The interaction of the spatial characteristics of a sanctuary (size, shape and location) with the spatial and temporal aspects of the hydrodynamic environment will have a large impact on the movement of propagules and, therefore, on the magnitude of the larval-export process (Carr & Reed 1993, Rowley 1994, Tilney *et al.* 1996, McManus & Meñez 1997, Roberts 1997a, 1998b, Dayton *et al.* 2000). Water movements or currents at several scales have the potential to play a role in the export of larvae, from very small-scale phenomena, such as wind-generated currents or tidal currents, to meso-scale phenomena such as eddies or upwelling, to ocean-basin scale structures, such as prevailing continental boundary currents.

The degree to which these water movements advect larvae away from sanctuaries will depend on the strength, direction and timing of the currents, relative to the location and timing of reproduction, among other factors (Tilney *et al.* 1996). The hydrodynamic features will interact with the spatial characteristics of sanctuaries and the dispersal characteristics of the species in question (Rowley 1994, Fogarty *et al.* 2000). In the case of a species with a very short dispersal period (days), weak currents sweeping over a large sanctuary would be expected to advect only a small proportion of that species' production from the reserve. The proportion could be very high if the currents were strong or the sanctuary very small. Conversely, it is likely that export would be very high for a species with a very long dispersal period (months), regardless of the size of the reserve or strengths of the currents (although this may be modified by the behaviour of the propagule in relation to ecosystem characteristics such as substrate topography). The complexity of the situation is increased when the shape and orientation of a sanctuary is considered. For example, a long-thin sanctuary (e.g. fringing reef) with its long-axis perpendicular to prevailing currents would be expected to have much higher export rates than a round sanctuary (e.g. patch reef) of the same size, which, in turn, would have a higher rate of export than the long-thin sanctuary if its long-axis was parallel to the prevailing currents (Rowley 1994). But even these generalisations will be affected by fine scale details, such as the timing and location of propagule release in relation to dominant current patterns. The export of reproductive output by the few species that do not have planktonic larvae (e.g. surf-perches, Embiotocidae, many crustacean and gastropods, live-bearing or brooding fishes) will be governed by other factors (Carr & Reed 1993).

'Spillover' and 'larval export' are the two processes by which reserves are hypothesised to contribute to populations outside reserves in the short- to medium-term. We have described the likely primary pathways from the establishment of a reserve (protection from fishing) that culminate in these processes. Secondary pathways that are hypothesised to operate within reserves and that have the potential to enhance the processes of spillover and larval export are discussed in the following Sections (4.7 to 4.9).

4.7 Recovery from habitat damage

4.7.1 Model Expectation

The cessation of fishing activity in sanctuaries is expected to halt the decline in habitat quality and secondary effects on species that results from the effects of fishing (Figure 1—Box 12). This change is expected to result, over time, in the improvement or recovery of habitats within sanctuaries (Box 13), including those habitats critical to the reproduction of the focal species (Box 14). It is reasonable to expect that these improvements will have beneficial effects on many species, possibly improving the rates of processes such as settlement and recruitment (Box 15), survivorship, and reproduction (covered elsewhere). The improvements to spawning habitats, and habitats in general, are expected to enhance spillover and larval export through a variety of pathways.

4.7.2 Effects of Fishing

Many fishing activities are known to cause damage to habitats (see reviews by McClanahan & Muthiga 1988, Hutchings 1990, Russ 1991, Jones 1992, Dayton *et al.* 1995, NRC 1995, Roberts 1995a, Auster *et al.* 1996, Jennings & Lock 1996, Jennings and Polunin 1996, Goñi 1998, Jennings & Kaiser 1998, Thrush *et al.* 1998, Hall 1999, Turner *et al.* 1999).

Trawling and dredging can impact benthic environments by crushing organisms, dislodging and scattering sessile organisms from their substrates (especially erect foliose and reef-building species), damaging their hard structures, damaging burrows or other refuges, exposing organisms to predators, resuspending sediments, and disturbing the fluxes of nutrients and other chemicals between the sediment and water column (Hutchings 1990, Jones 1992, Dayton *et al.* 1995, Auster *et al.* 1996, Collie *et al.* 1997, Goñi 1998, Hall 1999). These impacts can directly cause mortality, injuries that may lead to death later, and stress or energetic costs that may decrease longevity. Mortality rates may be even greater for those individuals that are caught by nets or dredges, and brought to the surface before being discarded (Jamieson 1993, Dayton *et al.* 1995, Attwood *et al.* 1997b, Auster & Shackell 1997). In general, the extent of the effect of trawling or dredging will depend on the interactions between species characteristics, habitat characteristics (e.g. substrate type) and the type of gear and fishing technique used (Collie *et al.* 1997, Goñi 1998). The frequency and extent of disturbance by trawling can be extremely high (e.g. Caddy 1973, de Groot 1984, Messieh *et al.* 1991, Dayton *et al.* 1995, McGarvey & Willison 1995, Auster *et al.* 1996), and its impacts may persist for decades (references in Jennings & Kaiser 1998). For example, Churchill (1989) found that in some latitude-longitude boxes on shelf areas in the northeast United States, the area trawled in one year exceeded the area of the box by up to 3 times, and that in some areas trawling was the major cause of sediment resuspension. Recently, Safina (1998) estimated that enough trawling occurs every year to cover half the world's continental shelves. A synthesis of data on the effects of trawling on benthic species in the North Sea found mortality rates as high as 50–75% (see Table 3.2 in Hall 1999). The impacts will vary among species (Jennings *et al.* 1999, Tegner & Dayton 1999). Long-lived, slow-growth 'K-selected' species are examples of those species most highly susceptible to the damaging effects of fishing (e.g. deep-water corals). Other species, such as those adapted to high-energy habitats with significant natural disturbance rates, may be more resilient and could even benefit (e.g. Eleftheriou & Robertson 1992, Hall & Harding 1997).

Many tropical coral reefs are subject to the highly destructive fishing practices of blasting, drive netting, which involves the dropping or dragging of weighted scare lines, and poisoning (see references in Russ 1991, Jennings and Kaiser 1998, McClanahan *et al.* 1999). Blasting and the use of weighted lines can destroy or severely alter the physical structure of coral reefs, reduce the structural complexity and diversity, and eliminate food and shelter for a host of species (e.g. Munro *et al.* 1987, Russ & Alcala 1989, Roberts & Polunin 1991, Russ 1991, Bohnsack 1993), a process that may take decades or centuries to reverse (Saila *et al.* 1993). Carpenter and Alcala (1977) estimated that 6% of coral was damaged during one scare-line fishing episode.

In extreme cases, one target species after another is fished out ('serial overfishing'; Munro & Williams 1985, Russ & Alcala 1989, Dugan & Davis 1993, Ault *et al.* 1997a, Goñi 1998, Orensanz *et al.* 1998, Pauly *et al.* 1998a), changing community structure and, potentially, ecosystem functioning. Population changes in focal species can have 'second-order' or indirect effects on other species, causing some to decrease and others to increase, perhaps replacing those lost because of fishing. Fishing pressure can be so intense that its detrimental effects extend to other species (e.g. Eldredge 1987, Russ 1991, Dayton *et al.* 1995), and replacement does not occur fully, a pattern called 'ecosystem overfishing' (Pauly *et al.* 1989). As more and more species are depleted eventually economically impoverished fishers may turn to the highly destructive fishing techniques described above and create major resource disruption and habitat destruction in an effort to maintain their incomes, in a process termed 'Malthusian overfishing' (Pauly 1988b, Pauly *et al.* 1989, Russ 1991, Roberts & Polunin 1993, McManus 1996, McManus & Meñez 1997); [note: many authors appear to use the terms 'ecosystem overfishing' and 'Malthusian overfishing' interchangeably]. In short, destructive fishing practices have the potential to greatly alter the abundance of target species, the species composition of communities, and the structure of the habitat.

Over time, habitats subject to heavy fishing pressure can become severely degraded (e.g. Collie *et al.* 1997, Tegner & Dayton 1999), which may lead to impacts on some species, such as increased mortality rates, reduced rates of settlement and establishment, and/or reduced growth and reproductive rates (Jones 1992, Halliday 1998, Auster & Malatesta 1995, Dayton *et al.* 1995, Hutchings 1995, Lindholm *et al.* 1998, 1999, Tegner & Dayton 1999). Local extinction of species can result, species diversity may decline, and apparently permanent shifts in the community or habitat types can occur as a result of the direct and indirect effects of fishing (e.g. Sale 1980a, Sano *et al.* 1984, Bouchon-Navaro *et al.* 1985, Castilla & Durán 1985, Moreno *et al.* 1986, Koslow *et al.* 1988, Russ & Alcala 1989, Alcala & Russ 1990, McClanahan & Shafir 1990, Claro 1991, Russ 1991, Dawson Shepherd *et al.* 1992, Jones 1992, McClanahan 1994, Sebens 1994, Auster & Malatesta 1995, Dayton *et al.* 1995, Roberts 1995a, Kaiser & Spencer 1996, McClanahan 1997a, Öhman *et al.* 1997, Roberts 1997b,c, Ault *et al.* 1997a, Goñi 1998, Jennings & Kaiser 1998, Pitcher & Pauly 1998, Tuck *et al.* 1998, Frid & Hall 1999, Tegner & Dayton 1999, Dayton *et al.* 2000). In extreme cases, structurally complex habitats with high biodiversity can be reduced to simple, low diversity habitats (e.g. Collie *et al.* 1997), or large shifts in community organisation can occur (Pauly 1998b).

As with most impacts on environments, while some species are affected negatively others may benefit. Scavenging species may increase in abundance as a result of the effects of fishing on populations and habitats (Jones 1992, Dayton *et al.* 1995, Fogarty & Murawski 1998). Species specialised to feed or settle on coral rubble may increase following the destruction of coral by explosives or drive netting (Russ 1991). Other species may experience population increases because of release from predation by, or competition with, species directly effected by destructive fishing (e.g. Russ & Alcala 1989, Claro 1991, Parsons 1992, McClanahan 1994, 1997a, Eggleston *et al.* 1997, Fogarty & Murawski 1998). Marine environments are subject to a variety of natural disturbances (Hughes 1994, Rogers 1993, Brown 1997, Connell 1997), some of which can produce effects similar to those caused by destructive fishing. Thus, it is not unreasonable to expect that some species will be adapted to take advantage of disturbances (e.g. Eleftheriou & Robertson 1992, Hall & Harding 1997), a phenomenon well known in many environments, and so increases in those opportunistic species may occur following fishing.

4.7.3 Sanctuary Effects

Sanctuary establishment in areas affected by fishing is expected, over time, to lead to improvements in habitat characteristics known to be impacted by fishing, such as structural complexity, system functioning and integrity, and species composition and diversity (Roberts *et al.* 1995). It is not unreasonable to expect that such habitat improvements will lead to benefits for at least some focal species, improving survivorship and reproduction (Thresher 1985, Auster & Malatesta 1995). Although evidence supporting this link is incomplete, numerous studies have shown correlations between habitat complexity and fish-species diversity or abundance (see references in Roberts 1996, Jones & Syms 1998), and most studies of marine reserves have found protection brought about increases in species diversity (Halpern in press). In situations where community composition has been severely altered, recovery may lead to a restoration of the original, historic or 'normal' composition. However, in other cases recovery may result in a qualitatively different community composition, indicative of an alternative steady state (Done 1992, Knowlton 1992, Hughes 1994). In many situations, habitat recovery may take much longer periods of time than is required for over-exploited populations to rebuild (Roberts & Hawkins 2000). In the case of species adapted to disturbed habitats or those species that benefit from discards, a reduction in the fishing and disturbance rate following sanctuary establishment could lead to population decreases. Thus, in general it will be difficult to predict the effect of a sanctuary on individual focal species, without considerable knowledge of their population and community dynamics (Roberts & Hawkins 2000). Nonetheless, it is generally argued that sanctuaries will benefit many, if not most, of the most valued species.

The improvement of habitat quality in MFSs is expected to lead to improvements in the rates of settlement and ecological recruitment through direct and indirect pathways. Directly, improved habitat quality is expected to increase the attractiveness of sanctuary areas, thus increasing settlement rates, and to improve the survival of newly settled individuals, thereby increasing recruitment rates. Indirectly, the sanctuary improvement process is expected to increase the size of the larval pool, which should in some cases result in increased settlement rates. As described earlier, improvement of spawning habitats is expected contribute to an increase in spawning activity and efficiency. This is expected to occur simply through the increase in the amount of habitat suitable for spawning, and, perhaps, through improving the quality of that habitat. Thus, to the extent that improved habitat quality contributes to increased reproductive output, and in proportion to the degree of larval retention, habitat improvements will increase the number of larvae available for, and achieving, settlement in sanctuaries. In addition, improved habitat quality should contribute to increased survivorship of individuals of some species, thus enhancing the processes associated with the increasing population abundance. This could have direct impacts on settlement for those species known to settle preferentially near conspecifics (Shepherd 1990) or have higher survival rates near conspecifics (Tegner & Dayton 1977). Secondarily, it could contribute by feeding back through increased reproduction to further enhance settlement.

Increased settlement and recruitment is expected, under certain circumstances, to result in population increases (see discussion in Section 4.13). For a given level of larval supply, settlement and subsequent survival appears to be most strongly dependent on habitat type, complexity and quality (Sale *et al.* 1984, Shulman 1984, 1985, Roberts & Polunin 1991, Dayton *et al.* 1995, Booth & Wellington 1998, Lindholm *et al.* 1999, Dayton *et al.* 2000), to the extent that, when recruitment or mortality rates are dependent on resource availability, habitat quality will regulate population size (Jones 1988). Thus, within the limits set by population regulation mechanisms, it is possible that increased settlement and survivorship rates, due to habitat quality improvements in sanctuaries, will result in increased numbers and densities of individuals in sanctuaries, and ultimately may contribute to increasing the size of the spawning population (Dayton *et al.* 2000).

Increased settlement will alter the size/age composition of reserve populations, reducing the rate of increase in mean age and size of individuals that is expected as part of the process of 'sanctuary improvement' (Section 4.2) although not the size of older age classes. Mortality rates for newly settled larvae typically are very high (Sale & Ferrell 1988, Carr & Hixon 1995, Roberts 1996, Caley 1998, McCormick 1998, Caselle 1999). Therefore, sanctuary-improvement population increases in species that prey on, or cannibalise, new or recent recruits may inhibit settlement and reduce ecological recruitment (e.g. Tupper & Juanes 1999), countering the tendency for recruitment to be enhanced by habitat improvements.

4.8 Benefits beyond focal species

4.8.1 Model Expectation

Eliminating the destructive impacts of fishing on habitats and species will produce far-ranging improvements beyond those of immediate importance to focal species (Box 16). Improvements are expected at the biological level (e.g. increased biodiversity, restoration of 'normal' ecological functions, stabilisation of community composition, increased habitat complexity), and at the human level (e.g. increased tourism value, creation of opportunities for research and education).

4.8.2 Effects of Fishing

In many cases, overfishing and habitat damage have led to reduced biodiversity (e.g. Russ & Alcala 1989, Russ 1991, Roberts 1995a, NRC 1995, Jennings & Lock 1996, Jennings & Kaiser 1998, Hall 1999, McClanahan & Arthur 2001; but see Greenstreet & Hall 1996, Watson *et al.* 1996 for counter-examples). This pattern is not surprising given the large number of studies that have shown a relationship between the abundance and diversity of coral reef fishes and coral cover (references in Jones & Syms 1998). As fishing pressure increases, diversity may rise first due to an increase in 'evenness' as the most common species are fished down moderately, but then decline as population sizes of more and more species are driven to low levels (Hall 1999). The 'intermediate disturbance hypothesis' (Connell 1978) predicts that in some situations moderate levels of fishing disturbance may increase biodiversity relative to the extremes of low or high disturbance (e.g. Hixon & Brostoff 1983, McClanahan & Shafir 1990, Rogers 1993, Aronson & Precht 1995, McKenna 1997), thus making it difficult to predict the outcome of reserve establishment on biodiversity, although there is little doubt that intense fishing pressure will have a negative effect on biodiversity.

Predation has the potential to function as an organizing process in marine ecosystems (e.g. Kerfoot & Sih 1987, Hixon 1991, Jones 1991, Jennings & Polunin 1997, McClanahan 1997c), thus it is not surprising that fishing has the potential to severely alter community composition and ecosystem dynamics (ecosystem overfishing). The overfishing of many highly desirable species, which often are top predators, can lead to the ecological release of their prey and competitors, and the subsequent increases in their biomass. There is a large theoretical and empirical literature that addresses the influence of competitive and predator-prey relationships on community composition (see Jennings & Kaiser 1998, and Hall 1999 for recent discussions).

Although the literature contains numerous cases of 'top-down control', in which removal of a predator apparently led to the release of prey populations, some have suggested that the evidence for compensatory prey release is equivocal (Jennings & Polunin 1997; also, see references in Roberts & Polunin 1991). Most studies are able to provide evidence consistent with this effect, but fall short of providing 'proof' or a clear demonstration of the mechanism. For example, Roberts and Polunin (1992) found that in areas where groupers had been fished down, one of their prey species (surgeonfish) were nearly three times more abundant than in unfished areas, a difference consistent with this hypothesis but one that could have had other causes. Similarly, the fishing down of mackerel populations in the North Sea in the 1970s apparently lead to the subsequent ecological release of sandeel populations (Jones 1983), but the link was only correlative.

Russ (1991, Russ & Alcala 1989) argued that 'prey release' is uncommon and should not be expected on coral reefs, because of the large number of potential generalist, 'replacement' predator species and the fact that many reef-fish populations may be limited by recruitment rather than predation. McClanahan (1994) pointed out that, for fishes, the evidence suggests that the phenomenon occurs only in diodontids and small-bodied labrids and pomacentrids. In contrast, Edgar & Barrett (1999), working on temperate reefs, suggested that secondary interactions in marine ecosystems are common, and, therefore, it is not obvious that any given no-take reserve will achieve its objectives for more than a small number of focal species.

The best evidence for top-down control comes from several tropical reef systems (Kenya, Caribbean, Red Sea, Mediterranean). Researchers have found that predatory fish apparently control the populations of certain urchin species, and removing those fish by fishing results in increases in urchin population sizes, sometimes to very high levels (references in Roberts 1995a, Sala *et al.* 1998a, Steneck 1998, and McClanahan & Arthur 2001). McClanahan and colleagues have shown that the overfishing of sea urchin predators such as triggerfish on coral reefs in East Africa leads to the ecological release of urchins. Intense grazing by the urchins, and habitat destruction by some fishing practices, results in the reduction in coral coverage, coral diversity and the abundance of grazing fishes (McClanahan & Muthiga 1988, McClanahan *et al.* 1995, McClanahan 1997b,c). Such reefs shift from being dominated by coral, coralline algae and diverse communities of grazing and predatory fishes, to being dominated by urchins and algal mats (McClanahan & Shafir 1990, McClanahan 1997c, McClanahan & Arthur 2001).

In some situations, the removal of a key predator may have a more far-reaching impact, such as when it initiates a 'trophic cascade' of effects, as has been documented in the orca—sea otter—urchin—kelp system in the North Pacific (Estes & Palmisano 1974, Estes & Duggins 1995, Estes *et al.* 1998). These systems and their responses to fishing and the removal of top predators are complex and open to alternative interpretations (Steneck 1998). Nonetheless, in situations where fishing precipitates a 'trophic cascade', the associated changes to community composition and ecosystem function have the potential to affect the productivity, viability and sustainability of exploited species in the system (Plan Development Team 1990). Viewed over a longer historical perspective, it is evident that ecological communities in many coastal areas around the world have been profoundly altered by centuries of human exploitation, as Jackson (1997) has shown for the Caribbean region.

4.8.3 Sanctuary Effects

As habitats improve after sanctuary establishment, given time, it is likely that locally extirpated species will reappear and that the 'normal' community composition will be re-established. As biological communities recover and return to 'normal', it is expected that 'normal' ecological functioning should become re-established. Because of the large impacts of intense fishing pressure on the populations of many species, protection should result in substantial changes in community composition within sanctuaries (Palumbi manuscript). These changes to the natural environment will have benefits for humans in a number of ways. For example, the re-establishment of 'natural' environments, as well as fostering the reappearance of rare and high-interest species (e.g. large, predatory fish), will lead to improved opportunities for non-destructive and non-exploitative recreation and tourism, provide for some of the needs of local communities, create opportunities for research and educational organisations to study those environments, and enhance the ecosystem services provided by the environment (Dixon 1993, Arcese & Sinclair 1997, Bohnsack 1998, Dustan 1999, Roberts & Hawkins 2000). However, if a system has been altered too severely (see discussion and examples in Hall 1999), it is possible that an alternative 'stable' state will have been reached which could impede and interfere with the process of sanctuary improvement and, ultimately, fisheries enhancement (McClanahan 1997b, 2000). A sanctuary isolated from potential sources of recruits could fail to re-establish its 'normal' state, and suffer a further loss of biodiversity in time (Roberts 1997a, Roberts & Hawkins 2000).

These environmental changes and improvements within sanctuaries may further enhance, through indirect pathways, the processes of spillover and larval export, by improving conditions for the focal species (e.g. prey availability, densities of commensals) and, in turn, the improved health of focal species populations should further contribute to non-focal species benefits. It should be recognized, however, that the same processes could have an inhibitory effect on spillover and larval export. In many situations, fisheries have found it is economically viable to target predation-released prey species, in part because of the economic extirpation, or near extirpation, of their predators, and in part because of increased abundance of the prey stocks. This is one aspect of the process termed 'fishing down marine food webs', which is characterised by fisheries gradually shifting their target from high trophic level, long-lived, low-productivity, piscivorous bottom fish to low-trophic level, short-lived, high-productivity invertebrates and planktivorous pelagic fish (Pauly *et al.* 1998a). Pitcher & Pauly (1998) provided several examples of systems in which high-quality fish (e.g. cod, halibut, grouper) have been replaced as the primary targets of fisheries by low-quality species (e.g. small pelagics, demersal omnivores, jellyfish). Thus, the re-establishment of 'normal' species composition within reserves may actually result in the decline in abundance and, therefore, reproductive output of prey species such as these, although it may also result in the increase in stocks of preferred commercial species.

Protection from fishing would see the return of many predator species and an increase in their biomass. To the extent that those species were predators of newly settled individuals and juveniles, the recovery of predatory species could act to inhibit settlement turning the sanctuary into a recruitment sink (Roberts & Polunin 1991). At least three studies comparing fishing and unfished sites have found an inverse relationship between the abundance of large age-classes and the abundance or survival of small age-classes (Goeden 1979, Tupper & Juanes 1999, Paddack & Estes 2000), but Macpherson *et al.* (1997) in their study of the survival of juvenile fish did not find evidence to support this idea.

In general, indirect effects may make it very difficult to predict the outcome of sanctuary establishment for any given species (Palumbi manuscript), which may help to explain why many studies have found that sanctuaries do not improve conditions for all species. In some cases, protection from human interference may result in particular suites of species being replaced by others without an overall change in density. However, this does not change the fact that sanctuaries will have a beneficial effect on a large number of exploited and unexploited species. This complexity suggests that sanctuary success cannot be based on the outcomes for single species, or even small suites of species, but rather should be assessed across all focal species, and their fisheries and environments. Palumbi (manuscript) further noted that the effect of reserve protection on species diversity will be difficult to predict. In some cases changes to species diversity may be due largely to the reappearance of extirpated species (i.e. an increase in species richness), but in other cases species diversity may change significantly due to changes in species densities without a significant alteration to the number of species. Nonetheless, most studies have found that area protection increases species diversity (Halpern in press).

4.9 Long-term benefits to focal populations

4.9.1 Model Expectation

Most of the enhancements to exploited species discussed so far are expected to be first realised within relatively few years (i.e. in the short- to medium-term). As conditions continue to improve, and populations and communities return to 'normal', those benefits are expected to continue to accrue. Over longer periods at least three other improvements to exploited populations should occur. First, in the absence of fishing mortality the 'natural' age/size structure should re-establish itself (Figure 1—Box 17). Second, as with other effects of fishing, the impacts of fishing selection on populations will be reduced with the establishment of sanctuaries, and may reverse in some circumstances (Box 18). Third, sanctuaries should reduce the loss of genetic diversity that occurs through the process of fishing selection and through the reduction of populations to very small sizes (Box 19).

4.9.2 Effects of Fishing

Most fishing is highly selective with respect to the size (see discussion in Section 4.2), and, therefore, the age of individuals caught. Nets and traps are often mandated by regulations to have a mesh size that will allow the escape of small (young) individuals, and fishing may be prohibited or restricted on nursery or spawning grounds. As result, the 'natural' age and size structure of the population becomes distorted in proportion to the fishing pressure (e.g. Russ 1991, Pope & Knights 1982, Rowling 1990, Rice & Gislason 1996, Goñi 1998, Rochet 1998). In extreme cases, most large, mature individuals can be removed from the population (e.g. Borisov 1978, Davis & Dodrill 1980, 1989, Rice *et al.* 1989, Russ 1991, Trippel *et al.* 1997, Roberts 1998a), and because these are the most productive individuals the loss affects the productivity of the population and, therefore, its potential fisheries yield (Bergh & Getz 1989). As discussed earlier, in sequentially hermaphroditic species (e.g. groupers, labrids and scarids) the removal of the oldest individuals may lead to a distortion of the sex ratio and, thereby, reduce productivity, especially in those species in which the transformation from one sex to the other is under endogenous control. Besides having the obvious effects on reproductive performance, distortions of the 'normal' age/size structure and sex ratio are believed to have detrimental impacts on behaviour patterns and social structure (Plan Development Team 1990, Shumway 1999). Disruptions to normal behaviour and social structure, in turn, are believed to have a negative effect on survivorship and reproduction (Shumway 1999). Behaviour is thought to play a central role in the expression of Allee effects. When population sizes are very low, individuals may have difficulties locating mates, schooling may break down exposing individuals to greater predation risk, observational learning may be impaired, and social facilitation necessary for some functions such as spawning may be diminished (Shumway 1999, Stephens & Sutherland 1999).

Fishing does not always push size distributions 'to the left' by removing larger individuals. In situations in which fishing is not size-specific, or the catch/bycatch of juveniles is high (e.g. Penn *et al.* 1997), large numbers of individuals can be removed before they have a chance to enter the reproductive age-classes (Dayton *et al.* 1995). This type of distortion of the natural size/age structure, 'to the right', may have less impact on populations, unless it leads to recruitment overfishing.

It has long been recognized that fishing mortality has the potential to produce artificial selection on life history characteristics (Ricker 1981, Bergh & Getz 1989, Smith *et al.* 1991, Policansky 1993, Rijnsdorp 1993, Jennings *et al.* 1999). The Plan Development Team (1990, after Ralston 1987) presented 28 estimates of natural and fishing mortality rates for reef fishes. The ratio of fishing to natural mortality rate was greater than 1.0 in 21 cases (75%), and the 6 highest values ranged from just over 2.2 to 5.6, which led them to conclude that fishing is likely to be the dominant selective agent for most exploited reef fishes. Life history characteristics most often thought to be selected for by fishing mortality are lower growth rate, smaller age- and size-at-maturity, smaller adult size, shorter life-span, altered timing of spawning, and reduced reproductive output (Plan Development Team 1990, Policansky & Magnuson 1998), all characteristics that could be detrimental to fisheries yield (e.g. smaller individuals are less desirable and less fecund, Roberts & Polunin 1991). Although very few empirical studies have been able to verify the predicted effects of this form of selection (Ricker 1981, Buxton 1993, Jennings *et al.* 1999), the theoretical arguments are sufficiently convincing to argue that the threat to a stock from fishing selection should be taken seriously (Roberts *et al.* 1995). Other characteristics that have the potential to affect the effectiveness of sanctuaries, for example aggressiveness or movement patterns, may also respond to fishing selection (Attwood *et al.* 1997b).

Overfishing is expected to result in a reduction in genetic diversity within the target population (Bergh & Getz 1989). Because the ability of populations to respond to environmental change is related to genetic variability (Lande & Barrowclough 1987, Nelson & Soulé 1987), reduced genetic diversity may decrease the likelihood of the survival of over-exploited populations (Shepherd & Brown 1993, McManus & Meñez 1997). The rate of loss of genetic information in finite populations is a function of the effective population size, which in turn is affected by several demographic factors that can be impacted by overfishing, such as the sex ratio, and generational overlap (Gaggiotti & Vetter 1999). The loss of genetic diversity will be greatest when populations go through very low effective population size bottlenecks, which can be caused by extreme overfishing. Relatively few studies have confirmed these impacts of fishing on populations. One of the most widely cited studies, demonstrated that intensive fishing on orange roughy, a ‘K-selected’ species, resulted in a loss of genetic diversity in a very short time (Smith *et al.* 1991). However, a recent study of a population of the squid *Illex argentinus* found very little loss of genetic diversity over a period when the population was subjected to intense fishing pressure (Adcock *et al.* 1999).

4.9.3 Sanctuary Effects

The establishment of a MFS should result in alterations to the age/size structure over time, presumably returning it to something like that seen in unexploited populations. Whether this change results in an enhancement of productivity within sanctuaries will depend on the degree to which the stocks were overfished and the balance between reproductive output and the ‘maturity’ of the age/size structure. Achieving the natural age/size structure, and sex ratio, should contribute to re-establishing the social environment that facilitates normal biological behaviour patterns and is associated with high productivity and population stability (Plan Development Team 1990, Zabala *et al.* 1997, Shumway 1999). However, predicting the population and reproductive effects of age/size structure and sex-ratio changes will be complicated by the competition between smaller age classes and larger age classes, and the effects of intra-specific predation.

The relaxation of fishing selection caused by size-selective fishing practices, will change the selective regime experienced by the population within the sanctuary to one primarily controlled by natural sources of mortality. It is likely that the change in selective regime will result in genetic changes in the population, but it is not at all clear whether those changes will in some sense ‘undo’ the selection caused by intense fishing. Some researchers argue that sanctuary protection has the potential to compensate for the damage done by fishing selection, although probably not in the case of single, small reserves (Roberts *et al.* 1995). Moreover, it will be difficult to predict the impact on the entire population of a change in selection regime for a portion of the population, without detailed information about the sizes of the portions and the gene flow between them. The open population structure of most marine species led to the view that there should be considerable gene flow between populations, which has been confirmed for many species, especially for those with long-distance dispersal (Carr *et al.* in press). However, recent work has found that effective long-distance dispersal may be relatively rare and that there is remarkably little demographic exchange in many species despite their considerable dispersal capabilities (Palumbi manuscript). In addition to changes to the genome, it is likely that fishing selection will have far-reaching impacts on the structure of meta-populations (e.g. reducing or eliminating demes in salmon populations, Policansky & Magnuson 1998), further complicating the prediction of population changes in response to sanctuary establishment. It is likely that biodiversity loss from a network of sanctuaries would not occur, or would be slower than the loss from a single sanctuary, especially if it was isolated from sources of recruits (Roberts 1997a).

Although the establishment of a sanctuary is unlikely to restore genetic diversity lost due to the effects of fishing, it should reduce the further loss of information, at least in proportion to the relative size of the sanctuary. Of course, changes in the loss of information will be influenced by many factors besides the size of the sanctuary. Protection of genetic diversity may be most effective when sanctuaries protect a number of local populations (Fujita *et al.* 1998b), as long as they are not separated by excessively large expanses of overfished habitat (Shepherd & Brown 1993). Auster & Shackell (1997) argued that a broad-scale network of sanctuaries would be more effective at conserving genetic diversity than would a single sanctuary. Further, McManus (1994) suggested that adaptation to local conditions may require semi-closed network of reserves connected by dispersal. In other words, local adaptation would not occur in a population with no retention or indirect gene flow. This role of marine sanctuaries may be especially important for those species with life history characteristics that make them most vulnerable to overfishing (Bohnsack 1998).

4.10 Reserve improvement and recovery

The improvement and recovery of stocks, communities and habitats within sanctuaries, as described in the previous sections, will depend in part on the biological and ecological potential for recovery. Evidence from field studies and surveys (see Section 5) shows that most populations subject to exploitation and/or the effects of fishing do recover once protected (Halpern in press), although it may take decades in some cases (Williams & Russ 1995, McClanahan 2000), and there are almost always some taxa that show no or little recovery. In general, recovery may be affected by several different factors that have the potential to prevent or greatly delay the process and, therefore, reduce the performance of a MFS.

4.10.1 Allee Effect

Very low densities may prevent population recovery by interfering with, or preventing, normal social and reproductive behaviour/performance, subjecting the population to the effects of demographic stochasticity, and inbreeding (the Allee Effect, or more generally inverse density dependence; Allee 1931, Levitan 1991, 1995, Dayton *et al.* 1995, Courchamp *et al.* 1999, Stephens & Sutherland 1999). Allee effects can occur because total densities are very low, the density of one sex is very low, or the effective population size is very small. The influence of Allee effects may increase the risk of extinction (Courchamp *et al.* 1999, Roberts & Hawkins 1999, Stephens & Sutherland 1999). Roberts (1997b) cites work suggesting that Allee effects are likely to lead to the extinction of giant clams in the Indo-Pacific region, and the white abalone in California.

4.10.2 Slow growth

Some of the most desirable and, therefore, most severely over-fished species (e.g. snappers, groupers, rockfish, giant clams, abalone) have K-selection life-history characteristics, such as low recruitment rates, low and variable fecundity, slow somatic growth rates, delayed maturity, and slow population growth rates, all of which are expected to contribute to long recovery times (Adams 1980, Palsson & Pacunski 1995, Russ & Alcala 1998b, Roberts 1998a, Murray *et al.* 1999a, McClanahan *et al.* in press, Palumbi manuscript, Roberts & Hawkins 2000).

4.10.3 Species interactions

The large changes that can occur in community composition and habitat structure as a result of overfishing and destructive fishing practices may prevent target species from recovering once a sanctuary has been established (Attwood *et al.* 1997b, Dayton *et al.* 2000, Roberts & Hawkins 2000). This lack of recovery may occur if previously extirpated species are unable to re-colonise a sanctuary because of the lack of necessary resources (e.g. shelter sites, essential habitat, or sufficient prey densities), the presence of a superior competitor, or high numbers of effective predators (Rowley 1994), especially if community changes have driven the system to an alternate stable state (McClanahan 1997b). For example, McClanahan found that the recovery of some Kenyan reserves appears to have been dependent on the abundance and species composition of urchins, and recovery could not be achieved until sufficient numbers had been removed (McClanahan *et al.* 1995, McClanahan 1997b). McClanahan also cautions that recovery time will depend on which component of the system is being considered: recovery of the process of triggerfish predation on urchins (5–10 years); reversal of urchin dominance (10-15 years); and recovery of triggerfish populations (>15 years) (McClanahan 2000).

4.10.4 Insufficient habitat diversity

Sanctuaries lacking in habitat diversity, or more specifically lacking the ecological features essential for settlement (nursery habitat), growth (food sources), and reproduction (spawning habitat) of the focal species may fail to show improvements and the recovery of overfished populations within their boundaries (Plan Development Team 1990, Rowley 1994). The constraint could be the habitat diversity required by generalist species, or some specific component required by a specialist species (e.g. obligate corallivores, Cox 1994, or obligate reef species).

4.10.5 Extensive habitat damage

Recovery through immigration can be rapid (see references in Lewis 1997, and artificial reef literature), but it depends on a network of habitat patches of the right type and at the right distances away to act as sources. If habitat destruction by fishing has been widespread and other sanctuaries are not located within reach of dispersers, then recovery may not be possible because of a lack of an adequate pool of potential immigrants. The same may be true with respect to recovery by recruitment (Rowley 1994).

4.10.6 Lack of refugia

Similarly, if a population experiences overfishing throughout its range and no refugia remain, then recovery would be slow due to a lack of sources of recruits. The severe depletion of shallow-water conch populations in the Caribbean has led to the fishing of deep-water stocks that previously had been an important source of recruits for the former, and may explain the slow recovery of subsequently protected shallow-water stocks (Jamieson 1993).

4.10.7 Unpredictability of recruitment

Recruitment can be notoriously sporadic and variable in magnitude, and in space and time (e.g. Sale *et al.* 1984, Doherty & Williams 1988, Lincoln-Smith *et al.* 1991, Robertson *et al.* 1993, Milicich & Doherty 1994, Tupper & Hunte 1994), thus creating delays in population recovery even in what otherwise may be good conditions (Jennings & Kaiser 1998). Williams & Russ (1995) stressed that coral reef systems "….may be highly resilient to acute disturbances such as the effects of fishing *provided that there is a supply of…… recruits outside the affected area*" [their emphasis]. Larval retention may be more important to this process than was previously realized (Swearer *et al.* 1999, Warner *et al.* 2000). If a sanctuary has been severely impacted by fishing, it is situated such that most of its recruitment comes from larvae produced locally, and it receives very little influx of recruits from other areas, then its recovery may be highly uncertain. Conversely, without retention sanctuary populations may be unsustainable in the absence of larval import, and, therefore, susceptible to the effects of overfishing beyond its boundaries (Carr & Reed 1993, Jennings *et al.* 1996, McClanahan 1997b, Palumbi manuscript). Roberts (1995b, 1997a) suggested that insufficient larval import has been responsible for the slow recovery rates of large groupers in a Caribbean marine reserve. McClanahan *et al.* (in press) pointed out that degraded sites that are a long distance from potential sources of recruits may have to wait decades for a year with good larval import, thus making recovery of such sites largely dependent on larval retention.

4.10.8 Poor location

Sanctuaries that are poorly placed with respect to habitat quality, species requirements, or the movements of larvae may receive insufficient numbers of recruits to allow recovery in a reasonable timeframe (Heslinga *et al.* 1984, Polunin 1990, MacDiarmid & Breen 1993, Dugan & Davis 1993, Tegner 1993, Armstrong *et al.* 1993, Attwood *et al.* 1997b, Roberts 1997a, 2000 , Roberts & Hawkins 2000, Fogarty *et al.* 2000). Roberts (1995b) found that even after 10 years of protection some grouper species had not recovered in a Caribbean marine park, which he attributed to a lack of recruits from outside the park due to widespread overfishing. In addition, if a sanctuary shows little larval retention and if its exported larvae have no place to settle, perhaps due to habitat damage or loss, then the sanctuary population may become poorly adapted to local conditions (McManus 1994), thus affecting its long term viability. Rowley (1994) pointed out the importance of having suitable habitat surrounding a reserve for dispersal of potential migrants, implying that its lack would inhibit recovery through immigration.

4.10.9 Small size

Species with large home-ranges or migratory movements that take them outside sanctuaries will be at risk of fishing mortality, especially if fisheries target spillover. Therefore, small sanctuaries are less likely than large reserves to provide effective refugia for all species (Davis 1989), and the recovery of populations in small sanctuaries may be incomplete (however, see Roberts & Polunin 1994, Roberts & Hawkins 1997, Jennings 1998, Halpern in press). Interestingly, a recent analysis of marine reserve studies found that the almost universal proportional differences in density, biomass, individual size and species diversity between protected and unprotected areas were not dependent on the size of the reserve (Halpern in press). In addition, small sanctuaries will be less likely to contain the diversity of habitats necessary for recovery of all species (Roberts & Hawkins 2000) and will be more susceptible to catastrophic impacts, such as cyclones, toxic spills (Halpern in press).

4.10.10 Inadequate numbers of sanctuaries

Several authors have argued that to be effective marine sanctuaries will have to consist of networks of protected areas (Dyer & Holland 1991, Dugan & Davis 1993, Ballantine 1995a, 1995b, 1997, Quinn *et al.* 1993, McManus 1994, Attwood *et al.* 1997b, Lauck *et al.* 1998, Roberts 1998b, Carr *et al.* in press, Fujita *et al.* 1998b, Roberts & Hawkins 2000). For example, it has been suggested that in the case of abalone in Southern California, a single sanctuary has failed to produce recovery of severely overfished populations, and that because of the limited larval dispersal capabilities of abalones a large number of sanctuaries would have been required to achieve recovery (Tegner 1993, Tegner *et al.* 1996).

4.10.11 Extreme environmental events

All of the factors that would promote sanctuary improvement and the recovery of populations from overfishing have the potential to be swamped by extreme, episodic events, such as El Nino, or large environmental changes, such as global warming (Allison *et al.* 1998), thus delaying recovery.

4.10.12 Illegal fishing

The potential for recovery is ultimately dependent on the elimination, or significant reduction, of fishing pressure in sanctuaries (Roberts 1998a, 2000). Evidence suggests that recovery may be prevented by relatively small amounts of illegal fishing (Jamieson 1993, Tegner 1993, Jennings & Polunin 1996, McClanahan & Kaunda-Arara 1996, Attwood *et al.* 1997b, Halliday & Pinhorn 1997, Gribble & Robertson 1998, Wallace 1999, Murray *et al.* 1999b, Rogers-Bennett *et al.* 2000), and it has been suggested as the cause for failure of populations of abalone in Southern California to recover from severe overfishing despite over 15 years of reserve protection (Tegner 1993). Unfortunately, as sanctuary improvement progresses the sanctuary is likely to become more attractive to poachers, perhaps limiting the degree of improvement that can be expected (Fogarty *et al.* 2000). More generally, the opportunity to achieve recovery may be lost by many forms of mis-management of the reserve or the target fishery (McClanahan 1997b).

4.11 Production stability enhancement

Up to this point we have described the primary and secondary pathways that lead to spillover and larval export. These process are considered to be important because they directly contribute potential recruits to exploited population, and have the potential to benefit fisheries.

Because of the better condition of habitats, populations and communities inside sanctuaries, it is expected that the contribution of larvae, recruits and adults from sanctuaries to fished areas should be more reliable and predictable than it would be from fished areas (i.e. have a lower year-to-year variability, and a smaller range of values). Thus, sanctuaries are expected to result in 1) a reduced variability in recruitment to fisheries (Palumbi manuscript; see evidence for this effect in McClanahan & Mangi 2000), 2) a reduced probability of recruitment failure (Davis 1989, Plan Development Team 1990), and 3) lower chance of stock collapse (Roberts & Polunin 1991). This effect should enhance system integrity, and increase ecosystem and fisheries resilience to a variety of environmental and anthropogenic stresses (Dayton *et al.* 2000). The effect of this suite of processes, which we term 'production stability enhancement', constitutes the third process contributing to fisheries enhancement (Figure 1—Box 20). Unlike 'spillover' and 'larval export', which physically contribute potential fisheries recruits, 'production stability' operates by enhancing the qualities of that contribution. We expect that stability will be significantly enhanced by long-term beneficial changes to the environment in sanctuaries (discussed above), and to focal populations (see below), especially when populations are exposed to environmental extremes (Carr & Reed 1993). Given the high degree of variability and uncertainty associated with recruitment, especially for exploited populations and ecosystems heavily impacted by fishing, the presence of an ideally located sanctuary, or network of sanctuaries, should greatly enhance the stability of those populations and the fisheries dependent on them (McManus 1994). The loss of natural refugia for many exploited populations has meant that entire populations are now exposed to the same fishing regime, thus increasing their risk of collapse if mistakes in management are made and/or large-scale environmental stresses strongly affect the population. Marine sanctuaries are hypothesised to reduce the probability of fisheries collapse by 'spreading the risk' or 'bet-hedging', a well established technique used in many fields (e.g. business and economics) for coping with uncertainty and lack of knowledge, and reducing risk (Lauck *et al.* 1998, Bohnsack 1999, Fujita *et al.* 1998b). By protecting a portion of the population from a major source of mortality and putting it under a different management regime, the population is less likely to suffer collapse from a single or small number of factors operating synergistically, or as a result of the inability of optimal management strategies to cope with the substantial and irreducible uncertainty inherent in natural systems. Some researchers have suggested that this benefit will be realized only in large sanctuaries or networks of sanctuaries (Clark 1996, Fogarty 1999). As discussed elsewhere, whether marine sanctuaries will increase or decrease the mean fisheries yield will depend on a variety of factors. Even when a marine sanctuary or network of sanctuaries is not expected to produce a significant improvement in mean yield, the overall or ultimate value of the sanctuary/sanctuaries should be viewed in terms of a tradeoff of the mean yield for reduced variability (Mangel pers. comm.).

As has been discussed earlier, the processes of spillover, larval export and/or stability enhancement are necessary if sanctuaries are going to enhance fisheries, but they may not be sufficient alone to produce that outcome. Next we will discuss the processes and pathways through which spillover and larval export resulting from improvement within sanctuaries can lead to fisheries enhancement. First, we consider the fate of spillover individuals.

4.12 Fishery enhancement from spillover

Initially we might imagine that emigrants from reserves would disperse throughout fished areas, thus increasing the number and density of individuals in fished areas. Presumably this effect would diminish with distance from sanctuaries, much in the manner of a random diffusion process. The magnitude of the effect should depend on sanctuary characteristics (e.g. size, shape, location and number) the characteristics of fished areas (e.g. habitat quality and influence of ocean currents) and the biological characteristics of the species (e.g. dispersal tendency, habitat affinities, or migratory behavior). In Section 4.4 we identified four elements to spillover: excursions, density changes outside sanctuaries, recruitment to fisheries, and fisheries enhancement. We dealt with elements 1 and 2 in Section 4.4, and we discuss elements 3 and 4 here.

4.12.1 Recruitment to fisheries

Spillover individuals may be of a size to be immediately, or in a short time, recruited to a fishery and, therefore, could enhance catches close to sanctuaries (Rowley 1994). Juvenile spillover individuals, however, may not recruit to the fishery for some time. This means that whether those individuals recruit to the fishery and therefore have an opportunity to provide fishery enhancement also will depend on the factors affecting their survival, growth and movements. If we assume that their probability of recruiting is not significantly different from individuals that originally settled in the same areas, then their potential contribution to the fishery would be proportional to the addition they made to the size of the juvenile age classes. However, several factors could mean that their contribution to the fishery is disproportionately greater than their numerical contribution (Suthers 1998). First, in those cases where individuals leaving sanctuaries immediately recruit to fisheries, they may be larger than individuals recruiting developmentally within fished areas. Thus, such spillover would contribute greater biomass, higher value individuals, and individuals with higher fecundity to the stock. Second, the improved conditions within sanctuaries relative to those in fished areas may mean that pre-recruit spillover individuals are in better physiological condition, have a competitive advantage, and greater probability of avoiding predation (Mesa *et al.* 1994, McCormick 1998), which could translate into higher growth rates, lower mortality rates, and, therefore, higher rates of recruitment to the fishery. These advantages should carry-over into the post-recruitment period, and apply to spillover individuals that recruit to the fishery immediately. In addition, this advantage would confer a greater reproductive potential compared to individuals of the same size that were raised in fished areas.

4.12.2 Fishery enhancement

Perhaps more important than the biological and ecological characteristics of the spillover individuals, will be the behaviour of the fishery and fishers in determining the degree of, and form of, enhancement that results from spillover. The establishment of a marine sanctuary is likely to alter the behaviour of fishers and the impact of their fisheries. The form of their response to sanctuary establishment is likely to differ depending on the fishery in question, its political and economic environment, and the other management controls that are in place (Ballantine 1995b). In many cases the distribution of fishing effort will shift to accommodate the presence of reserves. An important question with respect to marine sanctuaries is how the allocation of fishing effort will alter in response to the loss of fishing grounds. In the absence of any other changes in the fishery, the previous levels of fishing effort would be concentrated in the remaining fishing grounds. This would increase the fishing effort on a per-unit-area basis and, consequently, the fishing mortality rate (Roberts & Hawkins 2000), and, potentially, the rate of damage to the environment (Parrish 1999b). For this reason, fishery yields may decline immediately after sanctuary establishment, and total fishing effort would have to be reduced proportionally to avoid further stock declines (Carr & Reed 1993), which potentially could create a further loss to fishers (Roberts & Hawkins 2000). However, the allocation of fishing effort may adjust itself to avoid a large increase in effort in the remaining areas. This has been suggested by modelling effort allocation using 'ideal free distribution' models (e.g. Gillis *et al.* 1993, Abrahams & Healey 1990), and has been shown to be the case in one field study. McClanahan & Kaunda-Arara (1996) found that, following the establishment of a no-take area, fishing intensity did not increase in surrounding areas, apparently because some fishers chose to stop fishing and take up other work. However, in a later study, McClanahan & Mangi (2000) found that trap fishers targeted their effort at the boundary of a marine park and increased the number of traps the set.

A great deal remains to be understood about the behaviour of fishers in response to sanctuary creation. Will effort be redistributed to other sectors or fisheries? Will the total effort change, perhaps decreasing due to a perception that the availability of target species will have decreased? Will effort respond to perceived or detected benefits of marine sanctuaries such as spillover, and, if so, how long will it take for fishers to alter their behaviour?

Evidence suggests that fishers rapidly learn that enhancement within sanctuaries produces a spillover of relatively large, high-quality individuals in the vicinity of reserves (McClanahan & Kaunda-Arara 1996, Johnson *et al.* 1999, Piet & Rijnsdorp 1998, Roberts 1998a, Walls 1998, Roberts & Hawkins 2000, McClanahan & Mangi 2000). Theory and evidence suggest that this effect may not compensate for the loss of fishing area (e.g. Alcala & Russ 1990, Polacheck 1990, DeMartini 1993, Holland & Brazee 1996, McClanahan & Mangi 2000). In response to spillover some fishers concentrate fishing effort immediately outside the boundaries of sanctuaries (a behaviour termed 'fishing the line'), which can result in the removal of much, if not most, of the spillover that occurs (Davis & Dodrill 1989, MacDiarmid & Breen 1993, McClanahan & Kaunda-Arara 1996, Piet & Rijnsdorp 1998, Walls 1998, Johnson *et al.* 1999, Fogarty *et al.* 2000, McClanahan & Mangi 2000, Ballantine pers. comm.). Experience suggests that spillover will have, at best, a limited enhancement effect on such fisheries, primarily benefitting those fishers who concentrate their effort along sanctuary boundaries (Alcala & Russ 1990, Bennett & Attwood 1991, Rowley 1994, McClanahan & Kaunda-Arara 1996, McClanahan & Mangi 2000), fishers who specialise in catching high-value individuals rather than abundant size classes, and/or recreational trophy fisheries (Plan Development Team 1990, Bohnsack 1996b, Johnson *et al.* 1999). Rowley (1994) pointed out that reserves with a large perimeter-to-area ratio would be less susceptible to this problem. Russ and Alcala (1996b) raised the possibility that, in time, as densities increase within a reserve, the spillover rate would exceed the capacity of the 'boundary fishers', and densities would begin to rise in the vicinity of the reserve. However, it is not generally believed that this process alone could appreciably raise densities in fishing grounds distant from sanctuaries (Roberts & Polunin 1991, Russ & Alcala 1996b, however see Attwood & Bennett 1994). The one study to have examined this directly found that the CPUE of research fishing for spiny lobsters was similar when comparing boundary fishing near 3 reserves to CPUE from other nearby areas in New Zealand (Kelly *et al.* 2000a).

Whether this would result in an overall fisheries enhancement remains to be determined (studies described in Section 5). It is clear, however, that intensive fishing in the immediate vicinity of a sanctuary would affect densities of the target species inside the sanctuary, thus reducing the degree of improvement that occurs within sanctuaries. This effect would result in cross-boundary density gradients being gradual rather than something approximating a step function, and in very small sanctuaries it could have a large effect on the potential for the sanctuary to act as a source of juveniles and adults to surrounding areas (Kramer & Chapman 1999, Parrish 1999b). Other species-specific factors such as sedentarity and catchability would also affect the form of cross-boundary density gradients (Rakitin & Kramer 1996). In other words, targeting of the boundaries of small sanctuaries to catch focal species could have a negative feedback effect on the process that made that targeting feasible.

Because spillover adults caught outside a sanctuary are responsible, in part, for the reproductive output of the sanctuary, this type of impact could negatively affect larval export, and thus greatly reduce the effectiveness of a marine sanctuary as a fisheries management tool. To be effective as exporters of reproductive propagules, sanctuaries need to be large enough to maintain reproductive populations of the focal species (Attwood *et al.* 1997b, Bohnsack 1998). On the other hand, if the spillover is the primary means of fisheries enhancement, then intermediate-sized sanctuaries, with their higher perimeter-to-area ratios will be more effective (McClanahan & Kaunda-Arara 1996). In sanctuaries with large perimeter-to-area ratios much of the population will be too far from the boundaries to have a high spillover potential and in small sanctuaries spillover would inhibit sanctuary improvement. The spillover effect will primarily be a local phenomenon, as a widespread dispersal of spillover individuals from a small sanctuary will provide little enhancement of the surrounding fishery because of the dilution effect, except perhaps in the case of species that undertake large-scale movements as part of normal feeding behavior or ontogenetic habitat shifts (Rowley 1994). Exceptions to this rule may exist. A large reserve in South Africa appeared to produce sufficient numbers of a surf-zone fish species to replace the fish lost to fishing in adjacent, fished areas (Attwood & Bennett 1994). Finally, Kramer & Chapman (1999) suggested that excessive spillover could retard reserve improvement, thereby reducing its effectiveness at larval export, and, conversely, that minimal spillover would reduce local benefits and potentially erode public support. These considerations imply that careful thought must be given to the spatial design of prospective marine fisheries sanctuaries, and to the management regulations pertaining to fishing in their vicinity, if spillover effects are to be achieved.

4.13 Fishery enhancement from larval export

Sanctuaries are seen as having the potential to be significant sources of reproductive propagules to an exploited population (Roberts *et al.* 1995). The export of eggs and larvae from sanctuaries may provide the best possibility for sanctuaries to enhance fisheries (Plan Development Team 1990, Carr & Reed 1993, Rowley 1994), especially for the most vulnerable species (Roberts & Polunin 1991, 1993, Roberts *et al.* 1995). In the context of overfished species with depressed populations and reproductive output, sanctuaries have the potential to be significant hot spots in a source-and-sink population landscape and, therefore, keys to the recovery and sustainable exploitation of such species.

Historically, many exploited species were thought to have natural refugia created by the existence of areas that could not be fished (e.g. too deep, too remote, difficult to locate, unfishable), seasons in which fishing was not possible because of weather, or because they were not known to harbor exploitable stocks (Beverton & Holt 1957, Klima *et al.* 1986, Davis 1989, Russ *et al.* 1992, Bohnsack 1993, 1994, 1996a, Dugan & Davis 1993, Jamieson 1993, Lozano-Alverez *et al.* 1993, Walters *et al.* 1993, Walters & Maguire 1996, Fonteneau 1997, Bohnsack 1998, Walters 1998, Dayton *et al.* 2000, McClanahan *et al.* in press, Palumbi manuscript). In a few cases, fisheries regulations have maintained natural refugia that might have been lost otherwise (Tegner 1993), and in others, species characteristics (e.g. low detectability, lack of shoaling behaviour) may result in low catchability (Dugan & Davis 1993). Both World Wars inadvertently provided a pseudo-experimental confirmation of this idea, by effectively creating large sanctuaries in the North Sea, which produced significant recoveries of overfished stocks (Cushing 1975). Hutchings (1995) suggested that offshore closures of the northern cod fishery during winter and spring would re-establish the natural deep-water refugia that had historically sustained the fishery. Such natural refugia are apparently the ultimate source of a significant proportion of the recruits to some fisheries, and, therefore, the reason why some apparently severely over-exploited fisheries have not collapsed (Campbell & Robinson 1983, Polacheck 1990, Smith & Jamieson 1991, Dugan & Davis 1993, Fonteneau 1997). Fishery over-capitalisation, open access, technological advances, and increased knowledge have eliminated many such natural refugia (Davis 1989, Dugan & Davis 1993), so that MFSs are now seen in some situations as possible replacements for natural refugia.

The extent to which larval export from MFSs can supplement the productivity of natural refugia, and enhance fisheries, will depend on numerous factors associated with the sanctuary, the focal species and the environmental characteristics of the fished areas. Rowley (1994) has proposed that regional fisheries enhancement will occur only if 1) exported larvae constitute a significant proportion to the total larval pool, 2) exported larvae disperse to areas suitable to recruiting to the fishery, 3) there is a correlation between the numbers of larvae produced and larvae that settle, and 4) larval settlement is limiting to recruitment to the fishery.

4.13.1 Spatial characteristics and hydrodynamics

The placement, size and shape of a sanctuary, with respect to the fished areas and ocean currents, will have a large effect on the potential for larval export from sanctuaries to contribute to fisheries. Determining the relationship between a sanctuary's location and the fate of its reproductive output is a complex problem for several reasons, such as:

- the complexity and unpredictability of hydrodynamic spatio-temporal patterns, at least at certain scales
- the long periods of time many larvae spend in the plankton (Doherty & Williams 1988)
- the use of swimming, buoyancy control, orientation to small-scale hydrodynamic features, and alteration of the timing of metamorphosis by larvae to modulate their drift (Norcross & Shaw 1984, Power 1984, Leis 1991, Rowley 1994, Stobutzki & Bellwood 1994, Sponaugle & Cowen 1997), and
- the numerous other factors that affect a larvae's survivorship, such as food availability and predator densities.

Viewed in a different context, whether a sanctuary is placed in a larval 'source' or 'sink' area will have a profound effect on its success (Roberts 1997a). If marine sanctuaries are going to contribute to the recovery of exploited populations and the enhancement of fisheries, then the sizes, number, shape, character and, most importantly, location of sanctuaries have to be carefully considered (Roberts & Polunin 1991, Rowley 1994, Williams & Russ 1995, Allison *et al.* 1998, Bohnsack 1998). Mangel (pers. comm.) has suggested that the effective placement of marine sanctuaries is an extremely difficult problem, and fluctuations in ocean currents may render the potential long-term success of even the most carefully sited reserves highly problematic. Fogarty *et al.* 2000 have suggested that understanding the relationship between oceanographic conditions and dispersal characteristics is the most challenging and difficult problem associated with designing effective reserves, and is the problem with the greatest level of uncertainty and poorest understanding. The complexity of this relationship and the problem it presents have been identified by a number of authors:

- Roberts (1997a, 1998b) proposed that if recruitment from reserves is to enhance stocks in fished areas, then reserves need to be placed upstream of habitat patches for recruitment within fished areas
- Rowley (1994) pointed out that those habitat patches could have been destroyed by fishing, leaving no place for exported larvae to settle
- Jamieson (1993) identified a related issue, namely that the reproductive output of reserves located 'downstream' from fishing grounds could be lost, in the sense of never contributing to the larval pool from which recruitment to the focal stock occurs
- Dayton *et al.* (2000) emphasised that the relationship between reserve characteristics and hydrodynamics has to be examined at the appropriate scale, which will be strongly influenced by the scale of the larval dispersal patterns of the focal species (Roberts & Polunin 1991, Carr & Reed 1993, Tegner *et al.* 1996, Allison *et al.* 1998)
- Dayton *et al.* (2000) and Halpern (in press) also cautioned that if the protected proportion of the stock is too small it will be unable to provide fisheries enhancement
- Palumbi (manuscript) pointed out that in the case of species with long-distance dispersal that the dilution effect would mean that reserves could at best make only a small contribution to the larval pool
- Ballantine (1997) argued that, in practice, marine topography and the pattern of habitat distribution will strongly influence the placement and shape of reserves
- Carr & Reed (1993) referred to the "effective range of replenishment" as the area within which a successful reserve produces enough recruits to maintain focal populations, and they suggested that range would be a function of the interaction of environmental conditions and the developmental, behavioural and ecological characteristics of the focal species
- Warner *et al.* (2000) pointed out that to simultaneously achieve success at exporting larvae and sustaining populations within reserves, the right balance of export and import or retention of larvae will be required, but this balance may be unattainable in most situations (Roberts in press), and
- Williams & Russ (1995) reduced the problem to minimising the size of the reserve network while maximising the number of habitat patches to which the network contributes recruits, and cautioned that reserves created in 'sink' areas would be completely ineffective.

However, in some cases, location considerations may be relatively unimportant because:

- larvae do not disperse in the plankton (e.g. surf-perches and many gastropods)
- planktonic dispersal is highly restricted in space or time (e.g. Olson 1985, Shepherd & Brown 1993,Tegner *et al.* 1996)
- populations are closed at the scale of the reserve (Allison *et al.* 1998)
- habitat destruction by fishing outside reserves has eliminated most suitable habitat upon which larvae can settle (Roberts & Polunin 1993)
- the hydrographic situation is too complex to be able to decide what is upstream or downstream, such as may be the case when larvae (a) spend months, and cover very long distances, in the plankton, (b) are capable of directed movements by swimming or buoyancy control, or (c) can control the timing of metamorphosis (Norcross & Shaw 1984, Power 1984, Leis 1991, Stobutzki & Bellwood 1994, Sponaugle & Cowen 1997), or
- location, and other characteristics, of individual reserves are of secondary importance when reserves are established as demographically connected networks (Ballantine 1995a).

4.13.2 Networks of sanctuaries

Although local population enhancements (sanctuary improvement) have been observed commonly in single, small sanctuaries (e.g. Russ 1985, 1989, Roberts & Polunin 1994, Roberts 1995b, Jennings *et al.* 1996, Roberts & Hawkins 1997, Jennings 1998, Palsson 1998, Halpern in press), it is unlikely that a single sanctuary, especially if it is small, could be effective at enhancing a fishery exploiting a much larger area (MacDiarmid & Breen 1993, Attwood *et al.* 1997b, Bohnsack 1998, Dayton *et al.* 2000). Therefore, several authors have suggested that effective fisheries enhancement will depend on a network of 'connected' MFSs, particularly when the network encompasses a variety of habitats (Dyer & Holland 1991, Carr & Reed 1993, Dugan & Davis 1993, McManus 1994, Ballantine 1995a, 1995b, 1997, Quinn *et al.* 1993, Rowley 1994, Attwood *et al.* 1997b, Lauck *et al.* 1998, Roberts 1998b, Carr *et al.* in press, Fujita *et al.* 1998b). The simple fact that most marine species have one or more highly dispersive life-stages (e.g. planktonic larvae) means that a network of sanctuaries will be a much more effective tool to manage such open populations than will a single sanctuary (Ballantine 1995a), no matter how well the latter may be designed. Because many, if not most, sanctuaries would not be large enough to be self-sustaining, unless currents produce significant larval retention, sanctuaries will be dependent on non-sanctuary areas or other reserves for supplies of recruits (Roberts & Hawkins 2000). Thus, networks of connected sanctuaries may be required to ensure reserve success, especially in cases where little reproduction occurs outside sanctuaries (Carr *et al.* in press). In addition, networks may be an effective way to increase the total area protected, because single large sanctuaries may be politically very difficult to establish, and by spreading the risk they provide some insurance against sanctuary failures due to local or regional events (Allison *et al.* 1998, Fujita *et al.* 1998b).

If MFSs or MFS networks are to enhance fisheries they need to be self-recruiting or self-sustaining, otherwise they will be dependent on recruits from fished areas, which would defeat the purpose of establishing the sanctuary for overfished species (Carr & Reed 1993, Ballantine 1997, Roberts 1998b, Warner *et al.* 2000). In theory, and under certain circumstances, a single or small number of large sanctuaries could be highly effective (Plan Development Team 1990). Several authors have referred to the 'SLOSS' (single large or several small) debate in terrestrial conservation science. However, this distinction is less relevant in the marine context because the extreme resistance shown by commercial and recreational fishers to the concept of no-take reserves means that most marine reserves are, and will continue to be, small. The SLOSS debate is also less popular in marine conservation biology because of the poor understanding of the processes that would act to connect several small reserves in an effective manner. Given the very small proportion of the global oceans that is completely protected from fishing and the resistance to sanctuary establishment, choices regarding the number and placement of sanctuaries will probably be driven more by the probability of success than by size and complexity. Nonetheless, aspects of the debate associated with factors such as species diversity, representation and edge-effects are pertinent to the design of any reserve or reserve network. Bohnsack (1998) suggested that as long as each reserve is large enough to retain reproductive populations, the high reproductive rates and wide dispersal of most marine organisms means that a network of small reserves would be more successful than a few large reserves. Roberts & Hawkins (2000) suggested that a network of small reserves would contain, on the average presumably, a greater range of habitats than a single large reserve, thus suggesting a trade-off between achieving the objectives of ensuring self-sustaining reserves and sufficient habitat diversity. Ballantine (1995a, 1997) argued that the individual characteristics of reserves and their connectivity are of secondary importance; more important is designing a network that is representative (e.g. of different biogeographic regions, habitats and communities), is redundant (i.e. contains replicates for insurance against accidents), and is sufficiently large (number and area) to ensure sustainability of resources. Considering these different arguments, McManus & Meñez (1997) suggested that the ideal network would have many small and a few large reserves.

4.13.3 Larval pool contribution

The primary pathway from larval export to fisheries enhancement will have to include, at least, the processes of movement and survival during the dispersal phase, settlement and ecological recruitment, and growth to age/size of recruitment to the fishery. These processes will affect all larvae that could potentially settle in fished areas, regardless of where they were produced and, in that context, the enhancement should be proportional to the magnitude of the contribution made by sanctuaries to the larval pool relative to that made from fished areas (Rowley 1994, Roberts & Hawkins 2000). Populations subject to severe recruitment overfishing may have very low rates of reproduction from fished areas, in which case a small, highly productive sanctuary could have a large impact on the population as a whole (Polunin 1990, Roberts & Polunin 1991, Rowley 1994). On the other hand, even a high rate of reproduction in a small sanctuary will be unable to compensate for a very large difference in size between the sanctuary and the surrounding fished areas (MacDiarmid & Breen 1993).

The distribution and fates of exported larvae will not always be the same as that of larvae produced outside of sanctuaries. Several factors could lead to larvae produced within sanctuaries having a greater probability of successfully recruiting to the fishery, thus increasing the degree to which sanctuaries are responsible for fishery enhancement.

4.13.4 Placement

The placement of sanctuaries will play an important role in determining the fate of larvae that are exported. Larvae produced in sanctuaries in ideal locations, with respect to the distribution of habitat and the patterns of advective currents, will have a greater probability of settling on high quality habitat patches and eventually recruiting to the fishery (McManus 1994, McManus & Meñez 1997, Roberts 1998b).

4.13.5 Seasonality

In areas where hydrodynamic and/or nutrient conditions change seasonally, the timing of reproduction, and the synchrony of spawning can significantly influence larval dispersal and survival (Tilney *et al.* 1996, McManus & Meñez 1997, Trippel *et al.* 1997). The dispersal of larvae to suitable locations and habitats for successful settlement may depend on current regimes that occur seasonally (Dayton & Tegner 1990, Carr & Reed 1993, McManus & Meñez 1997, Dayton *et al.* 2000). Timing of the production of larvae to peaks in pelagic productivity and environmental suitability, and settlement conditions, may be critical to their survival and rapid growth (Leggett & DeBlois 1994, Tilney *et al.* 1996, McManus & Meñez 1997, Dayton *et al.* 2000). And, where the length of the 'growing season' is limiting (Chambers 1997), early spawning would increase the chances of larvae completing development before conditions deteriorate. Thus, if the effects of fishing include a disruption of the normal timing of reproduction, then sanctuaries could produce a much larger proportion of larvae that would experience 'normal' dispersal, achieve rapid growth while planktonic, and complete their development.

4.13.6 Adult characteristics

To the extent that characteristics of adults in sanctuaries (e.g. larger size, older, better physiological condition) result in better gametes (e.g. larger, better provisioned eggs), higher hatching success and superior larvae (e.g. greater reserves, larger, faster growing), and these characteristics are persistent, then those larvae will have a greater probability of surviving the larval stage to recruitment (see references in Sargent *et al.* 1987, Chambers & Legget 1996, Chambers 1997, Trippel *et al.* 1997, Suthers 1998, McCormick 1998). Higher survival could result from higher instantaneous survival rates (perhaps due to better larval condition), and/or from faster growth rates, which should result in less time spent in the plankton (Dayton *et al.* 2000). Because mortality rates during the planktonic stage and immediately after settlement can be very high (Sale & Ferrell 1988, Carr & Hixon 1995, Roberts 1996, Caley 1998, McCormick 1998, Caselle 1999), faster growth rates can, in theory, translate into higher survival rates (Shepherd & Cushing 1980, Houde 1987). However, empirical support for this idea is scant (see Frank & Leggett 1994).

4.13.7 Larval condition

Superior larval condition may confer superior juvenile condition, which in turn could mean improved juvenile survival rates and earlier recruitment to the fishery (references in McCormick 1998, Suthers 1998). McCormick (1998) notes from several field studies that 30-85% of juvenile fish are removed by predation very shortly after settlement, and, therefore, that it is logical to assume that juvenile condition will be related to survival probability.

4.13.8 Consistency

A consistent production of larvae from sanctuaries, compared to fished areas where recruitment may be highly sporadic and subject to failures, should result in sanctuaries making a disproportionate contribution to recruitment when averaged over years, and stabilise recruitment to fisheries (McManus 1994).

4.13.9 Stock-recruitment relationships

Viewed in a different light, the potential of marine sanctuaries to enhance fisheries depends to a large extent on stock-recruitment relationships. It is easy to see that fishery enhancement is dependent on the larger reproductive output of sanctuaries producing higher settlement and fishery recruitment rates (Rowley 1994), and, ultimately, larger stocks (McClanahan 1997b). Fisheries science has provided two basic models to describe this relationship. The Beverton-Holt Model shows a positive relationship at low stock levels that reaches an asymptote, after which there is effectively no relationship (i.e. recruitment remains constant as stock size increases) (Beverton & Holt 1957), while the Ricker Model starts the same, but becomes negative after reaching a peak (i.e. recruitment increases and then declines as stock size increases) (Ricker 1954; see Roberts 1996 Figure 4.3 for a comparison). Empirical studies have shown that the relationship is subject to a large amount of noise and measurement error, and it is often very difficult to achieve a close fit of data to the model, let alone distinguish between the models. There is an extensive literature dealing with these issues, the difficulties involved in demonstrating stock-recruitment relationships, and with their importance to the dynamics of exploited populations (e.g. Ricker 1954, Beverton & Holt 1957, Pitcher & Hart 1982, Beverton *et al.* 1984, Rothschild 1986, Hilborn & Walters 1992, Gilbert 1997). As discussed below, a central assumption behind these models is that stock-recruitment relationship is driven by density-dependent dynamics (Jamieson 1993).

Despite substantial noise and uncertainty in the relationship, there are good reasons to expect that many species will show a positive stock-recruitment relationship (i.e. a change in stock size will produce a change in recruitment that is proportional and in the same direction, and vice versa), at least at low stock levels (although some would suggest only at low stock levels; Cushing 1975). Meta-analyses of collections of data sets have generally supported this view (Roberts & Polunin 1991, Iles 1994, Myers & Barrowman 1996; however, see Gilbert 1997, Myers 1997a). Based on the strength of the stock-recruitment relationship at low stock levels, Roberts & Polunin (1991) argued that reserves will significantly contribute to recruitment in fished areas when stocks are low there but high in reserves—in other words in the case of a reserve established to aid the management of an overfished stock. Without a positive relationship at low stock levels, there would be little justification for establishing a fisheries sanctuary, as increasing stock size and reproductive output in protected areas would have no effect on recruitment to the population as a whole and, therefore, provide no or little enhancement to fisheries. The lack of a relationship, or the presence of a negative relationship, at high stock levels may be relatively unimportant when the objective is the conservation and recovery of overfished stocks. However, it has to be taken into account when considering the efficacy of sanctuary establishment for moderately fished species or assessing the long-term performance of a sanctuary established for overfished species, especially given the different predictions of the Ricker and the Beverton-Holt models.

A stock-recruitment relationship is one expression of density-dependent population regulation, a central issue in marine ecology in last several decades. Up until mid-1970s population sizes of coral-reef fishes were thought to be controlled by density-dependent processes operating on juveniles and adults, and their communities were thought to be equilibrial and structured by competition (e.g. Smith 1978, Anderson *et al.* 1981). Consideration of the natural spatio-temporal variation in these systems spawned an alternative view in the 1980s, namely that variation in population size and therefore community structure, is largely determined by typically low rates of highly variable recruitment (Sale & Dybdahl 1975, Talbot *et al.* 1978, Doherty 1981, Victor 1983, Sale *et al.* 1984, Doherty & Williams 1988, Doherty & Fowler 1994a, b), a view that eventually spread beyond the scope of coral-reef fishes (Caley *et al.* 1996, Tegner *et al.* 1989, Shepherd 1990). In many cases, populations were considered to be under-saturated, i.e. below levels at which post-settlement density-dependent processes would have a chance to be important, because of insufficient recruitment (Doherty & Williams 1988), a view supported by numerous coral-reef studies that have failed to find evidence of post-settlement density-dependent regulation. However, recent research has suggested that the phenomenon may have been missed in earlier studies because it appears to operate only in the first few hours or days after settlement (Carr & Hixon 1995, McCormick 1998, Caselle 1999 and references therein). In addition, several studies of other systems have found density-dependent effects on juvenile growth rates (references in Frank & Leggett 1994).

These two hypotheses and the relative importance of recruitment and post-recruitment processes in population dynamics and community structure have been extensively investigated, analysed, reviewed and debated in the last 15 years (e.g. Sissenwine 1984, Lewin 1986, Doherty & Williams 1988, Mapstone & Fowler 1988, Underwood & Fairweather 1989, Sale 1990, Fogarty *et al.* 1991, Jones 1991, Booth & Brosnan 1995, Hixon 1998). Based on analyses of the two processes and studies of their interaction (e.g. Connell 1985, Doherty & Sale 1985, Shulman & Ogden 1987, Jones 1991, Caley 1993, Hixon & Beets 1993, Carr & Hixon 1995, Eggleston *et al.* 1997, Chesson 1998, Levin 1998, Caselle 1999), a compromise view is emerging in which stochastic processes are seen to produce a high degree of spatial and temporal variability in settlement, and that this pattern has a strong influence on population size and community composition, but that it is modified by density-dependent post-settlement processes affecting growth and survival, such as habitat selection, predation, competition and migration (Shulman & Ogden 1987, Warner & Hughes 1988, Hixon 1991, Jones 1991, Caley *et al.* 1996, Roberts 1996, Ault & Johnson 1998, Booth & Wellington 1998, Hixon 1998, Caselle 1999). The relative importance of these two processes appears to vary among species (Tolimieri *et al.* 1998), among years depending on the level of recruitment (Jones 1990, Caselle 1999), and depends on the scale of the study (Ault & Johnson 1998).

It could be argued that, from the perspective of the objectives of MFSs, it is unimportant when or which density-dependent process is operating, as long as there is a positive relationship between the stock size (population density) and recruitment to the fishery. Indeed, it is possible that density-dependent control could occur at the time of reproduction or during the planktonic phase. We have not seen a discussion of density-dependent control of reproductive output, and density-dependent control operating on planktonic larvae seems an area of study with insurmountable logistic difficulties (Hixon 1998). Nonetheless, the existence of a positive stock-recruitment relationship, especially at low stock levels, provides strong support for the claim that sanctuaries have the potential to enhance depleted fisheries. However, while post-settlement density dependence processes would enhance the effectiveness of marine sanctuaries, density dependence operating on adult growth or reproductive rates could easily reduce their effectiveness, at least in the long run (Parrish 1999b, Mangel pers. comm.)

The large degree of uncertainty associated with stock-recruitment relationships, the lack of consensus regarding the forms of density-dependent regulation, the large spatial-scales involved, the high degree of variability in recruitment, and difficulties involved in studying the movements and fates of larvae makes studying the larval-export pathway very difficult in the absence of more advanced techniques (references in Dugan & Davis 1993, Allison *et al.* 1998). Carr & Reed (1993) pointed out that the relationship between egg production in reserves and recruitment to the fishery is dependent on several processes acting on larvae (e.g. retainment, advection, predation, starvation, settlement), all of which are very difficult to study. As a result most researchers have recommended, or have turned to, the use of models to study the potential for fisheries enhancement through larval export.

In summary, it appears that MFSs have the potential to enhance severely depleted fisheries. However, it is not obvious whether they have the potential to do so for moderately or lightly depleted fisheries. Their most important function in the latter circumstances may be in contributing to the prevention of overfishing and providing a hedge against stock collapse due to mis-management and/or environmental stresses. Further, it appears that the successful replenishment of overfished stocks by sanctuaries will depend on the interaction between the biological characteristics of the focal species and its ecosystem, the spatial characteristics of the reserve(s), and the hydrodynamic characteristics of their environment. Although, theory and evidence suggest that sanctuaries will be successful in general, predicting how successful they will be, and for which species, will be extremely difficult.

4.14 Summary

It is generally held in the literature that the primary pathway leading from sanctuary establishment to fisheries enhancement must involve the process of larval export. In a sense, this pathway can be seen as chain of processes or events necessary to produce fisheries enhancement. If we consider the claim that sanctuary establishment will produce fisheries enhancement as a hypothesis, then breaking any link in that chain, what Dayton *et al.* (2000) identified as a "bottleneck", may discredit that hypothesis. The links themselves are not important, because if a direct connection between sanctuary establishment and fishery enhancement could be made, then the claim would be supported. That connection could be made most simply, from a logical standpoint, by an experiment showing that fisheries benefited from reserves being established without studying or having any knowledge of the intervening processes. Of course, it is difficult to design such an experiment, given the difficulty of achieving replication and proper controls. Alternatively, the connection could be made by supporting the existence of the intervening links, as long as the connection was made between establishment and first link, and the last link and fisheries enhancement. The conceptual model above represents that chain, with the links chosen to represent what we understand to be key ecological processes along that chain. This chain or pathway (shown with large arrows in Figure 1) is summarized in Table 5 and described below.

Table 5. Summarised pathway illustrating the steps (A–G) leading from sanctuary establishment to larval export from that reserve.

Sanctuary Established (A)

↓

Fishing Activity & Mortality Ceases (B)

↓

Age/Size/Number/Density Increases (C)

↓

Spawning Biomass Increases (D)

↓

Spawning Activity/Efficiency Increases (E)

↓

Reproductive Output Increases (F)

↓

Net Larval Export Occurs (G)

Once a MFS has been established (A), the cessation of fishing activity and, therefore, fishing mortality are givens (B), and not generally subject to question, so long as the 'no-take' status of the sanctuary is effectively enforced. Fishing mortality rates may not reach zero if there is a small amount of poaching or if intense fishing at sanctuary boundaries depletes focal populations at the margins of the sanctuary. Nonetheless, these problems should be relatively easy to monitor and, as long as they are not serious, cessation of fishing activity and fishing mortality can be reasonably expected to occur almost automatically as a consequence of sanctuary establishment and protection.

As argued earlier, in the absence of fishing mortality, fishing-impacted populations within the sanctuary should begin the process of recovery, in what we have called 'sanctuary improvement', which has several components. Maturation of the age/size structure (individuals live longer, so mean ages and sizes increase) and increases in population size (C) are logical and well documented consequences of the lower overall mortality rates in sanctuaries (reviewed in Section 5). Unless the sanctuary has been placed in very poor habitat, the focal species is unsuitable (e.g. a migratory pelagic), the focal population was not depressed, the reserve is too small, or unforeseen secondary interactions interfere, these changes are almost certain to occur. In other words, this step can be easily assured with a modest amount of attention given to the design of the sanctuary (Roberts 2000).

An increase in spawning biomass (D) is a logical consequence of this last step (more individuals of larger size and age must eventually increase the spawning biomass), and can be verified for those studies in which enough is known about the biology of species to identify which size classes belong to the spawning stock. Increased spawning biomass is most likely to produce an increase in spawning activity and, for the reasons given earlier, an increase in spawning efficiency (E). Once again, these changes may be dependent on judicious design.

For example, a sanctuary that did not contain spawning habitat, could build up a large spawning biomass without any spawning activity taking place. It is possible that other, uncommon situations, such as saturation of suitable habitat by a territorial species, would limit the increase in reproductive activity. Increasing reproductive activity and efficiency would, by definition, result in an increase in total reproductive output (F) for the sanctuary. Then assuming reasonable dispersive dynamics and a lower reproductive potential outside the sanctuary, a net export of eggs and/or larvae from the reserve would occur (G). Although the last three steps have not been seriously questioned in the literature, they seem a logical and inevitable consequence of the previous steps, but they are unverified in most studies of marine reserves. From a practical standpoint, if net larval export could be shown directly, it would not be necessary to demonstrate the earlier steps. However, direct demonstration of the larval-export step is generally considered to be difficult, which is one of the reasons why most studies have focussed on establishing its precursors (B & C), and relying on logical argument to infer that larval export is, or should be, occurring.

As discussed earlier, secondary pathways lead to the processes of spillover and stability enhancement (medium-sized arrows in Figure 1), and internal pathways involving ecological elements other than the focal species are seen to contribute to sanctuary improvement (small-sized arrows in Figure 1), and, therefore, to the three fisheries-enhancement processes. It is generally considered that these pathways will not be the primary mechanisms by which fisheries enhancement is achieved, but the effectiveness of the primary pathway may be strongly influenced by the strength of the other mechanisms, especially those that contribute to sanctuary improvement. Continuing the primary pathway we proceed from larval export to several aspects of short-term fisheries enhancement as shown in Table 6.

Table 6. Summarised pathway illustrating the steps (G to M) leading from the process of larval export from a sanctuary to several aspects of fisheries enhancement.

Net Larval Export (G)

↓

Larval Pool Size/Quality Increased (H)

↓

Settlement Enhanced (I)

↓

Increased Recruitment to Fishery (J)

↓

Increased Fisheries Yields (K)

↓

Benefits Flow to Fishing Industry (L)

↓

Benefits Flow to Communities & Socio-economic System (M)

If we accept that substantial larval export (G) occurs as the result of sanctuary establishment and improvement, and if sanctuary placement is appropriate, then it follows that the size of the larval pool of the focal stock will be increased in size, and possibly quality (H). Here, however, we encounter one of the biggest questions about the potential for sanctuaries to enhance fisheries. Will an increase in the number of larvae increase the rates of settlement and subsequent processes? This question gets to the heart of the uncertainty surrounding stock-recruitment relationships. If we assume that some density-dependent process is not limiting the rate of settlement, then more larvae should result in more settlement (I). Likewise, if density-dependent processes are not limiting the growth, survival and recruitment of post-settlement individuals, then increased settlement rates may mean increased recruitment to the fishery (J). However, these are big 'ifs'. Theory suggests that this link is most likely to be realised at low stock sizes, in other words for sanctuaries established to aid the recovery of an overfished stock. Otherwise, it will be very difficult to predict the effect of larval export.

Assuming that the link is made, numerous factors will influence the relationship between the size of the larval pool and recruitment rates, but unless those factors interact with sanctuary-specific characteristics, the contribution of larval export will be simply proportional to its contribution to the larval pool, scaled by the strength of the stock-recruitment relationship. If larval export does increase stock sizes, then it follows logically that catch-per-unit-effort would improve, and, assuming the size of the fishery does not change, that increases in yield would follow (K). Whether fisheries-yield improvements are lasting will depend on the behaviour of individual fishers and the responses of the fishery as a whole. The potential for increased yield could be lost if fisheries respond to increased CPUE by increasing fishing effort. It is possible that some fishers will benefit, at least in the short-term, if they are able to exploit the spatio-temporal characteristics of reserve-produced stock enhancements. However, fisheries as a whole may not improve, or may even suffer, as a result of an inappropriate response. Viewed in another way, increased stock may translate into larger catches, yields and profits for fisheries, or alternatively into improved stock status and reliability without increased catches. In the latter case, it is still possible that yields and profits may increase through improvements in CPUE. As in many situations, the sustainability of stocks and effectiveness of management actions may depend on the control of fishing capacity (Allison *et al.* 1998, Fogarty 1999). Measuring the fisheries benefits or costs of sanctuaries will be complicated, and should entail carefully assessing changes at different levels, such as:

- changes in the status, size and distribution of the stock
- changes in CPUE, size of catch and quality of catch for individual fishers
- fishing effort allocation responses, and
- total catch and yield for fisheries.

What we are broadly calling fisheries benefits will extend beyond the fisheries themselves. Benefits may be passed on to those institutions closely linked to fisheries (L), such as processing plants, shipping firms, retail outlets, boat builders and suppliers of fishing equipment. Finally, the growth and/or improved sustainability of fishing industries will have flow-on effects for fishing communities, the public and related regional development and socio-economic systems. Depending on the response of the fisheries, the type and quality of their products and services provided to the community may change, independently of whether their profit is improved. Sumaila (1998) argued that the comprehensive evaluation of the utility of MFSs must include bioeconomic criteria, such as the nutritional needs of the community and management costs.

In summary, we conclude that theoretical expectations suggest that MFSs have a strong potential to be highly effective fisheries management tools for many fully exploited and over-fished species. It is clear that fishing can have profound effects on marine resources, habitats and environments, and that fewer and fewer areas of the world's oceans are free from these impacts. There can be little doubt that protecting parts of the marine environment will help to lessen the impact of commercial and recreational fishing activities. There are good reasons to expect that environments damaged by fishing will improve when protected, although it is critical to note that accurately predicting the form and extent of improvement will be very difficult. Assuming that sanctuaries are carefully designed and that their 'no-take' status is enforced, then it is reasonable to expect that in time they will contain healthy populations of focal and non-focal species, and 'normal' habitats and ecosystems. Those populations will be comprised, on the average, of older, larger and more fecund individuals than would be the case for unprotected, fished areas. It is assumed that these protected populations will become sources of excess production that will enhance exploited populations outside sanctuaries. While this is certainly possible, it depends on specific conditions being true. Fisheries enhancement through the 'spillover' of juveniles and adults that is more significant in quantity and geographic scale will depend on critical features, such as focal species selection, and the size, location, number and shapes of sanctuaries. Fisheries enhancement through 'larval export' will be even more problematic, depending on 'sanctuary improvement' actually producing net larval export, that export making a significant contribution to the total larval pool, and, most importantly, the increase in the size of the larval pool translating into an increase in settlement, and ultimately, fisheries recruitment rates. Again, these outcomes are highly dependent on the species selected and the characteristics of the reserves. Overall, there is convincing theoretical support for the idea that well designed sanctuaries will provide significant fisheries enhancement for those species of greatest concern—the overfished high value species most in need of improved fisheries management tools.

5. THE EVIDENCE

In this Section, we consider the empirical evidence relating to the potential benefits of marine sanctuaries for commercial species and their fisheries, and consider some aspects of the size/area required for sanctuaries. The research papers that contain relevant evidence are summarised in Appendices 1 and 2. In the text here we discuss some of that evidence.

5.1 Empirical Evidence for Improvements Within Reserves

The benefits within reserves are documented within three categories: increased abundance of focal species, increased size/age of species and increased fecundity of species. In all three cases, results are grouped as finfish or shellfish. Following these, some of the practical difficulties associated with studying marine reserves to capture reliable field data are discussed.

Despite the potential for marine reserves to assist with fisheries management issues, there are few well-documented examples of their actual application in fisheries systems. Moreover, studies of marine reserves have concentrated almost entirely on reef systems and other high topographic-relief habitats such as rocky substrate, seagrass beds, and kelp forests (Auster & Malatesta 1995). Because tropical and temperate reefs are critical habitat for many fish species, and are well defined environments amenable to detailed experimental investigations, research interest has focused on these habitats. Reef fish are also heavily targeted by inshore fisheries (Edgar & Barrett 1999). As a result, a substantial body of evidence has accrued to demonstrate the effect of marine reserves on reef fish populations (e.g. Roberts & Hawkins 1997). However, much less is known about the effect of marine reserves located in other types of ecosystems, and particularly continental shelf and open ocean environments.

Generally, the habitat requirements and life history strategies of deeper water species are uncertain and few reserves have been created to protect critical open ocean habitat. Where such reserves do exist, their remoteness often precludes scientific monitoring for evaluation purposes. Possibly one exception to this approach is the Georges Bank region off Canada where the importance of habitat to fish with extended ranges has been studied using remote techniques (Auster & Malatesta 1995).

The majority of studies of marine reserves have compared a reserve with other areas of similar habitat located nearby. Very few studies are designed as 'before and after' comparisons, or BACI comparisons ('before' and 'after' 'control' and 'impact'), which would provide the most convincing evidence of a reserve effect. Selecting control areas is a typical difficult design problem—there may be natural differences between areas studied that are initially undetectable to researchers and these differences may distort results on the effects of reserves (more design problems are discussed in Section 5.1.4). Many studies focus solely on abundance/density and size/biomass changes of fish species, with few documenting changes to reproductive output. Whilst most studies have compared reserves with harvested areas after less than five years protection, a number of time-series studies have been undertaken in the Philippines, Kenya and Tasmania (refer to Appendices 1 and 2). Halpern (in press) recently reviewed 89 empirical studies that examine the reserve effect in 73 temperate and tropical no-take reserves, covering a range of sizes and using 112 independent measures—but most were restricted to reef habitats.

5.1.1 Increased abundance of focal species

Changes to the abundance of focal species inside a marine reserve are an obvious (and often the most detectable) benefit from creation of a reserve. Many studies have reported rapid increases of in-reserve abundance following the creation of marine reserves, especially of large piscivorous fish, which are notably absent from exploited areas (Roberts & Polunin 1991, Rowley 1994, Ferreira & Russ 1995). Positive changes typically occur within 2 to 4 years following area protection (Carter & Sedberry 1997). Conversely, once the protection afforded by a marine reserve is removed, stocks of focal species are quickly depleted, and species abundance falls to pre-reservation levels (Russell 1997). After review of 89 studies covering 73 reserves (mainly reefs), Halpern (in press) reported that, comparing densities inside the reserve to outside the reserve, higher densities were found inside the reserve for carnivorous fish (66% of reserves), planktivorous and benthic invertebrate-eating fish (62% of reserves), and herbivorous fish (53% of reserves).

Finfish species

Increased abundance of finfish species has been documented in many marine reserve studies, most notably in relation to the density of previously harvested species. The majority of studies of species abundance have concentrated on coral reef predatory fish, which are the major target fish in many tropical fisheries and the most severely affected by fishing mortality. Large predatory fish are slow growing, have low reproductive rate and are generally territorial, reducing their resilience to fishing impacts (Russ & Alcala 1998b). Measuring the reserve effect for such species is difficult because of uncertainties about the length of time it might takes their populations to recover, especially if these target fish were previously exploited intensively. Studies on the effects of reserves have regularly reported abundances of target species up to 25 times greater within reserved areas than in comparable fished areas. Typically, abundances increase by 200-400% within several years (refer to Appendix 1). A six-year study of the effect of reserve protection on coral trout (*Plectropomus leopardus*) at the Houtman Abrolhos Islands in Western Australia found that all size classes increased between 8 and 16-fold in the reserved areas (Nardi *et al.* manuscript). Based upon these and other studies, and despite some variability in the documented outcomes of reserve protection for such finfish species, it appears that density differences are maximised about 6-8 years following area protection. It is therefore clear that studies intended to measure the reserve effect must cover at least 3 years, and preferably 5 years at a minimum, and should aim to continue for 10 years in order to confirm that the reserve effect persists.

Following closure of Bramble Reef on the Great Barrier Reef to fishing, as reported by Russell (1997), coral trout increased greatly in size and numbers on the reef. This was due in part to a large pulse in recruitment which occurred independently of area protection. In evaluating reserve outcomes, it is therefore important to be able to recognise the interaction of natural dynamics with the effects of area protection, and to ensure that sanctuary success is not confounded with a pulse in natural recruitment or other episodic factors that may be transient. Similarly, interpretation problems were encountered by Bennett & Attwood (1993) who attributed episodic catch rate patterns in their South African data to the sampling design. Also, the migratory nature of some species (*Umbrina canariensis*, *Argyrosomus hololepidotus*, *Pomatomus saltatrix*) was considered to account for the absence of any detected changes in abundance following area protection. The dominance of recruitment in fish life history strategies means that, in field sampling, designs to assess increases in species' density following area protection should incorporate recruitment patterns that may be episodic rather than regular and cyclical (Russ & Alcala 1989, Dugan & Davis 1993).

Changes in abundance flowing from area protection are not always direct. A common observation is that the abundance of predators increases, but there is a stabilisation or even decrease in the abundance of non-focal species (Chiappone & Sealey 2000) and juvenile herbivorous fish (Roberts & Polunin 1991, Macpherson *et al.* 1997). This phenomenon was evident in the Bahamas where non-target grouper species were more abundant in the fished areas than in the reserve (Chiappone & Sealey, 2000) due possibly to reduced competition for resources between target and non-target species, or because non-target grouper species affected post-settlement survivorship of target groupers through competition or predation. Samoilys (1988) noted no increase in total fish abundance following area protection, although groupers were significantly more abundant, and became depleted once protection was removed.

Dufour *et al.* (1995) compared the abundance of fish inside and outside reserves in 1992 with an earlier 1980 census and noted that no consistent pattern in abundance had occurred. Also, the mortality of juvenile fish inside the reserve was higher than that outside. The authors interpreted the presence of transient predators outside the reserves as indicating increased predation on smaller fish inside the reserved areas. Similarly, Roberts & Polunin (1992) reported that the surgeonfish (*Acanthurus migrofuscus*) in the Mediterranean were nearly three times more abundant in areas where fishing occurred than in unfished areas. This phenomenon was attributed to predation—the focal species [groupers] were fished down, allowing numbers of its surgeonfish prey species to increase. McClanahan (1996) similarly showed how fishing resulted in lower yields by changing predator-prey interactions on coral reefs.

Predator-prey effects clearly occur in and around reserves, but snapshot sampling designs make it difficult to detect the influence of other variables, such as recruitment and habitat differences, on changes in fish abundance inside and outside reserves. While the effects of exploitation and protection on individual species are relatively easily documented, community effects are less predictable and their implications less apparent (Buxton 1996).

Another behavioural factor that may complicate sampling designs and the interpretation of experimental data is territoriality. Large fish (commonly found in reserves) require larger territories, therefore a decrease in density or absolute number of fish may be observed in a reserve due to spillover, forced because of the enlarging territories required by larger and more mature fish (Paddack & Estes 2000). Also, some species may be aggressive and drive out members of their own species (interference competition). Problems can also arise if the fish preys upon juveniles of its own species, e.g. rockfish. The larger adults in the reserve can potentially consume a greater number of individuals than smaller, less numerous adults in unprotected areas (Paddack & Estes 2000), therefore no change may be apparent or even a decrease in the density of focal species may occur in a reserve.

Shellfish species

A number of studies—both theoretical and empirical—have examined how marine reserves benefit populations of invertebrate species and many have reported increases in abundance or density. For example, the mean size of abalone in a reserve was greater than those in non-reserved areas, as a result of the increased abundance of large abalone in the reserve. However, there was no overall increase in abalone density in the reserve, because smaller abalone were found to decline in abundance (Edgar & Barrett 1999). This pattern of changes in abalone was considered to be possibly caused by intraspecific competition for space and other resources (Edgar & Barrett 1999).

Lasiak (1998) determined that the effects of area protection in rocky infratidal zones in South Africa vary from species to species. Removing brown mussels and large grazing gastropods caused an increase in algae due to an increase in available space, which led to a decrease in abundance and biomass of sessile filter feeders and microalgal grazers and an increase in species which are associated with macroalgae.

Rock lobsters (also known as spiny lobsters) have been observed to increase in density in marine reserves, by as much as 260 percent (MacDiarmid & Breen 1993, Kelly *et al.* 2000a). Using the age of each of 4 reserves (3 years to 21 years after creation), the mean density of spiny lobsters (*Jasus edwardsii*) have been estimated to increase in abundance between 3.9 and 9.5% per year of the reserves' life (Kelly *et al.* 2000b). Lobsters can play a critical role in structuring reef invertebrate assemblages—in high densities they have the ability to prey on mussels and other filter feeders causing a change in ecosystem dynamics (Barkai & Branch 1988, Edgar & Barrett 1999). Large lobsters have been observed to undertake summer migrations to deep offshore patch reefs to scavenge for bivalves, and to aggregate into groups; so the sampling design is clearly an important factor affecting the accuracy of reserve evaluations for lobsters (MacDiarmid & Breen 1993, Kelly *et al.* 1999). Other beneficiaries of reserves include: Queen conch, where the density of adults and larvae have been found to be much greater in reserves (Stoner & Ray 1996); and Atlantic sea scallops which have shown increases in abundance and biomass when protected from fishing (Murawski *et al.* 2000).

Not all studies have reported increases in abundance following the establishment of a marine reserve. No noticeable differences in sea urchin (*Evechinus chloroticus*) numbers were observed inside or outside a marine reserve in New Zealand, and there was no obvious explanation for this pattern (Cole *et al.* 1990). It was thought that the benefits of area protection had perhaps already been expressed before monitoring commenced. In California, red abalone populations responded positively to 10 years of area protection, but green and pink abalone populations did not recover in protected areas until mature adults were translocated (Tegner 1993). These findings indicate that recovery may not occur naturally in MFSs where broodstock numbers are depleted below recoverable levels because of overfishing, or where habitats are marginal.

It has been suggested that sea urchins may not benefit from marine reserves at all. A decline in *Paracentrotus lividus* has been observed in protected areas attributable to increased predation by predatory fish (Sala *et al.* 1998b, McClanahan *et al.* 1999). However, significant sampling difficulties have been identified that confound sampling data that compares sea urchin distributions inside and outside of reserves (Cole *et al.* 1990, Castilla 1996, Sala *et al.* 1998b).

The failure of some species of shellfish to respond to area protection may also be due to poor selection of sanctuary areas relative to the species' habitat needs. Marine reserves created in low quality habitat did not enhance populations of hard clam (*M. mercenaria*) and trochus snails (*Trochus niloticus*) even after twenty years (Dugan & Davis 1993). Similarly, the red king crab (*Paralithodes camtschaticus*) did not benefit from a refuge created in the Bering Sea because only adults and sub-adults were protected, but not their critical breeding, spawning or nursery habitats (Armstrong *et al.* 1993).

5.1.2 Age and size gains

Many marine organisms live longer and grow larger when protected in sanctuaries (Roberts 1997c) and the elimination of fishing mortality allows the population age structure of organisms to re-establish (Novaczek 1995). Changes in size of focal species may be easier to detect statistically than changes in total abundance. Edgar & Barrett (1997) report that an increase in mean size of 10% was statistically significant, whereas abundance may need to be doubled before the same level of significance can be assigned, using the sampling techniques of their study. With careful sampling design, changes in size may be able to be interpreted with less ambiguity than statistically significant changes in abundance, which may be distorted by observer presence using some sampling techniques. However, increases in the average size of many species may take longer to be realised, compared with more immediate increases in abundance, and so the resolving power of mean size of focal species may vary depending on the species in question.

In the case of hermaphroditic fishes, the taking of larger size individuals can have highly detrimental effects on the abundance of the species and its success in sanctuaries in general. Beets & Friedlander (1999) showed how fishing in the Virgin Islands had the potential to wipe out red hind because of distortions in the sex ratio, which was observed to be 15 females to one male. After seven years of protection, the age structure normalised and the sex ratio became 4 females to 1 male. Examining the sex ratio can be misleading, however, as shown in a study of coral groupers in the Great Barrier Reef. Larger individuals decreased in abundance through fishing pressure, but the ratio of males to females nonetheless stabilised, suggesting the species adapted to change sex from female to male at a younger age to compensate for a reduction in mean size (Ferreira & Russ 1995). To examine just the sex ratio would disguise the fact that structural change to the population was being induced through fishing, and it is not clear how the sex ratios in such adapted populations would respond in a MFS.

Finfish Species

Observations of increased mean size, age and biomass of finfish were common amongst almost all the case studies on the effects of marine sanctuaries (see Appendix 1). The studies surveyed were diverse in terms of species studied, reserve location, fishing method and period of protection. This diversity in context strengthens the weight of evidence argument that marine sanctuaries can produce an increase in average fish size within sanctuaries. Focal species have been reported as benefiting the most in terms of increased size inside sanctuaries (Carter & Sedberry 1997, Chiappone & Sealey 2000). A ten-year study in the Philippines provides one of the most convincing examples of the effect of marine sanctuaries on reef finfish size. Two sanctuary and two non-sanctuary sites were sampled over periods ranging from –2 years (i.e. two years of fishing prior to protection) to 9 years of protection, providing a comprehensive set of information (Russ & Alcala 1996a). The biomass of the fish communities increased by a factor of 1.53 after six years of protection and increased further by a factor of 1.55 after nine years of protection (Russ & Alcala 1998a).

Halpern's review of the empirical studies in 73 (mainly reef) reserves (Halpern in press) found that, for carnivorous fish, 84% and 83% reserves had higher biomass and larger individuals respectively compared to outside the reserve. For plankton and benthic invertebrate eating fish, 55% of reserves had larger biomass, and 89% had larger individuals, compared to outside the reserve. For herbivorous fish, 63% of reserves had a larger biomass compared to outside the reserve, but no statistically difference existed between reserve and non-reserve herbivorous fish size (although only one study reported herbivorous fish smaller inside than outside the reserve) (Halpern in press).

Shellfish Species

Increases in size have been observed for many different shellfish species. In a study on reef biota conducted by Edgar & Barrett (1999), mean abalone size increased 8 mm after only 7 months of protection. Similarly, the biomass of scallop has been found to increase in sanctuaries. Increases in mean size of sea urchins, however, have differed between studies. The sea urchins in a sanctuary in Chile were found to be up to 25% larger than in fished areas (Castilla 1996), but there were no significant increases in the mean size of two species of sea urchin (*Paracentrotus lividus* and *Arbacia lixula*) in a sanctuary studied at Medes Island. It was proposed that the lack of increase in size was due to density-dependent growth rates of sea urchins—increased numbers of urchins prevented individuals from growing as large as they could where they occur in lower densities.

In the case of rock lobsters (*Jasus edwardsii*), an increase in both density and size was noted in a study on sanctuaries in New Zealand (MacDiarmid & Breen 1993, Kelly *et al.* 2000a). The mean size of the lobsters in these populations was estimated to increase by 1.14mm for each year of reserve protection, while the mean biomass was estimated to increase by between 5.4 and 10.9% for each year of reserve protection (Kelly *et al.* 2000b). In another study, increases in biomass and carapace length were observed in the lobster populations located in sanctuaries and it appeared that these results were more pronounced the larger the sanctuary (Edgar & Barrett 1999). The effects of the sanctuary were only observable to within 1km outside the boundaries, and beyond this buffer zone the rock lobsters were very rare. Therefore, spillover appeared to be limited to within 1 km from the sanctuary boundary for this species in this location.

5.1.3 Enhanced fecundity or reproductive capacity

A benefit of marine sanctuaries is their contribution to egg production, as older and larger fish are most likely to spawn and have a higher carrying capacity for eggs (Novaczek 1995, Roberts 1997b) and the eggs of older fish are also more likely to survive (Trippel *et al.* 1997, Ballantine 1999). Enhanced output per individual, and elevated numbers of individuals, can result in 80-600% greater egg production in protected fish populations (Dugan & Davis 1993, Ballantine 1999). Sanctuaries also provide insurance against recruitment overfishing of species such as the seabream (*Acanthropagus australis*) and abalone (Attwood *et al.* 1997b). Simply removing fishing disturbances and trauma-induced morbidity and mortality can also enhance reproductive capacity.

Despite this beneficial increase in reproductive output, few studies have tracked recruitment following increased egg production, due partly to the difficulty in distinguishing species at the early juvenile stage. One exception is the work of Tupper & Juanes (1999), who showed that the increase in abundance of predators within a sanctuary increased the level of predation on early juvenile grunts, thereby decreasing recruitment despite enhanced egg production. It is important to realise, therefore, that an increase in egg production in a sanctuary does not necessarily result in an increase in ecological recruitment in the reserve, although there may be an increased supply of propagules to fished areas outside the sanctuary.

Finfish Species

There have been few studies observing increases in fecundity and reproductive output of fish in sanctuaries. However, in the studies that have been conducted and evaluated there have been many positive results (refer to Appendix 1). Nassau grouper in a reserve in the Bahamas were reported as having a reproductive capacity of six times the capacity of those in fished areas (Sluka *et al.* 1997), coinciding with an increase in average size of the groupers. Other studies on grouper species have indicated similar results, with a massive difference in egg production of Nassau grouper reported in a four year old reserve in the Bahamas (8.6 million in the sanctuary contrasted to an average of 1.4 million in unprotected areas). A higher percentage of sexually mature grouper individuals (21% greater than the next most sexually mature site) was noted in this sanctuary (Chiappone & Sealey 2000). Other fish species reported to increase in reproductive capacity include groundfishes (Murawski *et al.* 2000) lincod, and especially copper rockfish, as egg production was found to be 100 times greater for this species in a sanctuary (Pitcher (ed.) 1997). It has been determined that reserves have clearly greater potential egg production if they conserve the spawning stock biomass (Sluka *et al.* 1996a, Chiappone & Sealey 2000).

While Paddack & Estes (2000) found that in general there was an increase in reproductive output for reserve sites, one-year old reserves showed no significant difference in reproductive capacity between fished and unfished areas. It is clear that, in fish populations, it may take many years (perhaps longer than 10 years) for the benefits of marine reserves such as increased fecundity to be fully realised.

Shellfish species

Many invertebrate species are broadcast spawners—they reproduce by releasing gametes into the currents for chance fertilisation. Larval settlement from these propagules can be close to the spawning sites in areas where tidal currents and wave action are low or if spawning is conducted at times when currents are minimal, or they can be carried very great distances where currents are greater resulting in much broader dispersal. Prince *et al.* (1988) found that the greater the density of adults, the higher the number of recruits. The few studies that have been conducted on marine reserves to investigate the reproductive benefits to shellfish have generally reported highly positive results. For example, in a sanctuary at Vancouver Island, abalone were reported to be 1.2 and 1.4 times more fecund than abalone in the two less protected areas (Pitcher (ed.) 1997). A similar scenario was observed elsewhere in British Columbia with abalone (Wallace 1999). In the case of rock lobsters, increases in reproductive output were observed in a number of Tasmanian sanctuaries and it appeared that the reproductive output corresponded with sanctuary size (Edgar & Barrett 1999). In 4 New Zealand reserves, egg production from spiny lobster (*Jasus edwardsii*) populations has been estimated to increase between 4.8 and 9.1% for each year of reserve protection (Kelly *et al.* 2000b). Larval increases of Queen conch have also been observed (Stoner & Ray 1996, Chiappone & Sealey 2000). Although increasing the concentration of spawners should greatly increase the likelihood of effective reproduction, the reproductive potential of abalone declined in South Australia where the reserves created did not attain the threshold density of spawners in the spatial arrangement necessary for effective spawning and stock replenishment (Shepherd & Brown 1993).

5.1.4 Limitations with studies of marine sanctuary benefits

There are a number of problems associated with studying, quantifying and evaluating marine sanctuaries benefits. Problems fall into three basic categories: methodological, ecological and management. These limitations can seriously affect results and researchers need to be aware of the problems and develop ways of dealing with them within study designs.

Methodological Problems

Design issues

The rigour of the sampling design of studies intended to examine the benefits of marine sanctuaries is crucial to their success. Weak designs mean that factors may be confounded, and conclusions will not be robust either for the sanctuaries being studied or when extrapolated to other sanctuaries. Unfortunately, few published studies have reported pre-establishment information on the sanctuary being studied (e.g. baseline biological data and fishing effort data collected prior to creation of the sanctuary or before fishing took place) (Carter & Sedberry 1997) and they often contrast just one reserved and one unreserved site (see reviews by Bennett & Attwood 1991, Roberts & Polunin 1991, Guenette *et al.* 1998). Lack of 'before and after' studies, time-series data and control sites, coupled with weak enforcement of fishing bans, have created major difficulties in providing conclusive evidence on sanctuary effectiveness (Carter & Sedberry 1997, Halpern in press). Control sites are especially important, because without them the true impact of removing fishing cannot be determined. The lack of a comprehensive and defendable statistical basis for design means that outcomes and conclusions are tentative and of uncertain value for use in other locations.

Even more limiting are snapshot studies which sample changes in variables over short time horizons and are therefore, for example, unable to identify how recruitment events—a fundamental influence on fish populations—affect abundance on an annual basis (see studies by Cole *et al.* 1990, Dufour *et al.* 1995, Russell 1997). Failure to observe benefits from marine sanctuaries has also been related to problems such as severely depleted breeding stocks, which may take a very long time to recover and are difficult to sample effectively. Therefore, a time series monitoring program conducted over several years is needed for a thorough evaluation of the effects of fishing (Beets & Friedlander 1999) (these influences are discussed further in the next section).

Edgar *et al.* (1997) emphasised the importance of identifying sites with comparable environmental conditions in studies that compared marine sanctuaries with unprotected sites. Many studies compare sites inside and outside reserves, which does not (necessarily) adequately control for intrinsic differences in habitat or other variables. Indeed, the equivocal findings by Roberts & Polunin (1992) were attributed more to habitat differences than to fishing effects. Because sanctuaries and sanctuary studies are not often replicated, it is difficult to differentiate between protection effects and spatial effects (Carr & Reed 1993, Paddack & Estes 2000). This confounding means that differences observed between a reserve and an outside area may not be attributable to protection status but rather to natural differences in habitat. Paddack & Estes (2000) also argue that there are basic deficiencies in using an experimental approach to examine fish abundance and population structure in reserves—(a) there is little reliable information about the natural spatial distribution of most fish populations, (b) it is difficult to replicate experimental treatments due to different levels of exploitation, and (c) there is often confounding of spatial and temporal variation among experimental units. Ferreira & Russ's (1995) study of coral groupers showed that more replicate treatments were needed to increase the degrees of freedom and power of their analysis. And finally, but possibly most importantly, the choice of biological variables to measure may affect whether a study will detect a benefit of protection. Making precise and powerful measurements on variables that are not likely to be involved with the reserve effect is misleading and counter-productive.

Another important design problem is determining the length of the sampling period— it needs to be long enough to detect a recovery of fish populations. Recovery periods can be especially long if focal species are slow growing and they were previously exploited intensively. Russ & Alcala (1996) indicate that a density difference in reef fish may not occur for 4 to 6 years following area protection. Sampling can be hindered by limited access time, water-clarity difficulties with undertaking visual counts, and the high cost associated with research using submersibles.

The need for carefully designed reserves, including monitoring (time series) programs, has also been identified as a key issue in assessing the performance of reserves established for fisheries purposes (Carr & Raimondi 1999, NAS 2000). Reserves that fail to meet their objectives may invoke 'catastrophic costs', depending on how much managers and stakeholders rely on the success of that reserve, and the design and evaluation framework is considered crucial to successful studies of reserve effectiveness (Carr & Raimondi 1999).

Sampling sanctuaries is a very labour intensive and time consuming exercise, and there are always limitations on resourcing such studies (Paddack & Estes 2000) and these limitations may cause interpretation problems. The study of Dufour *et al.* (1995) was inconclusive because of the brevity in the sampling regime. Variability also complicates sampling designs, and designs with low statistical power may lead to inconclusive results, a problem encountered by Cole *et al.* (1990) in their study of New Zealand's Leigh Marine Reserve. The inconclusive results reported from that study were apparently caused, at least in part, by unpredicted differences in monitoring accuracy among observers.

The design problems experienced by these (and many other) investigators make it clear that, as with any scientific endeavour, very careful planning and design is crucial to the success of the outcomes. Assessing the benefits of a sanctuary should be conducted in such a way that the data collected will be statistically robust, and be focused on aspects of a sanctuary that could reasonably be expected to show a change as a result of the area protection. Depending on the focal species, on the sanctuary design and on the resources available for the study, such designs are best based on 'before and after' comparisons at sanctuaries and control sites, on analyses of spatial gradients in key variables, and involve long (decadal) time series of data. Suitable indicator variables may be chosen from the list presented in Section 7.

Sampling issues

In sampling of sanctuaries, it is unlikely that statistically significant results will be produced where small numbers of individuals are involved. Pooling species to the family level is one way of overcoming the limitations presented by low statistical power (Roberts & Polunin 1992, McClanahan & Kuanda-Arara 1996). However, changes at the species level are likely to be masked by pooling of data to the level of family (Vanderklift *et al.* 1998) which may not allow detection of important biological changes as a result of area protection. Pooling of species data to achieve higher statistical power but reducing the potential to recognise potentially important biological changes compromises the original intention of the sampling design, (sacrificing the objectives of the sampling to meet statistical requirements is termed pseudo-power— Ward & Jacoby 1992), and in doing so may fail to detect biologically important changes.

Uncertainties about the behaviour of fish during sampling may also affect interpretations of data on the effectiveness of sanctuaries. It is possible that the presence of divers may attract fish during a census count, thus inflating estimations of effectiveness (Edgar *et al.* 1997). This phenomenon has been considered by

Dufour *et al.* (1995) in relation to fish inside a sanctuary where the presence of researchers may have acted as a stimulus for feeding through association with recreational divers and therefore caused a bias in survey results. Cole *et al.* (1990) report that some fish are naturally inquisitive—and thereby inflate visual census results—but endeavoured to exclude such individuals from their censuses. Fish avoidance of surveyors has also been documented, thereby biasing results downwards, as demonstrated with snapper (Pitcher (ed.) 1997). A related problem associated with visual sampling (either by divers, or worse, from videos) is incorrect identification of species. The juveniles of many species of fish are difficult to distinguish to species level, particularly in visual census, and so are often not surveyed. Also, the juveniles may occur seasonally and utilize different habitats that are more difficult to sample (Paddack & Estes 2000). Lobsters are reported to aggregate offshore, at times, (Kelly *et al.* 1999), making sampling design and effectiveness a critical problem when assessing the nature and extent of the reserve effect on spiny lobsters.

Ecological Issues

The long natural life spans and the diversity of reproductive strategies amongst dominant marine species make assessments of the effectiveness of marine sanctuaries difficult. Many species may not display a response to the exclusion of fishing for several years—until new recruits have occupied the size classes which had previously been exploited (Edgar *et al.* 1997). In such circumstances, it may be easier to detect statistically significant sanctuary improvements using the mean size or age of individuals rather than abundance, depending on the species of interest. For example, Ferreira & Russ (1995) showed that age structure was useful in detecting fishing-related changes to coral grouper because this species was slow growing, and changes in size or abundance would have taken much longer to be detected in any reasonable sampling design. In situations where the basic ecological and natural history characteristics of the focal species are uncertain, it will prove difficult to interpret assessments of the effectiveness of sanctuaries. This will be particularly difficult for studies that are short-term, or do not use species that have been well studied, except in the situation where increased abundances in focal species are substantial and rapid.

The dispersal characteristics of some species can also confound assessments of sanctuary improvement. Where the spatial scale of larval and adult dispersal compared with the size of existing sanctuaries is unknown, detecting sanctuary improvement can be difficult (Sala *et al.* 1998b). When densities become high in reserves, adults may disperse to areas outside the reserve to establish new home ranges or territories. If dispersal of some of the species in a reserve is over a large area, larger than the reserve itself, differences in fish density or population structure between protected and unprotected areas may be difficult to detect, even if exploitation was previously extreme (Roberts & Polunin 1993, Roberts 1995b, Paddack & Estes 2000). Rockfish are an example, as they move from areas of high population density to areas of low density. In situations where dispersal characteristics are unknown, studies of sanctuary improvement may reach misleading conclusions because of the unknown scale of dispersion, and a failure of the sampling design to properly account for dispersion characteristics of the species of interest.

Large scale oceanographic and climatic features such as El Nino Southern Oscillation (ENSO) events have the ability to seriously affect habitats and may disrupt benthic populations and their reproductive success. If this is occurring while a sanctuary is being sampled for assessment, and the ENSO has different effects in the sanctuary than in the control areas, then it can seriously confound the results (Allison *et al.* 1998). The spatial and temporal variability of the biological effects of these events is poorly understood, but when coupled with a low-power or otherwise inadequate sampling design, the variability in such features may create severe difficulties with interpreting the results of sanctuary improvement studies.

Studies of invertebrates to examine reserve effects may also be confounded by trophic interactions within the reserve. Reserve creation may benefit populations of carnivorous fish, but these may reduce populations of invertebrate prey within reserves, and so measures of reserve performance that do not also include a range of trophic levels may be misleading (Halpern in press).

Management Limitations

Aside from sampling or scientific limitations associated with studying the effects of marine sanctuaries, there is the problem of compliance and enforcement of reserve controls, and whether these, as well as management operations, change throughout the sampling period (Jennings *et al.* 1996, Pitcher (ed.) 1997). Few sanctuaries are comprehensively monitored to ascertain the degree to which no-fishing requirements are being observed, and it is possible that fishing violations corrupt the results of sanctuary improvement studies (McClanahan & Kuanda-Arara 1996). There is a lack of information on how fish communities are affected by different management strategies, even after reserves have been established for a long period of time (15 years) (Jennings *et al.* 1996), but many managers suspect that reserves are occasionally violated. The key problem then becomes what frequency, location and what type of fishing violation would compromise the objectives of a reserve, and in evaluating the reserve effect what, if any, sampling designs can be implemented to account for, or estimate, illegal fishing and its effects.

Factors such as reef degradation within a sanctuary and illegal fishing may reduce the size of the reserve effect, as was found in one study where there appeared to be no real difference in fish populations between reserve and non-reserve areas (Russ & Alcala 1998a). Where violations are suspected, it may be appropriate to include, or conduct, pilot studies to estimate the nature of illegal fishing, before designing a sanctuary evaluation project. Little published data exists to gauge the extent of non-compliance, but a multi-year study in the Great Barrier Reef has reported high levels of intrusion into a no-take zone of the Great Barrier Reef Marine Park (Gribble & Robertson 1998). If rules and regulations are not being adhered to and fish exploitation is occurring in a sanctuary, a reduced contrast in comparisons between fished and unfished areas would be expected, and much more intensive sampling designs would need to be implemented in order to detect such differences than if illegal fishing was not occurring.

5.2 Evidence for Improvements to Fisheries

In this section we consider the empirical evidence in support of the contention that sanctuaries deliver benefits to fisheries.

Establishing sanctuaries to protect habitats that are important for a focal species will potentially cause an increase in abundance and size of these species within the sanctuary, as discussed in Section 3. Two pathways through which fisheries can benefit from larger and more fecund populations of target species inside MFSs are emigration of adults (spillover) and exportation of larvae (larval export) (see Section 4 and Figure 1).

However, there have been very few studies that have attempted to critically examine and measure the benefits that a fishery has derived from the declaration of a no-take marine reserve.

At present, much of the evidence that is used in arguments advocating the use of reserves for fisheries management is largely theoretical or circumstantial, both because of the newness of the topic and due to the difficulties involved with measuring or quantifying spillover and larval export. As a result, the precise role of reserves in providing benefits to fisheries is still poorly understood, despite the literature reviewed above. Efforts are increasingly turning to modelling to try to better understand the nature of the benefits and the way in which they might be delivered. Most effort is now focused on the two most important conceptual sets of potential benefits—spillover and larval export.

5.2.1 Spillover effects

A small but convincing body of evidence shows that sanctuaries can increase fish catch in surrounding harvested areas, or at least maintain current yields for some species (Booth 1979, Davis & Dodrill 1980, Alcala 1988, Rogers-Bennett *et al.* 1995, Hastings & Botsford 1999b, McClanahan & Mangi 2000). Spillover is thought to occur when an increase in density of an organism in a protected area reaches a threshold at which individuals migrate into available habitats in adjacent unprotected areas, and contribute to the fishery. Tupper & Juanes (1999) consider that spillover is caused by intense intraspecific and interspecific competition in reserves, and also suggest that this phenomenon may take a few years to occur before densities in the reserve reach their maximum level. The spillover potential of adults and juveniles depends on the species involved, the size of the sanctuaries, the behaviour and motility of the species, and the total area protected (see Section 3). Therefore, in order to optimise projected benefits to fisheries, knowledge of oceanographic conditions and distance of movement of adults (and also larvae) will need to be determined before boundary locations of sanctuaries are established (for discussion of management implications see section 5.2.3).

Apart from interpretations of a small number of tagging studies and CPUE data in fishable areas adjacent to reserves, the evidence that could be used to determine the processes that lead to enhancement of fisheries yield relies on conceptual arguments rather than direct observations (Rowley 1994, Attwood *et al.* 1997b). Below we examine the concept of home ranges (an essential consideration in spillover) before reviewing techniques for measuring spillover.

Home Ranges

A home range is the area in which animals spend a substantial period of time and where they conduct almost all of their activities, including feeding, mating and resting (Anderson 1982, Matthews 1996, Kramer & Chapman 1999) (see Section 4). Species that are associated with substrate (benthic), as well as some mid-water species, usually have home ranges. Home ranges may not occur (or presumably may be too large to be measurable) in pelagic or highly migratory marine fishes, such as tuna (Kramer & Chapman 1999), and some home ranges are known to be extremely large (e.g. sharks). Typically the distances involved for benthic species are several hundred metres, but some range over 10-15 km (Roberts & Polunin 1991). Generally, large and schooling species move further distances, and hence will be more likely to emigrate from a reserve than are small or solitary species (Tupper & Juanes 1999). A number of coral reef fish move between feeding sites and resting or reproductive sites on a daily basis. Sometimes different habitat types are required for these activities, which are often joined by a narrow movement path (Kramer & Chapman 1999). Roberts & Polunin (1991) argue that enhancement of fisheries by spillover alone of coral reef fish is expected to be limited to within 1km of a reserve, given the generally restricted home range of most of these species.

As an example of observational data on home ranges, Table 7 provides some information on the extent of movement of a number of temperate reef fishes of the families Labridae and Monacanthidae at Arch Rock in Tasmania.

Table 7 shows that some reef fish are territorial, and therefore are likely to have home ranges that do not overlap. Territorial behaviour is usually expressed by one individual chasing another individual of the same species out of its territory/home range. In these fish, population density may be substantially affected by territoriality. The table also shows that banded wrasse and brown-striped leatherjacket have large home ranges which could potentially take many of them outside the boundaries of a small (say $1km^2$) reserve, hence subjecting them to fishing mortality. Whilst the estimated range of *P. vittiger* was not determined, studies into the long term movement of this species show that individuals can travel as far as 4.5 km and, although rare, can even cross large areas of open sandy bottom. A notable observation in Barrett's study is that the size of fish was significantly related to range size—ranges increased with the length of an individual in four of six species. Goeden (1978) also concluded that movement of *P. leopardus* is positively correlated with fish size. Home range size was not related to the sex of the individual in any of the species studied.

Table 7. Behavioural observations (200 hrs) on six temperate reef fishes at Arch Rock, Tasmania (adapted from Barrett 1995).

Species	Estimated range	Territorial Behaviour
Blue throat wrasse *Notolabrus tetrus*	225–725m^2	Yes
Banded wrasse *Notalabrus fucicola*	>1750m^2	No
Senator wrasse *Pictilabrus laticlavis*	175m^2	Yes
Rosy wrasse *Pseudolabrus psittaculus*	280–375m^2	Yes
Toothbrush leatherjacket *Penicipelta vittiger*	?	No
Brown-striped leatherjacket *Meuschenia australis*	>1750m^2	No

In contrast to finfish, most shellfish have small home ranges once they have settled. Adult rock lobsters are highly site attached and individuals may move less than a kilometre over several years. Therefore, during sedentary phases of their lifecycles, shellfish such as rock lobster and abalone can potentially be protected in small sanctuaries (Edgar & Barrett 1999).

Although some reef species are site attached and stay within a localised area for most of their post-settlement lives, other species display ontogenetic habitat shifts during their life cycle (Samoilys 1997, Tupper & Juanes 1999). Queen conch have ontogentic shifts in habitat: early juveniles inhabit mainly shallow zones where they spend their time buried under the sand; 1-2 year old juveniles form aggregations near tidal inlets with deeper seagrass beds. Similarly, spiny lobsters and Nassau grouper inhabit shallow bank habitats, comprising algal and seagrass patches, and patch reefs, during the juvenile stage, whereas the adults prefer shelf hard-bottom habitats (Herrnkind & Lipcius 1986, Eggleston 1995, Chiappone & Sealey 2000). Western rock lobsters (*Panulirus cygnus*) settle from the plankton onto the nearshore limestone reefs of Western Australia, then as they grow, migrate across the continental shelf towards deeper (shelf) waters. There are four stages in the life cycle of this lobster: (1) 9-11 month long planktonic period, when they are advected large distances into the Indian Ocean, (2) settlement of the peurulus stage in shallow water reefs where they grow for 3-5 years, (3) migration to offshore waters, (4) maturation in offshore waters and spawning (Phillips 1981, Phillips 1983, Morgan *et al.* 1982). Another example is butterfly fish, which appear to settle in nearshore habitats but later move offshore to deeper habitat, a behaviour displayed by many shelf species over distances up to several kilometres. In some species movement may also occur cyclically (seasonally and diurnally) for feeding or breeding purposes (Roberts & Polunin 1991).

Empirical evidence pertaining to spillover is discussed below by reference to the two different techniques used to detect it—tag and recapture studies, and CPUE/yield data from adjacent fishable areas.

Tagging studies

Tagging is a technique employed by researchers to detect fish movement and hence determine the size of a species' home range. A number of tagging studies indicate that movement out of reserves occurs for some species, although none have been able to link these movements to benefits for fisheries. Considerable movement was observed with tagged sport fishes into and out of a reserve in Florida, and for one species, *Lutjanus griseus*, migration was up to 18km (Bryant *et al.* 1989). In a study examining spillover from a reserve in Monterey Bay, movement was much reduced; ten to fifty per cent of adult rock fish tagged were found to move up to 1.6 km to re-establish in a newly created artificial reef (Matthews 1985, Paddack & Estes 2000).

Although coral trout (*Plectropomus leopardus*) are relatively sedentary in the short term with a home range of approximately 1200m^2, they can disperse as far as 12–28 km (Samoilys 1997). The degree of movement differs between the seasons, with coral trout moving less in summer (cleaning behaviour) and becoming more active in spring (pre-spawning behaviour).

In the case of shellfish, a tagging study by Davis (1989) showed that juvenile spiny lobster (*Panulirus argus*) remained in their nursery area in Florida Bay for 3 years before dispersing to the Gulf of Mexico and the Atlantic Coast. Based on this knowledge of lobster movement, Davis hypothesised that a sanctuary in the bay would enhance the lobster fishery, although no supportive data or models were presented. Likewise, dispersal into fished areas from a reserve has been shown for snow crabs (Yamasaki & Kuwarha 1990) and pink shrimp (Gitschlag 1986) using tag and recapture studies.

Other tagging evidence of spillover effects is not so convincing. Buxton & Allen (1989) conducted a study on a reserve in South Africa and found that tagged fish did not emigrate out of the reserve as most fish were relatively sedentary, and therefore protected entirely by the reserve. Similarly, in relation to a reserve in Tasmania, Barrett (1995) argued that if emigration does occur for *N. tetricus, N. fucicola, P. psittaculus and M. australis*, rates must be minimal based upon extrapolated calculations of mortality rates and tag recovery. Barrett did not measure in-reserve density, however, which other studies show is crucial to developing a correct understanding of spillover.

Attwood & Bennett (1994) suggest that the De Hoop Marine Reserve in South Africa contributed to the adjacent fishery by supplying a continuous source of fish. A tagging study of 1100 fish showed that most recaptures (83%) occurred within the reserve, suggesting that, overall, the species concerned (*Dichistius capensis*—galjoen) did not spillover in large numbers. However, some individuals were reported to travel as far as 1040 km to adjacent exploited areas. In another South Africa study on galjoen (*Coarcinus capensis*), some individuals also migrated large distances whilst others remained in a localised area (reported in Edgar & Barrett 1999).

Overall, it appears that both fish and shellfish species with small home ranges can spillover from reserves. Generally, the extent to which spillover occurs, and its timing, is related to the design and size of the reserve, the biological characteristics of the species involved, and the management system in place to enforce sanctuary controls.

CPUE/measuring yields

Another technique used to determine spillover from a reserve is measuring yields in the adjacent fishable areas, an approach which has been successfully used in several studies. At the De Hoop Marine Reserve, CPUE improved for 6 out of 10 inshore angling species following reserve creation (Bennett & Attwood 1991) and highly migratory species accounted for 3 of the 4 remaining species that did not show considerable recoveries, and so the documented improvement in CPUE may underestimate the true reserve effect. Likewise, in a ten-year old temporary reserve at Sumilon Island (45ha) in the Philippines, high yields were maintained adjacent to the reserve in fished areas (Alcala & Russ 1990). Emigration of adult fishes from the reserve to outside areas was hypothesised as the most likely reason for this result. Spillover is especially possible with Caesionids as they are highly mobile and large schools of these fish require large areas in the form of sleeping sites. When the reserve was re-opened to fishing, marked reductions in abundance of fish taken in the island fishery fell. The mean CPUE for the island one year prior to breakdown of the reserve was 1.98kg/trip, but had dropped by half (0.99kg/trip) 18 months after the reserve was opened to fishing. Over this same period, total yield from Sumilon Island fell from 36.9t/km^2 to 19.87t/km^2 (Alcala & Russ 1990). The Sumilon reserve comprised only 25% of the entire reef area of the island. From this 'natural experiment', the authors concluded that long-term closure of reef portions—rather than closing entire coral reefs—has a role in managing reef fisheries through spillover (Alcala & Russ 1990).

CPUE data has also been used to assess the spillover effects of coral reef area protection in Kenya. After the Mombasa Marine Park was created in 1991, the area available to fishing was reduced from 8 to 3 km^2 and as a result there was a 65% reduction in the number of fishers. Because of a similar reduction in percentage of both fishers and available fishing area, the pre-reservation fishing intensity was maintained. Catch per fisher increased from 20kg/person/month to 43 kg/person/month and benthic catch per unit area increased by 74%

during the initial part of the study. The estimated yield from the reef of 8t/yr/km^2 is close to the maximum sustained yield for coral reefs (McClanahan & Kaunda-Arara 1996). The study was based on landing data and therefore did not investigate biological changes to fish occurring within the reserve, so the effect of recruitment pulses or environmental factors cannot be assessed. Figure 2 depicts catch trends for eight months before the reservation, and for two and a half years following the reservation, indicating the possibility of spillover occurring and its benefits for the fishery. Towards the end of the study the total fish landing and the CPUE decreased although fish abundance increased, and this was attributed to changes in gear types implemented during the period of protection.

More recent work in the Mombasa Marine Park (McClanahan & Mangi 2000) documented the spillover of adults in three main target families (Siganidae, Acanthuridae, Lethrinidae) contributing to adjacent fisheries. Catches (weight and numbers) and size of these fish were greatest closest to the Park boundaries, although the magnitude of spillover was influenced by management controls and habitat characteristics in the fished areas. Spillover into the fishing grounds was considered to be limited to a few hundred m on the northern side of the Park (where fishing is not controlled) but to possibly extend for up to 2 km beyond the southern boundary of the Park (where gear types are restricted).

Further work by Russ & Alcala (1996b) relying on CPUE data indicated that spillover might be occurring from a protected area into adjacent waters. The density and species richness of large predatory fish (Serranidae, Lutjanidae, Lethrinidae, Carangidae) recorded by visual census correlated positively with the duration of the 22.5 ha reserve at Apo Island. The study rejected the proposition that populations were naturally increasing and diversifying due to high successful recruitment. Rather, the pattern of change suggested that as density inside the reserve increased, large predators tended to move from the reserve into the adjacent fished waters. This occurrence was expressed as a ratio of observed fish density inside the reserve relative to that outside. After 1 year of protection this ratio was 6:1, increasing to 16:1 after eight years of protection, and thereafter decreasing to a ratio of 8:1 (11 yr), as abundance increased outside the reserve. This supports the hypothesis that movement of large predators off the reserve was a function of density. Although fishers reported a doubling of catch only two years after the reserve was created, eight years of monitoring was required before the increase in biomass could be attributed to spillover (threshold density of 6/1000m^2) from the reserve, rather than merely natural population fluctuations. After the threshold density was reached, the density of large predators continued to increase both inside and outside the protected area (Russ & Alcala 1996b).

Sluka *et al.* (1997) used CPUE data to measure spillover in a study of 75 sites inside and outside Exuma Park in the Bahamas, and to reveal the scale of spillover of Nassau grouper (*Epinephelus striatus*). Figure 3 shows that biomass of groupers decreased markedly within 10 km of the centre of Exuma Park, suggesting that the reserve was exporting biomass to adjacent waters through adult emigration and also indicating the spatial extent of grouper movement (Sluka *et al.* 1997). However, an alternative explanation that has been advanced for this spatial pattern is that the distribution of groupers correlates highly with poaching pressure, which is least at the centre of the Park where the Ranger station is situated. Others (Chiappone & Sealey 2000) also suggest that greater fishing pressure north and south of the reserve is another possible reason for the drastic difference in biomass between the area within 10 km of the reserve and the area beyond 10 km of the reserve.

Figure 2. Time series landing of fish at Kenyatta Beach, Kenya. The Mombasa Marine Park was declared at month 8, and these landings are from the area outside the reserve (adapted from McClanahan & Kaunda-Arara 1996).

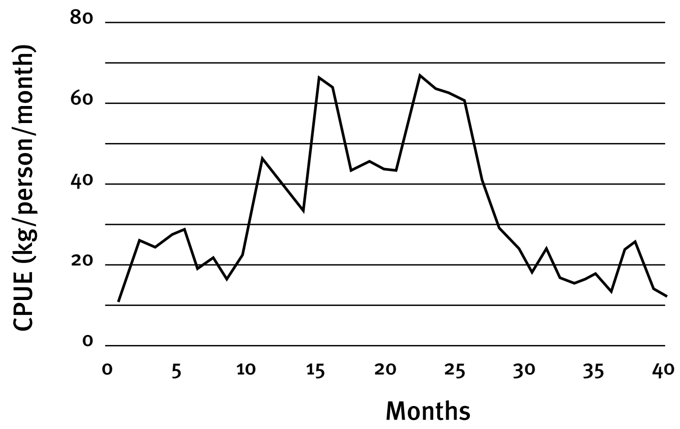
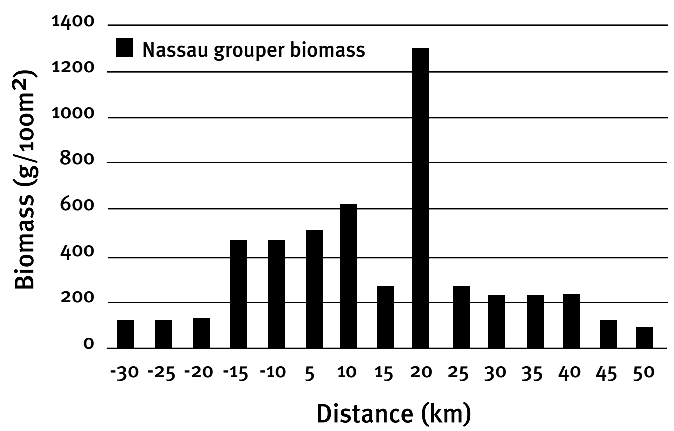


Figure 3. Relationship between distance south (-) and north (+) of Ranger station at the Exuma Cays Land and Sea Park and Nassau grouper biomass (Sluka *et al.* 1997).



For southern Florida fisheries, Bohnsack (1998) comments that three important fisheries (pink shrimp, stone crab and spiny lobster) have all had large area closures, and suggests that these closures account for the sustainability of these fisheries despite the increase in fishing effort they have experienced. By contrast, many other Florida fisheries—including king mackerel, grouper, jewfish, snook and queen conch—have collapsed.

A reserve in Tasmania is thought to export substantial quantities of rock lobster to an adjacent fishery, although the information is anecdotal and spillover benefits to the fishery have yet to be proven (Edgar & Barrett 1999). Similarly, MacDiarmid & Breen (1992) argued that a reserve in New Zealand contributes to increased catches of rock lobster (*Jasus edwardsii*) outside its boundary. The CPUE of research fishing near the reserve is similar to that in other nearby areas, and is maintained by spillover from the reserve, at a level of CPUE higher than the regional mean CPUE in the broader fishery for this species (Kelly *et al.* 2000a).

5.2.2 Export of eggs and larvae

Whilst spillover effects are expected to be localised, the export of pre-recruits can possibly enhance fisheries over much larger regions (Rowley 1994). Restrictions on fishing within a highly productive area can benefit a fishery through the dispersal of eggs and larvae to the surrounding areas (Novaczek 1995, Paddack & Estes 2000). Larval export is believed to benefit fisheries if spawning areas are contained within sanctuaries, and water currents transfer the increased concentration of larvae to fishing grounds for ecological recruitment. Although factors such as post-settlement predation are important influences on density of reef species, larval supply (and subsequent recruitment) may be a principal determinant of abundance (Russ & Alcala 1989). Because reserves are likely to produce dense populations of larger, older and more fecund individuals, the ability of reserves to seed outside areas and enhance recruitment is potentially high (see Section 3).

The majority of the literature related to larval export focuses on the larval characteristics of particular species and the oceanographic conditions required to enhance larval movement, rather than reporting evidence of export from reserves and subsequent recruitment. This lack of direct evidence is due to the newness of interest on this topic, and modelling studies are often used to provide support for the role of reserves. One of the biggest obstacles is the cost of acquiring field data on plankton over vast areas of ocean, and few studies have been conducted that relate directly to reserves. Most conclusions are circumstantial, based on combined modelling and limited field observational data. Schmidt (1997) found that larvae in the Caribbean drift for 50 days on average and can settle in an area 1900 km by 800 km, and since larvae may settle in areas far from where spawning occurred, it is presumed that reserves may enhance distant fish populations (Jennings *et al.* 1996, Roberts 1997a). The larvae and peurulus stages of Western rock lobster drift for many months in the Indian Ocean, and since the larvae from all sources are considered to be highly mixed during this long oceanic phase (Phillips 1983, Morgan *et al.* 1982), a few small areas of reserve where adequate breeding stocks were maintained could probably ensure the maintenance of an adequate supply of peurulus to the planktonic stage, and subsequently recruits to the fishery on the shelf reef systems of Western Australia.

Sources and Sinks

Areas that contribute greatly to population replenishment by supplying large numbers of offspring are known as sources, while those that supply few recruits, but accept larvae or juveniles, are referred to as sinks. Conceptually, designs for marine reserves should take account of the need to have reserves in both source and sink areas. Reserves in source areas will potentially be able to export the mainly planktonic larvae of marine organisms to both suitable habitats and fished areas, thereby providing the larval export benefit (Brown & Roughgarden 1995, Lauck *et al.* 1998). Reserves situated in sink areas may be very important in re-establishing connectivity between habitat patches. In time, areas considered to be sinks may ultimately become sources. However, identifying source and sink areas is one of the greatest challenges of reserve design—neither can be easily identified with confidence and there are likely to be many species-specific differences (Rowley 1994, Murawski *et al.* 2000, Roberts 1997a).

Replenishment of populations within reserves may depend on sources outside the reserve, and establishing that a reserve population is self-sustaining is a key issue in reserve design. Carr & Reed (1993) provide a framework under which replenishment of adjacent populations can occur through larval export from reserves. The four models proposed are:

- closed population—protected populations are self-recruiting and replenish themselves only
- single source populations—a single source of larvae supplies recruits to several populations
- multiple source populations—a metapopulation exists where several isolated populations contribute to a common larval pool from which each population is eventually replenished, and
- limited distance population—short planktonic phase larvae with limited dispersal abilities supply proximal rather than distant populations.

This conceptual framework is useful in indicating that, amongst others, the design and best location of reserves will differ depending on the species. An understanding of the mode of replenishment undertaken by focal species is crucial in the successful design of marine reserves aiming to rebuild or maintain fisheries through larval export.

Spawning aggregations and nursery grounds can generally be classified as sources, but many such sites are used by only a single species. Some sites may also alternate between being sinks and sources; a site may be a sink if the conditions for growth and reproduction are poor. Alternatively, if conditions are conducive, the site could also be a source. Because of the species' selectivity of source and sink areas, and highly uncertain knowledge of these influences, the role and placement of reserves in source and sink areas are uncertain, and, except for known spawning aggregations and grounds, the nature of benefits they may bring to fisheries is also uncertain.

Larval Drift

In order to understand the concept of larval drift, it is first important to understand the differing methods of reproduction employed by species. Viviparous species produce a small number of large, well-developed juveniles that disperse only a short distance from the birth site. Other species are demersal spawners and produce eggs that settle to the bottom of the ocean floor and then hatch into planktonically dispersed larvae. Another form of reproduction is broadcast spawning where broadcast gametes are fertilized and dispersed in the planktonic phase. Larvae hatched from demersal eggs usually are more developed than broadcast-spawned larvae when entering the planktonic phase, and more developed larvae will be the first to settle to bottom habitats.

Eggs and larvae of broadcast and demersal spawning species—even coastal or near-shore species—can rapidly disperse over large distances. Isolated oceanic habitats must of necessity be considered as self-recruiting units for many species that have only limited dispersal capacity. Coastal reefs display a high degree of larval natality; that is, larvae are retained and recruitment occurs in proximal reefs. For broadcast and demersal spawners settlement will therefore be greatest in reserves that are either very large in area or have an extensive perimeter relative to adjacent unreserved areas. Otherwise, a network system of reserves will be required to ensure successful export of eggs or larvae between reserved areas. The characteristics of larval export therefore mean that permanently closing whole reefs is unlikely to enhance local reef yields through larval processes alone as the larvae may disperse over tens or hundreds of kilometres (Alcala & Russ 1990).

Long durations of pelagic drift probably increase the distance over which larvae are likely to be spread (Table 8). Sparid larvae have been reported to move up to 70 km offshore and 240 km longitudinally before settling on a reef in the Tsitsikamma National Park in South Africa (Buxton 1996). Although this drift is probably exceptional, larval export is certainly species-specific and depends on a species' life history characteristics. Tegner (1993) attributed the failure of pink and green abalone (*H. corrugata*, *fulgens*) to recolonise depleted areas to their limited larval dispersal abilities, unlike red abalone (*H. rugescens*) which was able to export larvae and successfully recolonise. However, Thompson (1981) argued that the larvae of abalone has the potential to travel to areas outside reserves if the currents are fast enough, given that abalone are broadcast aggregate spawners. The daily minimum ebb and flood currents of 1.8 m/second and 1.5 m/second respectively that occurred at the reserve sites studied in British Columbia were found to be adequate for broad dispersal.

Lipcius *et al.* (1997) argue that a reserve in the Bahamas may be an important source of Queen conch larvae to the surrounding fishable area. The reserve is thought to be a recruitment source for populations north of the reserve in Exuma Sound. Larvae are transported to nurseries in the northern Exuma Cays and Southern Eluethera through an along-shore drift of about 1.5-3 km per day and a meso-scale gyre (Chiappone & Sealey 2000).

Table 8 shows that the planktonic phase of reef fish differs between species, and ranges have been recorded from 14 to greater than 130 days. The longer the planktonic phase of the larvae, the greater the transport potential. The actual distance of transportation of larvae also depends on the hydrographic features of the area, and both the larval characteristics and oceanographic conditions therefore need to be understood to be able to assess how much benefit a specific reserve would contribute to a specific fishery.

Table 8. Planktonic phase of temperate Californian reef fish (adapted from Carr & Reed 1993)

Species	Planktonic drift (days)
DEMERSAL SPAWNERS	
Chromis punctipinnis (Blacksmith)	35 ± 3
Heterostichus rostratus (Giant kelpfish)	14–60
Hypsypops rubicundus (Garibaldi)	20 ± 2
BROADCAST SPAWNERS	
Atractoscion noblis (White seabass)	32 ± 3
Girella nigricansi (Opaleye)	>60
Halichoeres semicinctus (Rock wrasse)	30 ± 4
Medialuna californiensis (Halfmoon)	>60
Oxyjulis californica (Senorita)	39 ± 4
Paralabrax clathratus (Kelpbass)	20–30
Scorpaena guttata (California scorpionfish)	30
Sebastes mystinus (Blue rockfish)	>130
Semicossyphus pulcher (California sheephead)	37–78

5.2.3 Implications for management

Sanctuary location, design and management arrangements are crucial to the efficacy of sanctuaries in providing spillover and larval export to fisheries. Opinions differ about the optimum size, shape and design of sanctuaries; some researchers argue that sanctuaries do not need to cover the entire home range of migrating species, only specific locations like aggregation sites for spawning where individuals are vulnerable to fishing mortality (e.g. Kramer & Chapman 1999). However, Roberts *et al.* (1995) argue that a network of sanctuaries representing all habitats can benefit fisheries along the boundaries of the reserves and even tiny sanctuaries can produce increases in focal species, providing that these are situated in larval source rather than sink areas (Roberts 1997a). Conversely, Barrett (1998) proposes that, as a general rule, if the intention is the conservation of biodiversity, a sanctuary should be approximately ten times greater than the largest home range of the species it proposes to protect. Generally speaking, the available evidence indicates that a network of sanctuaries may be most effective if it includes individual sanctuaries at a range of sizes. This is considered both ecologically desirable and most effective for achieving a range of different management objectives (Attwood *et al.* 1997b).

The collapse of an abalone (*Haliotus laevigata*) metapopulation in South Australia has been attributed to poor sanctuary design relative to the species' recruitment strategy (Shepherd & Brown 1993). Between 1970 and 1990, the density of aggregated local populations fell by 68%, from 37.1 sexually mature abalone (>100mm shell length) per $100m^2$ to $11.9/100m^2$. Although poor recruitment in the late 1970s contributed to a decline in adult numbers, the reason that the metapopulation collapsed was the inadequate size of a sanctuary relative to larval dispersal. Once recruitment failure occurred the distance from other populations (12–15km) in combination with minimal tidal movement (1–4km around the reserve) prevented the local population from recruiting through the dispersal of larvae. Shepherd & Brown (1993) proposed that 40–50% of the potential abalone egg production needs to be protected from harvesting. The design of sanctuaries depends very much upon the individual abalone species, however. For compact populations of *H. laevigata* a few large sanctuaries are expected to maximise larval dispersal benefits. On the other hand, *H. rubra* aggregates in population strings along the coastline, and would benefit from a network of many small sanctuaries. Therefore, to design a sanctuary network based upon source and sink principles requires detailed knowledge of species characteristics, oceanic conditions and recruitment transport and fate.

Some researchers have suggested seasonal closures of areas are needed to protect spawning aggregations. However, this form of protection has been ineffective on a number of occasions, because of the increased level of fishing effort outside closed areas and the targeting of post-spawning aggregations after closures were re-opened, resulting in benefits being lost almost immediately (Halliday 1988, Brown *et al.* 1998, Murawski *et al.* 2000). The positive effects of marine sanctuaries are lost if the surrounding area is not managed effectively, therefore conventional fisheries management should continue to apply outside the reserve (Pollard 1993, Rogers-Bennett *et al.* 1995, McClanahan & Mangi 2000) although clearly, management models need to be adjusted to ensure that the reserve effect is taken into account when setting quotas, gear types, etc. for the fishery.

A further important consideration for sanctuary design is to ensure habitat continuity. The propensity for fish to move is clearly determined by the behavioural characteristics of the particular species. However, in some cases, organisms (e.g. spiny lobster) that are normally highly mobile show an unexpected trend towards residency within sanctuaries, actively choosing to stay within the protection conferred by the reserve (Bohnsack 1996b). Observations such as these indicate how dependant sanctuary design is on existing knowledge of species behaviour, and how such behaviour may be modified by fishing impacts.

In addition, many other factors such as the perimeter-to-area ratio of sanctuaries and habitat availability will also influence fish migration. Continuous habitat inside and outside a sanctuary should facilitate exchange between the two areas. The issue of continuity of habitat is an important one when choosing a sanctuary location designed for increasing the stock available for fisheries. For example, reef fish from the families Labridae and Monacanthidae are deterred from emigrating into areas that require crossing a boundary such as open sand between two reefs (Barrett 1995). Similarly, in another study on a reserve in Tasmania, bastard trumpeter, whilst increasing more than tenfold during five years of protection in a reserve, did not spillover into adjacent areas and remained at near zero levels outside the reserve (Barrett 1998, Barrett & Edgar 1998). The trumpeter were believed to be hindered in their movement by sandy beaches, and so individuals were confined to specific rocky headlands. These two studies indicate that the position of natural barriers, such as open sand, may be important factors in delivery of benefits from a MFS.

The geographic location of a sanctuary may hinder efforts to protect species. Although such temperate reef fishes as labrids, cheilodactylids, pomacentrids, rockfishes, surfperch, and bass are site attached, it is hypothesised that their tendency for year-round residency decreases with increasing latitude due to stress caused by environmental extremes (Barrett 1995). For example, some temperate regions experience vast seasonal variations in water temperature thereby forcing residents out of reefs and into offshore areas. Such environmental changes will interact with the capacity of spillover and larval export to make contributions to fisheries.

Based on data from the tropical coral reef systems of Mombasa Marine Park (Kenya) derived from closing and opening parts of the previous fishing grounds, McClanahan & Mangi (2000) consider that the sanctuaries covering 10 to 15% of Kenya's inshore fishing grounds appeared to be likely to be beneficial. They estimate that highest CPUE has been achieved by reducing the size of the Park to 50% of the total fishing grounds, but they consider that smaller sanctuaries would be more effective in enhancing the inshore fisheries provided that they were based on spillover. Where larval export was also involved, McClanahan & Mangi (2000) speculate that larger sanctuaries (and proportions of available area) would be needed.

McClanahan & Mangi warn that tropical fisheries like the Kenyan inshore fisheries they studied may be supported by fish populations that range well beyond the existing fishing grounds, in waters and depths too difficult for fishing, thus providing a natural refuge. Where these refuges become exploited, using advanced gear or other technology, the inshore fisheries may suffer. The implication is that the inshore fisheries are directly supported by spillover from deeper unfished areas that act as natural refuges for the fishery. McClanahan & Mangi (2000) conclude that sanctuary designs for Kenyan inshore fishing grounds intended to maintain the pre-reserve fish catch will require a careful balance of the extent and location of the fishing area in comparison to the extent of the reserve, and need to take account of a range of biological and fishery management factors.

Design constraints for MFSs will also include oceanographic patterns, as well as the activities allowed 'upstream' from the sanctuary (Allison *et al.* 1998), the incorporation of spawning aggregation sites (Stoner & Ray 1996, Chiappone & Sealey 2000), and possible barriers preventing larval drift. Egg production can be estimated from population structures and spawning behaviour, but the understanding of recruitment-settlement processes is very poorly developed for most species (Roberts & Polunin 1994).

5.3 Biodiversity Conservation Benefits of Marine Fishery Sanctuaries

In this section, we discuss the concept of how marine sanctuaries contribute to biodiversity conservation. We consider the empirical evidence in the categories of habitat, species and genetic diversity.

5.3.1 Habitat recovery

Protection of habitat in a MFS to provide benefits to fished species is also expected to confer benefits to many other (non-fished) species that also use the same habitat. After the implementation of a MFS, conditions in the reserve are expected to change, and a range of non-fished species are also likely to respond to the exclusion of fishing activity.

The community structure of impacted areas generally shows signs of recovery after exclusion of light fishing activity (i.e. one or two trawls a year), although many years are needed before a heavily trawled area recovers (Van Doolah *et al.* 1987, Rijnsdorp *et al.* 1991, Van Doolah *et al.* 1991). Despite the available evidence showing that benthos can return to pre-impact conditions after light fishing pressure within a year or so, the extent to which long term fishing affects seabed habitat, benthic fauna, and fishery productivity is generally not known (Attwood *et al.* 1997b). A detailed experiment of the effects of dredging in Port Phillip Bay suggests that soft bottoms recover after about a year of dredge exclusion. Currie & Parry (1996) report that dredge tracks disappeared after six months and the abundance of most species recovered after their next recruitment, although this recovery is by comparison to other recently fished areas.

In deep areas and on hard substrate, post-fishing recovery appears to be slower or irreversible. A study conducted in northern Tanzania, where dynamite fishing and pull-seines had been used, found that although there was an increased percentage of coral cover following reservation (20% greater), this result was not significant (McClanahan *et al.* 1999). A longer period of protection may be required before there is a marked difference in habitat quality between reserve and non-reserve sites, although one reserve had been protected for as long as 25 years without appreciable improvements. The reef degradation at this reserve also affected reef fish abundance and diversity of grazing and invertebrate-feeding species. A similar outcome was observed in Kenya, where the area protected had been previously damaged by dynamiting and the benefits of the reserve were not realised because the habitat was severely damaged (Samoilys 1988). It may take a number of years, depending on the extent of damage, for habitat recovery to take place and the many benefits of reservation, such as increased density and size, to occur.

5.3.2 Species and genetic diversity

Protecting biodiversity, including species and genetic diversity, means avoiding bycatch of non-target species, destruction of bottom habitat, over-harvesting of marine plants and overfishing of organisms that are, or may be linked to, prey for the focal species. The effects of fishing on species and genetic diversity depend on: (a) the fishing intensity and selectivity; (b) the focal species; (c) whether fishing targets species with important roles in maintaining community structure; and (c) whether the habitats of the taxa are degraded (Dayton *et al.* 1995, McManus 1997, Russ & Alcala 1998b).

Fishing has been strongly implicated with indirect effects on coral reefs. Sea urchins are able to quickly exploit niche openings provided by the fishing mortality of their main predators, such as triggerfish and wrasse. In East Africa, heavily fished coral reefs became colonised by sea urchins, which reduced primary production through over grazing and in turn decreased the abundance and diversity of important reef species (McClanahan 1995). In this case, interspecific competition was considered to be a factor controlling the abundance of species and their alteration by fishing. McClanahan *et al.* (1999) reported a reduced abundance and a change in generic composition in corals at four of five fished sites, which they hypothesised was caused by fishing.

A number of researchers have reported that marine reserves can reverse the decline in species richness and genetic diversity caused by fishing. Whilst studying the effects of a reserve in Kenya, Samoilys (1988) found that although abundance and biomass of target fish species did not increase, species richness was highest in the reserve compared with unprotected areas. A significant difference was observed between the three levels of protection: park, reserve and unprotected. Areas declared national parks (i.e. sanctuaries) had the highest species richness, while unprotected sites had the lowest. Similarly, increases in the species richness of macroalgal species were documented in a Tasmanian reserve and there was also a shift in dominance of the plant species from *Cystophora retroflexa* to *Ecklonia radiata* (Edgar & Barrett 1999). The Leigh Marine Reserve in New Zealand demonstrates the species richness benefits that flow from protection—Cole *et al.* (1990) report that the number of species within the Leigh sanctuary was 60% higher than in adjacent fished areas.

In Belize, a higher species diversity was observed in a marine reserve after only two years of establishment when compared with a heavily fished reef (16.1 versus 14.7 species per observation) (Sedberry *et al.* 1999). The most dominant species in the reserve were the snappers (*Lutjanus griseus*, *L. mahogan*, and *Ocyurus chrysurus*) which were rare outside the reserve. Nassau groupers (*Epinephelus striatus*) were also more abundant in the reserve, along with black groupers (*Mycteroroperca bonaci*) and graysby (*E. cruentatus*). Herbivorous fish, such as surgeonfishes (Acanthuridae), parrotfishes (Scaridae) and coney (*E. fulvus*) were more abundant outside the reserve, suggesting a prey-release effect, which has been found in a number of reserve studies. In these cases, prey fishes are more abundant outside the reserve, where predator densities are low, while relatively high predator densities in the reserve maintain lower, perhaps more 'natural' densities of prey fishes.

In contrast, declines in species richness have been observed in some cases following cessation of fishing pressure. This phenomenon may occur because of variable ecosystem changes or because certain species become dominant and prevent others from increasing (i.e. through predation or competition). Barkai & Branch (1988) found that rock lobsters, which increased in density in a reserve, began to eliminate mussels and other filter feeders. Nonetheless, Barrett & Edgar (1999) argue that there should be an increase in species diversity over a large spatial scale if a marine reserve is present, due to the increased habitat heterogeneity associated with protected and unprotected areas.

Some species are long-lived, slow growing and have a low fecundity (e.g. sharks), indicating that they may have evolved with relatively low rates of natural mortality. Other species are short-lived, quick to reproduce and grow but suffer higher natural mortality rates. Fishing can potentially alter the genetics of the long-lived species as well as their life history characteristics because fishers target the most desirable individuals of a population—the largest and oldest members—and create a selection pressure for faster growers, earlier maturation and a reduced age at first spawning.

Severe fishing mortality potentially alters genetic diversity and can cause a range of effects in fished populations. Effects of fishing that have been suspected to have a genetic component include selection for small size and early maturation, reduction in the age of sex change, selection for late spawning, disruptive selection (resulting from the targetting of a specific time of salmon run), and change (increase and decrease) in allozymic heterozygosity (Smith 1994).

Fishing can cause a loss of genetic diversity as extreme reductions in population size are experienced; this can occur within 6 years, as was seen with orange roughy (*Hoplostethus atlanticus*) populations in New Zealand (Smith *et al.* 1991, Auster & Shackell 1996). Loss of genetic diversity was believed to have occurred because the spawning populations were reduced by 70 percent. A similar situation occurred with Northern cod as there was a dramatic change in age structure with the larger fish virtually eliminated, thereby affecting recruitment and the number of eggs produced (Auster & Shackell 1996).

Growth overfishing (see the Glossary of Terms for definitions) occurs when fishers selectively target older, larger fish resulting in a younger and smaller population. Growth overfishing is particularly detrimental for protogynous hermaphrodite fish, such as red hind, as it can cause sperm limitation during spawning aggregations leading to spawning failure (Beets & Friedlander 1999) and can also reduce the ratio of males to females. Shift in the sex ratio may cause a change in life history traits such as fecundity, survival and size-at-age, potentially altering the pattern by which the population replaces itself (Shackell & Lien 1995).

Recruitment overfishing, conversely, occurs when the most targeted individuals are the breeding stock (due to their older age/larger size) hence creating a decrease in the number of spawners available to sustain a population. Not only does fishing of the spawning population distort the age structure of the species, but it can also reduce the number of fertilized eggs and can even affect the spawning behaviour of fish. It is not clear if these effects result in permanent genetic changes or whether the population would return to normal if fishing pressure is removed or reduced (Shackell & Lien 1995). It is also unclear within what time frame such genetic change operates, what type of genetic variability contributes to population viability (i.e. molecular, allelic, polygenic) and whether genetic variability is important in the regional design of a reserve. Equally uncertain is whether age structure can be maintained in a population whose individuals migrate out of a reserve, or even if reserves can be designed in a way that would fully compensate for the potential genetic effects of size-selective fishing.

Russ & Alcala (1998b) conducted a study to determine whether life history and fishing intensity together could predict rates of decline and recovery of abundance and species richness of reef fish in the presence and absence of fishing. Their information showed that fishing impacts are taxon specific. Fusiliers (Caesionidae) are resilient to fishing because they are abundant, short-lived, fast growing and have high reproductive rates; while Acanthuridae displayed weak effects of fishing on abundance and species richness. However, the Acanthuridae is a family highly diverse in behaviour, size and trophic category, and other studies (e.g. in the Caribbean) have found herbivorous fish to be highly susceptible to the damaging effects of fishing (Hughes 1994, Russ & Alcala 1998b). Anthidae were not affected by fishing in this study, and Labridae did not change significantly in terms of species richness and displayed complex patterns of change in density over time. Mullidae decreased when protected and displayed no significant changes in species richness over time, and Scarids declined in species richness when fishing resumed and density declined, although not significantly. Prey fish that are not targeted by fishers commonly increase in density, usually considered to be a consequence of the decrease in abundance of their predators.

Although there is little data to demonstrate that marine reserves protect genetic diversity by preventing (or compensating for) fishing-induced selection, a number of studies have indicated that this protection might occur. In some cases, sanctuaries have increased reproductive output and genetic diversity by limiting the degree of size selectivity applied by fishing and allowing for 'mixing' between fished and protected populations through spillover (Bohnsack 1996a, Buxton 1996). Marine reserves may thus have an important role to play in preserving community structure, and serve as reservoirs for some of the species that are impacted—either directly or indirectly—by fishing. Shepherd & Brown (1993) showed that the genetic diversity of abalone populations would be enhanced by the correct placement of refuges, subject to appropriate maintenance of connected habitat or intervening populations.

Overall, in order to adequately maintain genetic diversity, and given the large uncertainties in relation to managing the gene pool of a focal species, MFSs should sample faunal provinces, fish assemblages, sediment types, sensitive habitats/spawning/nursery areas (Auster & Shackell 1996). When designing MFSs, an understanding of how oceanographic processes, life history characteristics, and human activities affect the spatial and temporal aspects of habitat distribution is essential (Auster *et al.* 1998). Protection of the gene pool enables fish to respond and adapt quickly to changes in their habitat. Also, separating local fecundity and recruitment reduces the risk of inbreeding depression and genetic drift (Carr & Reed 1993). These conclusions apply also to species that are not directly targeted (such as bycatch species), although generally the nature of genetic protection that would be conferred by MFSs on these taxa is difficult to predict. In Australian reserves, although species richness increases and community compositional changes have been noted, the effects of area protection are less obvious than in overseas reserves, and this is considered to be because the areas set aside in Australia as reserves are too small (Porter, 1999).

5.4 Some Design Issues – size and area

The questions of optimal effective size of a reserve and the total area that should be protected have been widely debated. It has been suggested that 20% of the total shelf area should be closed to fishing in order to maintain stock reproductive output at 30% or more of that of an unexploited population (Plan Development Team 1990). Modelling suggests that even larger reserves (50% or more) are particularly beneficial to heavily exploited fisheries (Roberts, 1997b). Lauck *et al.* (1998) considers that reserves need to include up to 50% of the original population in order to prevent total collapse. Recent approaches to the reserve size question adopt a more flexible approach, indicating that set percentages are difficult to defend on ecological or fisheries grounds, and reserves are perhaps best designed to be a network, using a set of carefully developed design principles (Attwood *et al.* 1997b). The success of no-take reserves for fisheries purposes is considered by many authors to be critically dependent on underlying model structures, assumptions and design issues including size and the specific location of the reserve in relation to life history and dispersal characteristics of the species (e.g. Fogarty *et al.* 2000).

Single large protected areas are thought by some researchers to be the best option as the populations within the reserve will be large, thereby reducing the chance of inbreeding and random extinction (Nilsson 1998). The advantage of having a large marine reserve is that it assists with the problems of protecting migratory species as well as pollution and other indirect problems associated with coastal development. Large reserves also include many types of habitat, have a higher species richness, reduce the need for migration out of the protected area, and large organisms could be protected, which are usually keystone species requiring large spaces (Nilsson 1998). Nonetheless, small sanctuaries can also be highly beneficial, in terms of protecting biodiversity and providing habitat protection; these reserves typically however require intensive management. Sobel (1993) suggests that the two above options should be complementary—small, no-take reserves should be located within large multiple use reserves. Jennings *et al.* (1996) consider that small reserves are advantageous for managers as they can operate without depriving locals of all their fishing ground and are more easily regulated.

Reserves may need to be extremely large in order to be self-sustaining for large species, therefore, a network of reserves which allows movement from one reserve to another may be a better alternative (Ballantine 1999). Allison *et al.* (1998) maintain that reserve networks could provide replicate source populations and increase the potential benefits to non-reserve areas if properly designed (Allison *et al.* 1998). A network of small areas would also be useful as this would preserve more species and habitats per unit area, and better reflect natural genetic variation. Also, many species are dependent on areas that are located distant from each other so a network of reserves could protect particular habitats important for certain life stages. Having several reserves provides protection against the possible collapse of an entire protected area and builds a measure of replication into the reserve system (Nilsson 1998).

There have been few designed empirical studies of the questions surrounding the most effective size for marine reserves. McClanahan and Mangi (2000) consider that an effective size of reserves to enhance the inshore fisheries in Kenya would be about 10 to 15% of the total area, based on studies of landings and research data in Mombasa Marine Park. They recognised however, that these fisheries may also be supported by natural refuges for the fish they studied, in offshore and deep waters where exploitation pressure was limited, and that this may confound their estimates of effective size for reserves. A meta-analysis of data from 73 reserves indicated that reserve benefits (in terms of abundance, size, and weight of focal species, and overall species richness) was not closely related to reserve size, with small reserves achieving a similar range of per area benefits compared to larger reserves (Halpern in press).

6 THE SOCIAL DIMENSIONS OF MARINE PROTECTED AREAS

In this section we consider the social aspects of marine reserves, including issues such as social benefits, stakeholder views, management, and the spatial size and type of reserve.

6.1 Social Benefits

It is well recognised that marine protected areas can only be implemented effectively with the support of local communities (Gilman 1997, NAS 2000). However, few studies have considered the social consequences of declarations of marine reserves, even though there are some obvious potential economic impacts—some positive, others negative. One reason for the lack of information is the newness of the concept and the few known examples available for analysis. Tourism often follows from the creation of MPAs, benefiting coastal communities located near a reserve. However, the increase in tourism may be viewed by the local community as either positive or negative. Positive effects include increased employment, economy and livelihood of the adjacent coastal communities. On the other hand, some people may be opposed to the increase in tourism. In a reserve in New Zealand (Te Whanganui-a-Hei Marine Reserve) most of the community approved of a marine reserve, but others were concerned that the price of land would inflate and that the increase in tourists would change the nature of the town. A major complaint was that the reserve would restrict recreational fishing. In the event, ninety percent of the local community surveyed after the establishment of the reserve supported the idea of more marine reserves being implemented in New Zealand (Cocklin *et al.* 1998).

There are cases where a marine reserve has been documented to benefit a community and the local economy. The marine protected area at Cape Rodney in New Zealand is now a popular tourist destination and contributed greatly to the economy of the coastal town (Porter 1999). Similarly, the Leigh Marine Reserve in New Zealand is an example of how incorporating the community and all stakeholders into the design and management of a reserve can provide benefits to all involved, as well as the ecosystem (Cocklin *et al.* 1998). Many of these stakeholders believe that the reserve has lifted the profile of Leigh and the economy has benefited as the area is now a popular tourist destination. Even commercial and recreational fishermen approve of the reserve, stating that fishing has improved outside the boundary. Local fishers are now very protective of the reserve and are involved in policing any fishing or other illegal activity in the reserve. In contrast, Gribble & Dredge (1994) showed that community tension resulted from the creation of temporary reserves in the Queensland prawn fishery. Seasonal closures of the area are used to maximise yields, mainly for limiting growth overfishing on prawns (*Penaeus esculentus*). Area closures resulted in an increased effort by fishers in the region and movement of non-local fishers into the region aiming to capitalise on increased catches outside the reserves occurring through spillover.

Other uses of marine reserves are also rewarding for local communities and visitors, and recreational marine parks can be used for educational and interpretive purposes, which can encourage support for marine reserves and sustainable fisheries in general (Novaczek 1995). A series of Reef Observation Areas are proposed for the

Abrolhos Islands, Western Australia, as marine reserves for combined fisheries protection and community education purposes (Bunting 2001). Using reserves as educational facilities is useful in promoting an understanding of how the health of oceans can directly or indirectly benefit fisheries as well as the general community.

Tourism and conservation can sometimes conflict if management arrangements are inadequate. When a mutual relationship is formed though, the benefits can encompass cultural, ethical, economic and physical forms (Kelleher & Kenchington 1990). Experience has shown that the success of marine reserves, or any conservation strategy, works most effectively if there is support from the local community. Reserves to which access by the community is restricted, therefore, could prove to be more difficult to implement unless the community is well informed on the benefits the reserve will deliver (Ballantine 1999). Hence, education plays a very important role in the success of any marine reserve implementation.

6.2 Stakeholder Views

There has been much conflict over the development of marine reserves due to the difference in goals and the requirements of different marine users. Some of the views from opposing stakeholders in Australia are discussed below. These are presented as representative views of many such stakeholder groups, both in Australia and overseas.

6.2.1 Reserve Advocates

Many people with strong environmental and scientific views believe that more reserves should be established, with preference given to large no-take areas. Conservationists believe that the benefits to marine biodiversity through the protection afforded by reserves are numerous and that there is a drastic need for areas of the marine environment to be protected because of declining populations of target fish species and habitat degradation caused by fishing practices. Conservationists urge for areas of the ocean to be set aside for protection, as the amount of degradation in the marine environment is difficult to assess due to the invisibility of some impacts (ACIUCN/ANPWS 1991). They believe that there is a growing need for change to fisheries management because of the substantial depletion of many of Australia's (and indeed the world's) exploitable marine species. Many fisheries are overfished or fully exploited and advances in fishing technology are continuing to enhance the exploitation rate (ACIUCN/ANPWS 1991).

Documents produced by environmental groups and government agencies dealing with environmental issues tend to focus more on the potential and actual benefits of reserves to biodiversity and provide little evidence on the social and economic effects, especially as these relate to fisheries (e.g. Gubbay 1996). Such a focus may be entirely appropriate for specific localities and issues, but overall, reserves can only be effectively established and sustained if they have a broad base of support from all key stakeholders that have an interest in the area where the reserves are to be declared. This will always include fishing communities, and many other local users of marine resources, but too often, such communities and interests are overlooked.

6.2.2 Fishing Industry Opposition

In contrast to the beliefs held by conservationists about establishing reserves, there is much apprehension and hesitation by industries such as the seafood industry that rely either directly or indirectly on marine resources. A common complaint by fishers is that no-take marine reserves reduce yields, however there is very little evidence to suggest this occurs (CALM 1999) (but see McClanahan & Mangi 2000). Buxton, reported in the Queensland Fisherman's newsletter (Buxton 1999), considers that the proposed benefits of reserves are 'a little exaggerated' mainly because of the small size of most existing reserves, but that there is also insufficient evidence to show that biodiversity has been threatened by fishing. He considers that the conventional methods of fisheries management will be more likely to guarantee the future of Australia's fisheries.

The Australian Seafood Industry Council (ASIC 1998) believes that MPAs can "add up to a load of trouble for the (seafood) industry", and can be especially disastrous socially and economically if MPAs are badly planned. ASIC considers that MPAs should ensure certainty in employment, have sensible environmental goals, and that there should be less conflict associated with MPAs than in the past if the objectives are acceptable to the fishing industry. ASIC argues that MPAs should be planned and managed on a regional scale with clear and agreed objectives, and no-take zones should be limited and flexible for changing conditions. Also, existing MPAs in Australia should be assessed for their effectiveness, along with social and economic impacts, before new MPAs are established. ASIC believes that if an MPA is ineffective it should be removed or modified, and the fishing and seafood industries should be central to decision making. ASIC also suggests that MPAs be enacted under fisheries management arrangements.

The Tasmanian Fisheries Industry Council (TFIC; Lister 1998) considers that the current management arrangements in Tasmania for rock lobster and abalone (Total Allowable Catch) are adequate and sustainable, and reserves are therefore not needed. In relation to the theory that reserves create an increase in egg production due to increased size of focal species, TFIC considers that the relationship between eggs and weight of lobsters results in slightly fewer eggs produced by a tonne of large females than a tonne of small females (due to the increased number of small individuals in a tonne). This relationship would therefore mean, according to TFIC, that protecting females in a reserve would either maintain current yields or decrease them. Since the larval dispersal mechanism for lobster is unknown, Lister (1998) suggests that it would be safer to protect egg production regionally until there is more research conducted. He doubts that reserves allocated to increase growth will increase yields as effort would have increased elsewhere, thereby resulting in growth overfishing in the fishable areas. He concluded that while it is important to protect lobsters from harvest for the purposes of scientific research, the perceived benefits of reserves to the fishery will occur at the expense of areas outside the reserve (Lister 1998).

In response, Edgar & Barrett (1998) assert that an increase in density of rock lobsters in reserves would result in a density decrease in areas outside the reserve if the reserve was closed to fishing. However, in terms of Total Allowable Catch (TAC), emigration of protected specimens (which are usually about twice the weight of specimens in fished areas) from the reserve into surrounding areas would maintain the TAC and save at least two non-reserve organisms for each emigrated reserve lobster. Rock lobsters inside reserves grow to a much larger size than lobsters outside sanctuaries.

6.3 Management Considerations

In order for MPAs to be used in fisheries management, all stakeholders need to come to a consensus, and further research focused on key issues will help aid this process. Murawski *et al.* (2000) declare that fisheries failures are attributable to significant harvest overcapacity, combined with ineffective enforcement of regulations, little adaptability within management to changing stock conditions, technological improvements in fishing development, and difficulties in addressing allocation issues. It has been suggested that the most efficient fishing technologies such as trawls and seines be restricted, although not banned entirely, and bycatch and discard be minimised (Novaczek 1995). Hastings & Botsford (1999a) produced a model to determine differences in yield between marine reserves and traditional fisheries management and found there to be no difference between the two. They concluded that marine reserves would be a better alternative because of the protection against overfishing afforded by closed areas. In addition of course, there would, at least potentially, be many other benefits that accrued outside the fishing industry, including benefits to sectors such as tourism, and the broader conservation of biodiversity of non-focal species.

It is apparent from the experience of reserve declarations in many countries that community and industry support is essential if conservation and management goals for reserves are to be achieved and maintained on a lasting basis. Therefore, a collaborative management approach is necessary in the development of reserves, with governments, scientists, fishers, conservationists, community groups and marine resource agencies working together (Fiske 1992, Novaczek 1995, Pitcher (ed.) 1997). An example is the proposed La Parguera marine sanctuary in Puerto Rico where fishers felt that they were not included in the management plan development and they did not fully understand the details of the sanctuary and its consequences. One meeting was held in English only, which displeased them further and hence they developed an unswerving resistance to the sanctuary even though restrictions were minimal (Fiske 1992). In contrast, most fishers at St. Thomas are supportive of a permanently closed off area at a grouper aggregation site because of the perceived benefits in increase catch of these fish (Beets & Friedlander 1999). Similarly, fishers supported protection of spawning areas as a management tool at Georges Bank (Murawski *et al.* 2000).

In developing policies, strategies and proposals for MPAs, many countries (e.g. Australia, Sweden, Canada) have taken the approach of incorporating all stakeholders and the general community, and zoning areas into differing levels of protection depending on the objectives of the MPA (Nilsson 1998). The governments of Canada and British Columbia are developing a marine protected areas strategy coordinated across all jurisdictions and including the public in the decision making process, aiming to develop an extensive system of protected areas by the year 2010 (Canada and British Columbia Governments 1998). All the MPAs will protect areas from the damaging effects of ocean dumping, dredging and exploration and there will be multiple levels of protection depending on the objectives for each site.

Western Australia enacted the Acts Amendment (Marine Reserves) Act 1997 that enables the creation of a multiple-use marine conservation reserve system. Petroleum drilling and production, mining, fishing, pearling, aquaculture, tourism and recreation will not be permitted in zones which are highly protected and where such disturbance would be in conflict with the conservation purposes of the zone. The Ministers for Mines and Fisheries must both give their consent before a marine reserve is created or if there are any management changes within an already established reserve (Government of Western Australia 1997).

Considerable attention needs to be paid to many issues if environmental, social and economic benefits from reserves are to be realised. There needs to be a political commitment, effective legislation, comprehensible policies and sufficient funding (Eidsvik 1992, Allison *et al.* 1998). The frequency of surveys, cost effectiveness and degree of adaptability in fisheries management also needs to be addressed (Pitcher (ed.) 1997). When preparing a management plan for MFSs, a register of habitats and species, species range requirements, population stability and sensitivity should all be considered (Ballantine 1991, Eidsvik 1992). Also, the issues of cultural values and of aboriginal rights needs to be addressed to determine whether access for fishing in no-take areas is to be permitted (Pitcher (ed.) 1997). In Canada, aborigines are to be included in the management of MPAs and will be working together with scientists to share information and protect areas of cultural significance. Special consideration will be given to traditional aboriginal activities during the planning and establishment of reserves (Fisheries and Oceans Canada 1998). It is also suggested that stakeholders be adequately compensated, or provided with an alternative form of employment or income generation, if they are displaced and can no longer conduct their activities in the proposed reserve area (Fiske 1992).

Enforcement and sufficient penalties are necessary if MFSs are to work. In the Great Barrier Reef Marine Park, fifty boats per year trawled illegally during a study into reserve effectiveness, compromising research efforts and reducing the contrast between fished and unfished areas (Gribble & Robertson 1998). Large enclosures would be most affected by illegal fishing along the boundaries of the reserve, with little fishing occurring in the centre, whereas small enclosures are much more likely to be illegally trawled throughout the entire reserve (Gribble & Robertson 1998). Murawski *et al.* (2000) found that policing is effective through the use of high levels of ship and aircraft patrol, high penalties for violators, and satellite-based vessel monitoring.

6.4 Issues in Reserve Design

The spatial size of reserves and the type of management necessary to most benefit industry and the environment has been debated by many researchers. Roberts (1997c) and Porter (1999) believe that no-take reserves are more easily managed and work more efficiently than multiple use or zoned reserves. Prideaux *et al.* (1998) agree, stating that reserves should be strictly no-take areas with multiple use areas surrounding them and should be protected foremost for the marine ecosystem. Ballantine (1999) discussed the social benefits of marine reserves in New Zealand. He considers that no-take reserves are more efficient in terms of planning and management than multiple use reserves. Single-use reserves do not depend on detailed information and provide insurance and buffers against management error. He also considers that the public needs time to become accustomed to the idea of a reserve and to be shown examples of reserves in other locations that have worked. It may be more socially acceptable, however, if only certain areas are protected in a reserve and others are open to extractive uses. The Great Barrier Reef Marine Park is zoned into different sections each with different uses. Some of these uses include recreational fishing, conservation, scientific research, and commercial fishing, and the regulation and enforcement of these differs in response to the use permitted within a zone. Permits are used if activities have the potential to harm the reef, conflict with other uses, or need to be strictly controlled in a location (Alder 1993).

It has been suggested that the ideal design of an MPA will rarely be adopted in practice because of the need to satisfy multiple interests simultaneously, resulting in a compromised outcome (Attwood *et al.* 1997b). The reduction in risk to a fishery associated with marine area reservation may encourage their acceptance to otherwise disaffected communities (Holland & Brazee 1996). In fact, a concern has been expressed that future marine reserve successes may be exploited by fishers once initial reservations have been overcome (Hart 1996). It is clear that education of fishers and the broader community about the value of successful MFSs will be a crucial aspect of their ongoing management and sustained success (NAS 2000). The difficulty is the circular argument of having some successful MFSs that can be well documented and used as models for discussion and education within receptive coastal communities.

To conclude, there have not been many documented social benefits of MFSs, but increases in local tourism have been noted, hence benefiting the community and economy. The ocean is regarded as a 'commons' and so management requires a careful integration based on input from all stakeholders. For consideration of marine fisheries sanctuaries, the level of involvement should be equal among stakeholders, including the local community, the tourism industry, fishing industry, exploration industry, and the conservation sector, and should remain equal throughout the whole process from planning to implementation. The size of, and management arrangements for, any MFSs will depend on the planned objectives, which should be decided upon by all participants, to ensure that benefits flow to a broad range of stakeholders including the fishing industry.

7. AN EVALUATION FRAMEWORK

In this section we develop an approach for evaluating the benefits of marine fisheries sanctuaries and suggest a set of indicators and criteria as the basis for assessment.

7.1 Evaluating The Benefits

No-take marine fisheries reserves (MFSs) are rare, and there has been very limited opportunity for fisheries managers to develop operational procedures or measurement systems that can be used to evaluate their benefits. The limited global history and experience with the use of MPAs also means there are no well-tested approaches that can be used 'off the shelf' by fisheries managers to confidently evaluate the benefits of MFSs.

Here, we discuss the issues surrounding the evaluation of sanctuaries for fisheries management purposes, and develop procedures for their evaluation and a generic set of criteria and indicators that are appropriate for any fisheries reserve-related circumstances. The approach (framework) and the criteria and indicators may be used to assess the literature on the performance of marine reserves, in planning a set of fisheries reserves (to help with establishing objectives, and boundaries), to support the development of a performance monitoring program, as part of a management accreditation program, and contribute to the community debate on Ecologically Sustainable Development (ESD) of marine fisheries. A comprehensive and workable model for assessing the benefits of reserves will make an important addition to the toolkit of fisheries managers as they consider how to best assess the role of no-take areas, and where appropriate, conduct trials, and eventually build them into their more traditional fisheries management systems.

7.2 The Approach

Fisheries management is considered here to encompass the concepts of the management of fisheries and fishing in the context of ESD. This is to distinguish it from the simpler concept of management and sustainability of fish stocks alone, which is only one part of the broader concept of ESD for fisheries.

Ecologically sustainable fisheries management involves (amongst others) maintaining target stocks at acceptable levels, and managing fisheries to cause minimal and acceptable damage to non-target species and habitats, either directly or indirectly. Increasingly however, commercial fisheries management policies are being seen to have broader ramifications, particularly in relation to regional economies, rural employment, recreational aspirations, and quality of life matters (see for example Kenchington 1990, Halliday & Pinhorn 1997, Leadbitter *et al.* 1999).

Failures of traditional stock management approaches (e.g. Dayton *et al.* 1995, Larkin 1997, Ludwig *et al.* 1993, Roberts 1997b) have been a major motivation for the consideration of the use of marine protected areas as fisheries management tools in many countries (e.g. Roberts *et al.* 1995, Holland & Brazee 1996, Bohnsack 1996b, 1998). Although in Australia fisheries stocks have perhaps fared better than in many other countries, increasing calls for marine reserves for non-fisheries purposes, as well as concern about more precautionary management of existing fisheries, mean that MPAs have attracted the attention of many stakeholders with an interest in the conservation and uses of marine ecosystems.

Given the objectives of MFSs to protect both fished and non-fished species, MFSs will be evaluated for benefits within two very different contextual settings: first their ability to contribute to stock maintenance, enhancement, or sustainability of the fishery (the 'fishery benefits'); and second, for their ability to contribute to mitigation of the unavoidable environmental impacts of fishing and to the social, cultural, environmental and economic issues of local and regional communities (the 'non-fishery benefits'). In effect, no matter what the express intentions and objectives for a MFS are, they will be evaluated by a range of stakeholders in order to decide how effective they are at achieving a range of outcomes, only some of which will be the primary management responsibility of a fisheries agency (Bohnsack 1998). For example, the effectiveness of a MFS could be evaluated on, amongst others, its contribution to regional conservation goals for highly valued non-commercial species such as seabirds, or a highly valued and sensitive habitat such as coral reefs. These goals might be either explicit or implicit in the identification, selection and management of the MFS, but because marine ecosystems are 'common' property, a range of stakeholders will have a direct and legitimate interest in their conservation and use.

In the first context, sustenance of the stock and the fishery, the evaluation would be primarily managed by the fishing industries and their agencies. Comprehensive strategies are in place to keep track of exploited populations, including routine stock assessments. To evaluate fishery benefits, evaluation of the performance of MFSs could be readily achieved by using traditional stock assessment and fishery indicators, deployed at the appropriate time and space scales to match to fisheries management objectives, and with the addition of some specific indicators especially designed to assess the performance of the individual reserves.

In the second context, the evaluation process is much broader, and involves a wide range of interested stakeholders, including the fishers themselves, their local communities, NGOs, government agencies at a range of levels, and for some trans-boundary fisheries and issues, even international government agencies and NGOs. An evaluation of reserve performance for non-fishery benefits is much more complex, because it will interact with other efforts made to conserve the same elements of biodiversity. Complexities arise when individual jurisdictions develop different indicators and criteria for assessing the performance of a valued element of an ecosystem. Such complexities can be even further compounded if different methods are used to collect data and evaluate indicators within different jurisdictions.

There is, therefore, a critical need for an integrated approach to evaluation of the performance of marine sanctuaries. This includes, but is obviously not restricted to, an integrated approach to identifying criteria and developing appropriate indicators so that the performance of MFSs can be evaluated across the full range of ecosystem-protection and use objectives, including fisheries stock maintenance.

An evaluation of the effectiveness of a reserve should consider the purposes for which the reserve was intended, and evaluate outcomes of the reserve's functions in terms of its objectives. However, reserves established for purely stock management purposes will also have other biological values that are maintained in a purely coincidental (or at least unintended) manner. These additional values may result from objectives for management that are either implicit, or are simply coincidental. In either case, the reserve may have a range of values other than those specific fishery values for which it was originally intended, and overall, a MFS may have broad-ranging social and economic significance in the local area or in the broader region. For many stakeholders these incidental values will be of equal importance to those relating to the focal stocks of importance to the fisheries management system. Recognising these additional, and perhaps coincidental values, could add significantly to the recognition of MFSs as a legitimate strategy for conservation of marine ecosystems, and could assist substantially in gaining broader acceptance of fishing strategies in the wider community.

To be able to evaluate the effectiveness of such reserves against their intended objectives, the processes of reserve design and selection will need to considered, and evaluated to the extent possible, as will the ongoing management activities that relate to the reserve. Without this, characteristics of reserves that meet, or fail to meet, their objectives cannot be identified. For non-fishery benefits, which may be important elements of achieving ESD of fisheries in the eyes of many stakeholders, evaluations should also be based on local and regional conservation objectives for fishing-affected species, habitats and ecosystems.

7.3 Development of Criteria and Indicators

In determining whether MFSs have been (or are likely to be) effective for the maintenance, conservation and management of harvested species and non-commercial species and habitats, their effectiveness should be assessed using a set of criteria and indicators that cover the full range of potential reserve effects and interactions. If reserves are not assessed in a comprehensive manner, there is a significant risk that fisheries might be badly affected by poorly performing reserves, because such reserves convey a false sense of security (Carr & Reed 1993). A full evaluation would cover the extent to which:

- the reserves have been identified, planned and selected to deliver specific management outcomes, and the contribution of specific tools to this process;
- objectives for management of the reserve have been specified explicitly, or implicitly in some other form of statement of activity, and have been achieved;
- the reserves achieve (by coincidence or design) other valued outcomes, such as positive effects on local economies and other sector activities (such as tourism), and the provision of related functions such as support for research to increase knowledge on natural ecosystems or to assess the natural dynamics of ecosystem components; and
- appropriate management strategies, plans and actions are implemented for the reserve, including performance evaluation, security of tenure, control of activities in and around the reserve, compliance assessment, and reporting procedures to stakeholders.

A broad spread of types of indicators will ensure that the contribution of MFSs to regional ESD goals can be quantified, and for new MFSs, they will help to define management objectives that are intended to fulfill a broader role than simply support for the management of harvestable species.

For the purposes of this work we have adopted the FAO nomenclature on indicators of sustainable fisheries, where criteria are (usually) broad statements to guide decisions, with one or more measurable variable termed indicator that will assist to make an evaluation of each criterion. The indicators will usually be numerically based, and should be measurable variables in the context of the evaluation. The indicators and the criteria may be weighted as required for different purposes (such as use in evaluation models), but here we do not consider the use of weights (or specific models) for use in interpreting or evaluating indicators or criteria. These should be developed as required for each specific application circumstance. The indicators can also have target levels attached to them, in the form of reference points. Here, we suggest the direction of change that might be considered to be desirable (i.e. a change for the better), but identifying numeric targets is well beyond the scope of this review. Similarly, there are various systems for synthesis of numeric scores on multiple biodiversity assessment criteria, but such details are not the subject of this review.

We derive here a list of suggested criteria and indicators that can be used to make a comprehensive evaluation of existing or intended fisheries reserves. Evaluation of the performance of actual reserves against criteria and indicators is only feasible by using a system of ranked scores developed *a priori*. Various scoring systems might be applicable in different circumstances, but a generically applicable evaluation could use the following system:

na = not applicable to this reserve or situation
u = unknown situation (missing value)
0 = data not collected to permit an evaluation to be made
1 = condition undesirable
2 = condition slightly undesirable
3 = condition unchanged
4 = condition slightly desirable
5 = condition desirable.

For each indicator, the direction of 'desirable' (the converse of 'undesirable') will need to be defined and specified in detail in each specific application of the evaluation process.

7.4 The Criteria and Indicators

Not all these Criteria and Indicators will apply in all reserves or in all circumstances. This is a comprehensive set from which the relevant and appropriate Criteria and Indicators can be chosen to suit a specific set of circumstances. While not all the Indicators will apply in all reserve circumstances, the Criteria are likely to be used in most circumstances. In some specific cases, there may be alternative indicators that can be defendably used to evaluate the specific Criteria we identify below.

Selection Process (establishes boundaries, sizes, location, network interactions, from a set of previously identified candidate areas)

1. putative objectives developed?
2. selection models—area selection outcomes; scientifically robust?
3. precautionary approaches applied?
4. interactions with other uses/objectives integrated?
5. security of tenure (time and/or space)
6. adequate resources provided for planning activities?

Declaration Process (underpins broad sustainability of the reserve's existence)

7. participatory, to create local and stakeholder ownership of the outcomes?
8. explicit and accountable?

Management Planning (underpins the continued performance of the reserve)

9. management strategies, plans and actions in place?
10. operational goals and objectives in place?
11. participatory development of the management regime and activities?
12. enforcement of regulations, monitoring of compliance
13. appropriate penalties and disincentives agreed and implemented?
14. capacity to change strategies, plans and actions in the light of new information/data?
15. adequate resources provided for management activities?
16. active program of benchmarking management plans and actions?
17. active program of stakeholder education about the values of the reserve?

Performance Assessment Process

18. routine monitoring and evaluation used to assess achievements of goals and objectives?
19. processes underpinning reserve performance actively studied?
20. threatening processes known or being evaluated?
21. part of an integrated system or network of reserves?
22. functions as effective harvest refuge?

Biological Outcomes (after Roberts & Polunin 1991, Dugan & Davis 1993, Guenette *et al.* 1998)

Local Benefits (within the reserve)

Populations of Focal Species

23. enhanced abundance and/or density?
24. enhanced mean age and/or size?
25. natural sex ratio maintained?
26. natural age-size-sex population structure maintained?
27. reproductive output (eggs / larvae) enhanced?
28. spawning stock protected?

Community/Biodiversity

29. areas of undisturbed habitat established/maintained?
30. habitat complexity enhanced?
31. species diversity enhanced?

32. community complexity (e.g. trophic complexity) enhanced?
33. important local ecosystem processes maintained?

Regional Benefits (outside the reserve)

Population of Focal Species (for the stock as a whole)

34. fishery yields enhanced?
35. abundance and/or density enhanced?
36. reserve provides recruitment source through export of eggs and/or larvae?
37. reserve provides source of post-larval stages through emigration?
38. abundance maintained?
39. age-size-sex structure improved?
40. reserve provides insurance against management failures (i.e. stock collapse)?
41. intraspecific genetic diversity protected?

Community/Biodiversity

42. habitat complexity, species diversity and/or community complexity enhanced?
43. important regional ecosystem processes maintained?

Populations of other Targeted Species

44. fishery yields maintained?

Management Outcomes

45. enforcement simplified?
46. ease of public understanding and acceptance of management?
47. provides sites and facilitates multi-disciplinary scientific study of natural ecosystem structure, function and dynamics?
48. defends against non-sustainable development options for the reserve site, by excluding incompatible activities?
49. contributes to integrated ecosystem-based management of marine ecosystems?
50. data-collection requirements reduced?
51. contributes to improved estimates of focal species population parameters (such as natural mortality, population structure)
52. provides sites and facilitates education and training opportunities?

Economic Outcomes Local and Regional Effects

53. local economies augmented?
54. economic opportunities enhanced and diversified?
55. opportunities for employment in local industries enhanced?
56. opportunities for low-impact traditional or subsistence fishing or gathering of natural marine resources enhanced?

Social Outcomes

57. quality of life of the majority of stakeholders, particularly the local communities, improved?
58. social and cultural well-being of local communities maintained?.

7.5 A Minimum Set of Criteria

The objective of selecting a small subset from the criteria above is to provide a means of quantitatively evaluating the biological performance of a Marine Fisheries Sanctuary (or marine park, marine protected area or other form of harvest refugium) using real data that is either already available, or could be collected for a realistic cost. We recognise that, in many fisheries, there is already a substantial amount of available data and information that could be used as the basis for design and declaration of MFSs. However, for the MFSs to function fully in the intended manner, and to achieve fisheries and conservation objectives, the designs of initial reserves may need to be improved to optimise their performance. Here we identify a minimum set of criteria that can be used to determine if a MFS is performing effectively.

The critical issue is whether, for a managed species, a MFS (or other reserve) enhances fishery yields compared to the system without the reserve, and whether it does so in an environmentally and socially acceptable way. Very few direct assessments of this issue have ever been attempted, instead researchers have tried to answer the question indirectly. A marine reserve is expected to enhance fishery yield because it creates a number of changes to the dynamics of the stock. Within the reserve, in the absence of fishing mortality, the recruitment rate, size, age, number and/or density of fish is expected to increase. This is then expected to result in three phenomena that result in the overall enhancement of the stock: spill-over, the movement of 'excess' adult fish out of the reserve; larval export, the net movement of larvae out of the reserve; and stability, an insurance buffer against a failure of management practices or an unpredicted accident or natural event. Spillover and larval export are expected to produce, over time, discernible changes in the stock outside the reserve comparable to those seen inside the reserve, which is expected to result in an increased number of fish being caught, and, ultimately, an increased fishery yield.

However, the benefits of these biological processes may be offset by the aggregation of fishing effort into the peri-reserve district, such effort being either displaced from the reserve or attracted from elsewhere by the potential for bigger yields. Depending on the form of the fisheries management system, this may reduce effort in other areas, or permit increased effort in the peri-reserve area. In either case, the yield across the whole fishery may change as a direct result of the interaction between the reserve declaration and the fisheries management system, and this could happen independent of the biological processes described above. The displacement of fishing effort from the reserve area by the declaration process might also have detrimental effects on other fisheries located in nearby areas, as fishers from this fishery might choose to focus on different target species or different places in the nearby district. The community acceptability of a sanctuary (size, placement, management objectives) will relate to how the declaration of a reserve deals with the question of resource allocation. For example, will the reserve adequately enable other stakeholders (recreational fishers, traditional fishers, conservation) to see biological resources of concern to them equitably allocated; will the reserve create a subsidy for other sectors (such as tourism); or, will the displacement of fishing activity cause economic hardship to a local town.

In considering both the biological and management system issues surrounding marine fisheries reserves, there are five classes of evidence at a minimum that will provide defendable evidence of successful reserve performance for fisheries purposes, and these might be considered as the key benefits that a MFS stands to deliver:

1. enhanced conservation of fishing-affected species or habitats either in or outside the reserve;
2. stock enhancement within the reserve;
3. stock enhancement overall or outside the reserve;
4. improved overall fishery yields; and
5. improved socio-economic outcomes for local communities.

To evaluate these, a large number of indicators could be selected from the complex set of processes that begin within the reserve, produce changes in biological characteristics of the stock within and then outside the reserve, and, ultimately, result in enhanced fishery yields or other reserve benefits (see Section 4 and Section 5). However, below we list the minimum set of criteria, with some suggested indicators, that are considered to be essential to be able to provide adequate evidence of the performance of a MFS (or network of MFSs) in fishery enhancement. The indicators are arranged within 7 criteria, each of which is considered essential for reserve evaluation purposes. As for the broader set of criteria and indicators in Section 7.4, each criterion could be evaluated using a mix of different indicators, and the set below is presented as a suite of indicators from which specific indicators can be chosen to evaluate the 7 criteria within a particular reserve.

The indicators below are not necessarily the best for use in all circumstances, nor will they measure all of the potential benefits of fishery reserves. They also are not adequate on their own for establishing objectives and the planning for new marine fisheries reserves, because they take only limited account of the environmental, social and economic criteria that are important in developing and defending new reserves beyond the criteria of direct relevance to fisheries stocks. Also, all these indicators suffer, some more than others, from the methodological problems discussed in Section 5.1.4. In the circumstances of any specific MFS, the choice of an appropriate set of indicators will always be influenced by the potential for robust data and information to be captured for each indicator.

The minimum-set criteria below are listed roughly according to how close they are to providing direct evidence of fishery benefits that flow from marine fisheries sanctuaries. The indicators are drawn from, *inter alia*, a larger set based on the work of Roberts & Polunin 1991, Rowley 1992, Dugan & Davis 1993, Bohnsack 1998, and Guenette *et al.* 1998.

1. Biological Outcomes—fishery benefits, inside the reserve

- Increased size/age of focal species of fish
- Increased abundance (density) of focal species of fish
- Increased size of spawning stock
- Increased reproductive output at age for focal species of fish

2. Biological Outcomes—fishery benefits, outside the reserve

- Net movement of adult focal species of fish from inside to outside of reserve
- Increased abundance (density) of focal species (across total fishery)
- Increased individual size of focal species (across total fishery)
- Increased yield of focal species, standardised for fishing effort (across total fishery)
- Yields in other fisheries in region/district maintained

3. Biological Outcomes—non-fishery benefits, inside the reserve

- Establishment/maintenance of areas of undisturbed habitat
- Enhanced habitat complexity
- Enhanced species diversity
- Enhanced community complexity (e.g. trophic complexity)
- Improved populations of fishing-affected species

4. Biological Outcomes—non-fishery benefits, outside the reserve

- Maintenance/enhancement of habitat complexity, species diversity and/or community complexity
- Maintenance/enhancement of populations of fishing-affected species

5. Management Outcomes

- Simplified enforcement
- Contributes to integrated ecosystem-based management of marine ecosystems
- Reduced data-collection requirements

6. Economic Outcomes

- Enhanced and diversified local and regional economic opportunities
- Enhanced opportunities for employment in local industries
- Enhanced and diversified regional economic opportunities

7. Social Outcomes

- Maintenance and enhancement of the social and cultural well-being of local communities.

8. CONCLUSIONS

In this section we summarise our findings using the context of three key questions. We also identify some gaps in current knowledge, and make some suggestions for future strategies to resolve these.

8.1 Do sanctuaries help with fisheries management issues?

Sanctuaries could maintain, and possibly improve, economic benefits, but there are no well-documented examples

Several case studies document increases in yield to fisheries as a result of sanctuary creation; they cover a range of fishery types and durations (Alcala & Russ 1990, Bennett & Attwood 1991, McClanahan & Kaunda-Arara 1996, Sluka *et al.*1997). Also, many fisheries are considered to be able to maintain levels of harvest because large proportions of the populations of their target species are effectively isolated from fishing mortality within inaccessible areas that operate as *de facto* sanctuaries (e.g. Beverton & Holt 1957, Davis 1989, Dugan & Davis 1993, Jamieson 1993, Lozano-Alverez *et al.* 1993, Walters *et al.* 1993, Bohnsack 1996a, Walters & Maguire 1996, Ault *et al.* 1997b, Fonteneau 1997, Bohnsack 1998, Levy 1998, Walters 1998). However, there are no well-documented examples where marine fisheries sanctuaries have been shown to provide and maintain net economic benefits for previously existing fisheries. Net benefit is important in the (common) situation where MFSs are intended to be established within existing fisheries, and fishing effort overall is to be reduced or displaced to accommodate the sanctuary. Nonetheless, there are many arguments, and considerable ecological evidence, that indicates that marine fisheries sanctuaries could maintain, and possibly improve, economic benefits, across a whole fishery in the medium to long-term, even though some fishers might be displaced and suffer consequential loss in the process of reserve creation, especially in the short term.

Specific fisheries management measures such as a reduction in total effort may be capable of being implemented efficiently and effectively through the use of sanctuaries, with consequential whole-of-fishery benefits. These benefits however, will be achieved in only some fisheries. Key issues that will determine which fisheries will benefit from sanctuaries include the extent to which the biological benefits can be converted into economic or management benefits for the fishery, and thus depends on the life history characteristics of the target species, the intensity of the harvest regime, the susceptibility of the stock to external factors such as environmental change, and the willingness of fishers to incorporate sanctuaries into their traditional systems of fishery management and respect the controls and rules. Fisheries that stand to benefit most are:

Sanctuaries offer most benefit to fisheries that are over-exploited, harvest high trophic levels, or have big impacts on habitats

- Overfished or on the steep part of the stock/recruitment curve
- Exploit high trophic level, large, highly valued species, or
- Operate where ecological communities or habitats are heavily impacted by fishing operations.

Sanctuaries help to make fisheries management more precautionary and contribute to regional conservation goals

Nonetheless, the exact type and extent of benefits are difficult to predict, and the experience and predictions of many studies indicate that benefits will also depend on local environmental conditions, including oceanographic regimes, and the extent of acceptance of sanctuaries by fishers and local communities.

In addition, sanctuaries appear to be in the unique position of being able to assist traditional fisheries management systems to become considerably more precautionary, and, simultaneously, make a significant contribution to regional conservation goals for marine ecosystems. For species that are not broad ranging or highly migratory, and are affected by fishing gear, discards, trophic disruption, and bycatch effects, or other aspects of fishing, sanctuaries will form highly effective refuges. Such refuges will be especially important for those species whose 'natural' refugia have been recruitment overfished, or eliminated, or are at risk from refugia reduction through such factors as technology creep or coastal development. Reducing the impacts of fishing, by providing areas where species, assemblages and habitats that are affected by fishing can recover, and be conserved, will also assist a fishery in meeting broader obligations under the National Strategy for Ecologically Sustainable Development, the National Representative System of Marine Protected Areas and Australia's Oceans Policy.

8.2 What are the non-fishery benefits of fisheries sanctuaries?

Sanctuaries assist with biodiversity conservation by providing refugia for many species and reducing impacts of fishing on habitats

Sanctuaries that are designed to assist with fisheries management will also confer benefits on a range of non-commercial species. The nature and extent of these benefits will depend on the design of the sanctuary, but particularly on the nature of the focal species and its management system (because this will dictate the design, location and management system for the sanctuary), the effects of fishing, and the nature of the habitats the focal species normally occupy. Fisheries sanctuaries will assist with reducing the local effects of fishing, such as the direct damage of habitats by gear, the impacts of fishing on non-target species (diversity, size structure, life history traits), and trophic interactions (predator removal, prey removal, species replacement, scavengers and discards). Although the nature and extent of such local benefits are difficult to predict, many authors (such as NAS 2000) consider that sanctuaries will also assist to minimise the broader regional effects of fishing, provided sanctuary design and management is appropriate and fisheries impacts in non-reserved areas are managed in a manner consistent with the objectives of the sanctuaries.

Valuable for tourism, recreation, training and scientific research, and national biodiversity conservation

Fisheries sanctuaries are also likely to offer a range on non-biological benefits for local and regional economies. These include opportunities for non-destructive forms of tourism; recreation (such as nature appreciation and selected types of recreational fishing); education, research and training; and the indirect benefits these activities bring to local communities. In some locations, MFSs will also offer the opportunity for co-management with aboriginal owners and artisanal fishers to conserve their customs and traditions.

The non-fishery benefits conferred by sanctuaries are likely to make an important contribution to the conservation of biodiversity in Australia's jurisdiction because at present there are few reserves in the National Representative System of Marine Protected Areas (NRSMPA) that meet the criteria for a MFS. A well designed system of MFSs would meet the highest protection criteria of the NRSMPA, and could assist a jurisdiction to meet marine conservation goals for its region, depending on the scale of the fishery and the design of the sanctuaries.

8.3 How can sanctuaries deliver benefits?

Sanctuary benefits are delivered mainly through spillover and larval export

The two main processes for delivering benefits from fisheries sanctuaries are spillover and larval export. Spillover of juveniles or of target-sized fish will most likely benefit fisheries near the boundaries of sanctuaries, while larval export is more likely to deliver more broadly-based benefits, as larvae or other propagules are distributed widely into available settlement habitat. These benefits would be most extensive in fisheries that are overfished, and will depend on their stock-recruitment situation

Sanctuaries help to protect against management failures

Sanctuaries that are effective are also likely to confer considerable stability on fishing management systems, by reducing and spreading the risk of overfishing, environmental impacts on the fishery, or inadvertent failures of the management system. This benefit could be expected in all fisheries, not just overfished ones. Increasingly, fisheries are seeking to implement more precautionary management systems, and many authors consider that sanctuaries are an important opportunity to hedge the bets within a management system that has to deal with a number of substantial uncertainties.

Marine Fisheries Sanctuaries may be able to achieve their fisheries objectives as well as support a range of non-consumptive uses. Such uses, which may have high local value, may include some forms of recreation, tourism, education, research and training. Biodiversity benefits are conferred on the non-commercial species conserved in the sanctuary, and like fishery benefits, these might flow to areas outside the sanctuary, depending on the species and the precise nature of the reserve and the surrounding habitats.

A systematic approach to design of sanctuaries is essential

In order to optimise the range of benefits captured from sanctuaries, it seems most likely that in each fishery, networks of sanctuaries will be required, and that they will need to comprise a mix of large and small areas, strategically designed and located to maximise specific benefits. While there is no general agreement on a model for how such networks should be designed, it is clear that different species and habitats will have a range of spatial requirements, that for many, is variable through time. There is thus no clear consensus amongst authors on required sizes or locations of MFSs, but a range of sizes spatially allocated for different reasons will minimise the risk that the full range of spatial scales and habitat types that may be important to the fishery are not represented in the sanctuaries

8.4 Gaps in the evidence

Need to build on existing knowledge in 7 key areas

The information we have reviewed indicates that implementation of sanctuaries is likely to make an important contribution to the conservation of a focal species. Generally speaking, such sanctuaries could be designed and implemented in many fisheries now, with little additional knowledge beyond that already available. However, to optimise their success, and to enable other fisheries to learn from those experiences, we consider that there is additional knowledge that will make the process of designing and implementing

MFS in Australian fisheries more efficient and effective in the future. This need to build on existing knowledge is in 7 key areas; the first five are related directly to fisheries management systems, while the last two are crucial aspects of ecological knowledge.

1. A detailed understanding of the stock-recruitment relationship for the focal species, and what the variation in that relationship in space and time means to achieving benefits from a MFS system. Without a detailed understanding of how recruits to the fishery provide net economic benefit to fishers, it will be extremely difficult to design and locate MFSs that are completely effective.
2. Documented experience about the extent to which MFSs reduce the risk of fisheries collapse caused by environmental stresses, failure of the fisheries management system, or mis-management of the fishery. While protection from these factors are widely cited potential benefits of sanctuaries, and difficult to implement in other ways, there are no well-documented examples that can be used as the design basis for new MFSs.
3. Documented experiences on the response of fishers to the design and establishment of MFSs intended to assist with the management of their fishery. Many MFS benefits are likely to be realised in the medium and long-term, but fishers are subject to short term economic imperatives that may force them to trade-off the recognised long term benefits for short term survival. Documented experiences of the process of design and implementation of MFS that focuses on the behaviour of fishers in relation to MFS issues is crucial to enable efficient future sanctuary declaration processes and to minimise economic and social disruption to local communities. As summarised by the US National Research Council (NAS 2000): "MPA proposals often raise significant controversy…" "The controversy persists because we lack a scientific consensus on the optimal design and use of reserves and we have only limited experience in determining the costs and benefits relative to more conventional management approaches."
4. Empirical measurements of the benefits that are realised by an Australian fishery from the implementation of a network of MFSs, and supporting evidence of the processes responsible for delivering those benefits. This would involve knowledge based on a detailed assessment of such matters as catch, effort, costs, profits, resource allocation, compliance, employment in local communities, and indirect socio-economic impacts in local and regional communities.
5. The lack of explicit procedures and models for identifying which fisheries will benefit from MFSs, and experience with designing and implementing Australian MFSs that are optimised across the range of competing objectives of the range of stakeholders. This is particularly crucial to ensure that benefits for fisheries are considered in the light of the range of broader benefits that may accrue to other interests.
6. Knowledge about the ecological processes within an MFS that underpin larval export or spillover. Uncertainty about the extent to which spillover or larval export contribute to recruitment into the fishery make predictions about sanctuary improvements highly complex. Knowledge of how sanctuaries deliver benefits to fisheries is crucial to ensure that complementary stock management tools (such as quotas or effort allocation) are correctly applied taking into account the way in which the reserve contributes to the fishery-wide returns. Much existing information is based on knowledge derived from fishing grounds, but species may have very different characteristics in non-fished areas, and this will affect the way in which sanctuaries operate. The key processes include the interactions between the focal species and predators or competing species, both within and outside the sanctuary.
7. Detailed knowledge of the larval export characteristics of the focal species in fully exploited and over-exploited fisheries. Without this process-based knowledge, the potential for MFSs to contribute to more precautionary management systems for the focal species will be difficult to assess with any certainty. Likewise, it will be difficult to assess the potential for sanctuaries to maintain or improve stock sizes/yields in fished areas. Also, MFSs intended to assist such focal species may be incorrectly designed, located or managed because they are not matched to the needs of dispersal and settlement of propagules of the focal species. Critical areas of knowledge include the relationship between the species' dispersal characteristics and the hydrographic regime, and the interaction between that relationship and the design, placement and number of reserves.

8.5 The future

Benefits will be broad-ranging and extend beyond the fishery

Marine fisheries sanctuaries have many theoretical benefits for fisheries, but they are as yet poorly documented. The specific benefits that an individual fishery stands to gain cannot be predicted without a detailed knowledge of each fishery and careful design of each reserve set, but it is clear that benefits are likely to be broad-ranging and extend beyond the fishery itself.

Although the fishery benefits are not well documented and are difficult to predict precisely, non-stock benefits are perhaps easier to identify. The benefits for regional conservation goals, non-consumptive activities such as tourism, recreation, local employment, and baseline research, are likely to be substantial. The extent to which these non-stock issues are recognised and promoted will support attempts by a fishery to demonstrate its ecological sustainability in both stock and non-stock issues.

Benefits will need to be assessed, documented and promoted

It appears therefore that MFSs may be able to deliver a broad range of benefits, including to the fishery itself. However, the major challenge is to identify specific approaches and design methodologies that will produce reliable MFSs that achieve these benefits. In order to achieve maximum benefit for implementing MFSs, considerable effort will also be needed to document and promote the benefits to ensure that the fishing industry is properly recognised for its role in managing marine ecosystems in an ecologically sustainable manner. The important elements in this process are the careful and systematic design, identification, selection, management and monitoring of MFSs. We recognise that MFSs can be designed and implemented now in concert with other fisheries management tools, and in many fisheries this could be based on existing knowledge. However, we consider that this should be based on a systematic analysis and design process to ensure that, even though such MFSs may initially not be fully optimised, they will nonetheless function effectively in their early years to provide net benefit for fisheries. Without this, MFSs risk losing the confidence of fishers and fisheries managers. The design and implementation of effective MFSs will therefore have a high initial cost for the establishment phase, but routine fishery-wide management costs are likely be lower than at present, and environmental conflicts reduced because of the existence of demonstrated evidence of sustainability.

Fisheries sanctuaries will make an important contribution to marine conservation goals and fisheries management

Implementing networks of sanctuaries for fisheries purposes in Australia appears to provide the capture fisheries sector with an opportunity to demonstrate its leadership in marine conservation, and to confirm its commitments to the principles of precautionary management and to the practice of ecologically sustainable development.

Appendix 1

Summary of the Empirical Evidence for the Effect of Reserves on Focal Species

Taxa/locality	Abundance	Age & size	Fecundity	Reference source
FINFISH				
Red hind Virgin islands	Equivocal results	Increased average length; sex ratio normalization	Not reported	Beets & Friedlander 1999
Common fish assemblage South Africa	Key species recovered to non-exploited abundance levels in 4 years	Species protected by reserve attained non-exploited size	Not reported	Bennett & Attwood 1991
Galjoen South Africa	Catch rates (CPUE) within a marine reserve were at least double the CPUE outside	Not reported	Not reported	Bennett & Attwood 1993
Sparids South Africa	Abundance higher in reserve than in a similar but fished area	Average size and maximum size greater in reserve	Not reported	Buxton & Smale 1989
Sparids South Africa	Not reported	Size greater in reserve than in surrounding areas	Not reported	Buxton 1993
Grouper Bahamas	Nassau grouper more abundant in reserve; abundance non-target grouper greater in fished areas; higher spp. richness in reserve compared with outside	Higher mean size and biomass of target spp. of grouper in reserve; sig. greater densities of larger grouper spp. in reserve	Grouper more sexually mature in reserve; greater egg production of Nassau grouper	Chiappone & Sealey 2000
Reef fish Red moki, snapper, blue cod New Zealand	No clear trends in fish abundance	Larger snapper generally more abundant inside reserve	Not reported	Cole *et al.* 1990
Assemblage (41 fish spp) France	Equivocal results – no clear patterns in abundance of species	Large individuals significantly more populous inside reserve	Not reported	Dufour *et al.* 1995
Bastard trumpeter, ling, marble fish, draughtboard shark Tasmania	Sig. increase in abundance of fish in all but one reserve; increase of trumpeter in largest reserve; no increase in density of fishes at smallest reserve; increase in spp. richness in largest reserve	Large fish increased sig. in abundance over the years in reserves	Not reported	Edgar & Barrett 1999
Coral grouper Great Barrier Reef	Not specified	No significant difference in age and size structure between areas	Not reported	Ferreira & Russ 1995
Reef fish Seychelles	Spp. richness higher in highly protected reserves	Biomass in highly protected reserve sig. greater than in less protected areas	Not reported	Jennings *et al.* 1996
Littoral fishes Western Mediterranean Sea	Declines in abundance of juveniles in all three spp. after settlement both in and out of reserve	Not reported	Not reported	Macpherson *et al.* 1997
Common fringing reef taxa Kenya	Density and diversity 2x greater in reserves than outside; increase in spp. richness in reserve	Not reported	Not reported	McClanahan 1994

Summary of the Empirical Evidence for the Effect of Reserves on Focal Species

Taxa/locality	Abundance	Age & size	Fecundity	Reference source
FINFISH				
Eight families of reef fish Kenya	Density of fish 5 to 10 times higher inside protected areas	Not reported	Not reported	McClanahan 1997a
Reef fish Kenya	Poor recovery of fish in reserve (due to sea urchin abundance)	5 fold increase in total fish wet weight	Not reported	McClanahan 1997b
Reef fish communities Africa	Overall increase of fish abundance in reserves	Fish biomass 3x higher in reserve than outside	Not reported	McClanahan *et al.* 1999
Reef Siganidae, Acanthuridae, Lethrinidae Kenya	Increased abundance in fished areas adjacent to reserve	Increased size of fish in catches from areas adjacent to reserve	Not reported	McClanahan & Mangi 2000
Groundfishes New England	Abundance of groundfishes increased after reservation	Not reported	Spawning stock biomass increased after reservation	Murawski *et al.* 2000
Baldchin groper (wrasse—*Choerodon rubescens*) and coral trout (*Plectropomus leopardus*) Abrolhos Islands, Western Australia	In reserves: between 8 and 16 fold estimated increase in densities of *P. leopardus*; possible increase in *C. rubescens* density of large fish	All size classes of *P. leopardus* increased in reserves	Not reported	Nardi *et al.* manuscript
Reef fish California	Density of fish 12% & 35% greater at 2 reserve sites than non-reserve	Average lengths sig. greater at 2 reserve sites protected the longest (1yr reserve did not differ sig.); biomass >2x higher in reserve than non-reserve sites (no diff. in 1yr reserve)	Reproductive output greater for reserve sites but similar in 1yr reserve	Paddack & Estes 2000
Lincod and rockfish Puget Sound	Higher abundance of rockfish and lincod at reserve	Significantly larger lincod and rockfish; large rockfish not often observed in harvested sites	Egg production increased by many orders of magnitude inside reserve	Palsson 1997
36 families of tropical reef fish West Indies	25 of 36 recorded taxa more abundant inside reserve	18 of 24 recorded taxa were of larger mean size inside reserve	Not reported	Rakitin & Kramer 1996
Snapper, grunts St Lucia	Not reported	Biomass of fish inside reserve more than double that outside; predator biomass 4 x higher in reserve than outside	Not reported	Roberts & Hawkins 1997
Groupers, parrotfish, snappers, surgeonfish Red Sea	One grouper species more abundant in reserve; mixed results for other species	One grouper species an average of 14cm longer within reserve; equivocal results otherwise	Not reported	Roberts & Polunin 1992

Summary of the Empirical Evidence for the Effect of Reserves on Focal Species

Taxa/locality	Abundance	Age & size	Fecundity	Reference source
FINFISH				
Grunts, snappers, groupers Belize	Not specified	Biomass of commercially important fish 8 x higher in centre of reserve compared with outside	Not reported	Roberts & Polunin 1994
Perch, snapper, cod Philippines	Large predators were 9 times more abundant within reserve than in adjacent areas outside	Biomass of predatory fish increased 8-fold following reservation	Not reported	Russ & Alcala 1996a
Reef fish Philippines	Total community density not sig. affected by fishing; higher total density after 9yrs protection; increase spp. richness during periods of fishing exclusion	Biomass increase by factor of ≈1.56 over 6–9yr period	Not reported	Russ & Alcala 1998a
Coral trout Great Barrier Reef	Density of trout inside reserve tripled in 3.5 yrs due to removal of fishing and recruitment pulse	Legal size coral trout increased 400% before reserve was reopened to fishing	Not reported	Russell 1997
Reef fish Kenya	Fish no more abundant in reserve, density same in reserves as outside (reef degradation in some parks, illegal fishing); higher spp. richness in reserve than outside	Average size and biomass of Serranids was greater at less fished site, otherwise no difference in biomass between protection levels	Not reported	Samoilys 1988
Goby Mediterranean	Not reported	Fish inside marine reserve notably larger than outside	Not reported	Sasal *et al.* 1996
Nassau groupers Bahamas	Obvious increase in abundance of groupers inside reserve	Three times as many mature groupers (>50cm) inside reserve compared with outside	Reproductive capacity six times higher inside park than outside	Sluka *et al.* 1997
Grunts Barbados	Abundance of trappable grunts sig. higher in reserve	Size of trappable grunts sig. higher in reserve; overall biomass of grunts sig. greater in reserve	Recruitment of juvenile grunts sig. lower in reserve; inverse relationship between predator density and recruitment; post recruitment mortality of grunts	Tupper & Juanes 1999
Nine major families of fish New Caledonia	Sig. increase in overall density at reserve after 5 yrs; spp. richness increased in reserve after 5yrs	In-reserve biomass more than doubled after 5yrs (outside biomass unchanged); increased proportion of small fishes after 5yrs protection	Not reported	Wantiez *et al.* 1997
Coral trout Great Barrier Reef	Density of trout within reserve 20% higher than outside	Not reported	Not reported	Zeller & Russ 1998

Summary of the Empirical Evidence for the Effect of Reserves on Focal Species

Taxa/locality	Abundance	Age & size	Fecundity	Reference source
SHELLFISH				
Queen conch Bahamas	Sig. greater density of conch in reserve	Not specified	Larval densities of conch highest ever recorded in reserve	Chiappone & Sealey 2000
Sea urchins and rock lobster New Zealand	Sea urchins 20% more abundant inside reserve than outside; striking increase in abundance of rock lobster within reserve	Mean size of snapper and rock lobster greater in reserve than outside	Not reported	Cole *et al.* 1990
Spiny lobster *Jasus edwardsii* New Zealand	3.9% increase in shallow (<10m) sites and 9.5% increase in deep (>10m) per year of protection	Mean size increased by 1.14mm per year of protection in reserves; mean biomass increased by 5.4% per year of protection	Egg production increased by 4.8 and 9.1% per year of protection for shallow and deep sites respectively	Kelly *et al.* 2000b
Rocky infratidal macrofaunal assemblages South Africa	Higher abundance of 7 spp. in reserve compared with non-reserve	Biomass higher for some spp. inside reserve compared with non-reserve; many spp. found only within reserve	Not reported	Lasiak 1998
Spiny lobsters New Zealand	Spiny lobsters 3 to 50 times more abundant within reserve	Large individuals predominant inside reserve; biomass up to 10 times greater inside reserve	Not reported	MacDiarmid & Breen 1993
Sea urchins Kenya	Sea urchin decreased in reserve through predation	Not specified	Not reported	McClanahan 1997b
Atlantic sea scallop New England	Abundance of scallop increased following reservation	Biomass of scallop increased 14-fold in closed area after protection	Not reported	Murawski *et al.* 2000
Queen conch Bahamas	Adult density inside reserve up to 15 times greater than fished area	Increase in size not related to reservation	Larvae an order of magnitude more abundant inside reserve	Stoner & Ray 1996
Northern Abalone Vancouver Island	Abalone less abundant in reserve, densities lower than pre-exploitation levels as reserve area was not self-recruiting	Abalone significantly larger and older in reserve	Reserve area 1.2x and 1.4 x as fecund as two harvested areas	Wallace 1997
Abalone British Columbia	Equivocal results	Oldest reserve sig. larger abalone	Fecundity greater in enforced reserves than coast-wide reserve	Wallace 1999

Appendix 2

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Beets & Friedlander 1999	*Epinephelus guttatus*	Coral reef off St. Thomas, U.S. Virgin Islands (protected for 7 yrs); 48km²	Snapshot before and after study; visual census using transect and video transect, also angling samples; previous study (10yrs earlier) data obtained from fishers	Average length of red hind in reserve increased 70.7mm after 7yrs of protection; sex ratio skewed 15 females/male before closure, changed to 4 females/male after 7yrs of protection; abundance varied considerably throughout monitoring period
Bennett & Attwood 1991	Surf-zone species *Coraciuns capensis* *Diplodus sargus* *Diplodus cervinus* *Lithognathus lithognathu*, *Rhabdosargus holubi* *Sparodon durbanensis*	De Hoop Marine Reserve, South Africa; 46km long sandy beach and beach rock platform; patch rock	Exploited site survey from 2 yrs before reserve to 4.5 yr after reservation; non-exploited site monitored 2.5–4.5 yr after protection; samples collected by angling	Catch per unit effort of key species increased to and stabilised at 90% of CPUE recorded at unexploited site; slight increase in mean size of fish
Bennett & Attwood 1993	*Coracinus capensis* *Diplodus sargus*	De Hoop Marine Reserve (South Africa); 46km long sandy beach and beach rock platforms; patch rock	Two sites monitored by shore angling over time frames ranging from -2 yrs to 6.5yrs and 2.5 to 4 yrs protection	Reserved sites returned mean angling CPUE of 233 and 163 fish/hr; other non-reserve studies report 7 to 150 fish/hr
Buxton & Smale 1989	Sparids *Chrysoblephus laticeps* *C. cristiceps* *Petrus rupestris*	Tsitsikamma Coastal National Park (South Africa); 60 km long, 5 km seaward boundary for most of length; closed to fishing for <20 years	Comparative evaluation with a physiographically and biologically similar but exploited site 150 km east of the Park. Survey restricted to shallow component (<35 m) of species depth range	Abundances of *C. laticeps* and *P. rupestris* were significantly higher in reserve (0.025 and 0.013 m–² resp.) than at fished site (0.006 and 0.001 m–²)
Buxton 1993	Sparids *Chrysoblephus laticeps* *C. cristiceps*	Tsitsikamma Coastal National Park (South Africa)	Creel census of recreational catch in areas (several hundred km) surrounding the Park, compared to fish caught during research fishing conducted in the Park	Proportion of males significantly reduced in fished areas compared to reserve; the mean size and size distribution was greater in the reserve.
Castilla 1996	*Concholepas concholepas* *Loxechinus albus*	1–2 km² reserves (Chile) fished on a 2–4 yr rotational basis	Inside-outside contrast studies over five years; CPUE and visual census using transects inside (when fishing banned) and outside reserve	CPUE of gastropods 91–540/hr inside reserve (15–143 outside); sea urchin CPUE 409/hr inside reserve (129 outside)

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Chiappone & Sealey 2000	Serranidae, *Strombus gigas.*	Exuma Cays land and Sea park, Bahamas; closed to all types of fishing in 1986; covers 442km²; diversity of contiguous shallow-water habitats	Studies comparing reserve (after 4yrs reservation) and adjacent unprotected areas; visual census using transects, plankton tows, and also towing snorkeler behind boat (counts)	Greater spp. diversity, density, biomass, potential reproductive output, and larval densities for fishery target spp inside reserve; overall grouper spp. 35% sexually mature in reserve, (average 11% at other sites); Nassau grouper - 4.5-7x greater egg production in reserve, 2x as abundant and biomass 3x larger in reserve; other spp. greater biomass in areas outside reserve (prey-release effect); higher abundance of conch larvae in reserve; juvenile aggregations of conch covered nearly 4% of bank area surveyed, 1.6% at another site
Cole *et al.* 1990	Reef biota — *Pagrus auratus* *Evechinus chloroticus* *Parapercis colias* *Jasus edwardsii*	Leigh Marine Reserve (New Zealand) 4km long and 800m offshore, comprising rock habitat and kelp forests at depths greater than 10m	Longitudinal study from 1976 (when reserve declared) until 1988; inside-outside contrast undertaken in 1988; visual census using transects (fish) and quadrats (shellfish)	Red moki increased over 6yrs in reserve; other spp. showed no clear trend with time (study design issues, protection effect already in place, migration); sea urchin density 6/m² inside (5 outside) modal snapper size 20–40cm inside reserve (10–30cm outside); higher density and mean size of rock lobster inside reserve compared with outside
Dufour *et al.* 1995	*Diplodus sargus* *Diplodus vulgaris* *Mullus surmuletus* *Scorpaena porcus* *Oblada melanura* *Symphodus tinca*	Banyuls-sur-Mer Reserve (France) 15km² coastal reserve, rocky and sandy bottom	Comparison of visual census data gathered in 1992 with 1980 data; contrasting reserve and non-reserve	Six of 35 species more abundant inside reserve in 1992 than 1980; 9 species more abundant outside (prey-release effect); larger *D. vulgaris* specimens (>28cm) inside reserve

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Edgar & Barrett 1999	Reef biota — *Latridopsis forsteri* *Jasus edwardsii* *Notolabrus tetricus* *Haliotis rubra*	Maria Island Reserve— 7km length, Tinderbox Marine Reserve – 2km, Governor Island and Ninepin Point Marine reserves –1 km; reserves 7 mths old (Tasmania); shallow reef ecosystem	Visual census using transects and quadrats comparing reserves with adjacent unprotected areas and temporal changes within reserve over 5 yrs	Overall 243% increase in abundance of fish between fished and unfished areas; 2 orders of magnitude increase in abundance of trumpeter (absent outside reserve); sig. increase in abundance of rock lobster at largest reserve (260% inside and 12% outside reserve); biomass of rock lobster over legal size increased over 20x in 5yrs; fish >300mm increased in abundance and <300mm decreased at 2 largest reserves over time (unchanged outside); mean abalone size increased sig. at largest reserve from 128mm—136mm shell length; increase in spp. richness in largest reserve
Ferreira & Russ 1995	*Plectropomus leopardus*	Glow, Yankee, Hopkinson and Grub mid-shelf reefs (~4km²)100km offshore Townsville	Two open and two closed reefs sampled by angling twice annually 3 and 4 years following area protection; age determined from otoliths and gonads	Mean coral grouper size 44cm inside reserve (42.5cm outside); mean age in reserve 6.3 yr (5.5yr outside); sex ratios not sig. different between protected and unprotected sites
Jennings *et al.* 1996	Reef fish communities 16 families, 115 spp.	Seychelles – Inner Seychelles Group; 4 reserves established for <15yrs with varying degrees of protection; fringing coral reef and granitic reef	Visual census (random point counts) comparison of reserves with differing protection	Spp. richness of many families and communities higher where protection was greater; biomass 40–60% higher at most protected areas than less protected areas
Kelly *et al.* 2000b	Spiny lobster *Jasus edwardsii*	New Zealand; 4 reserves and nearby areas in north-eastern NZ; rocky reef and adjacent sand habitats; reserves of different sizes; protection from 3 to 21 years.	4 reserve and 4 control locations 2 sites in each location 2 depths in each site 5 visual transects in each depth	Reserves show increased abundance, larger individuals, higher biomass, and higher egg production; most of these greater effect in deeper water than in shallow.

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Lasiak 1998	Rocky infratidal macrofaunal assemblages	Mkambati, Hluleka and Dwesa nature reserves stretching 273km in Transkei, South Africa; protected since late 1970s; gently sloping rock platforms, strong wave action	Multivariate comparisons of samples collected with hammers and paint scrapers from random quadrats in several replicate shores situated within and adjacent to 3 reserves	Marked differences in community structure between reserves and exploited sites; biomass higher for a bivalve spp., a barnacle, a sea anemone, an opisthobranch and a chiton; higher biomass, or only found, in reserve: 9 molluscs, 2 echinoderms, 2 barnacles, a sea anemone and a crab; higher average abundance of 4 sessile species, 3 small grazers, lower average abundance of small phytal-associated spp. in reserve
MacDiarmid & Breen 1993	*Jasus edwardsii*	Leigh Marine Reserve (New Zealand); shallow (<10m) habitat of bedrock and tumbled boulders surveyed	Marine reserve sampled irregularly for 14 yrs following protection; compared to five outside sites; visual census using transects and quadrats	Lobsters <100mm comprised 90% of size classes inside reserve (outside ~36.5%); in-reserve biomass 4400–8481g/m² (outside 163–1192g/m²)
Macpherson *et al.* 1997	*Diplodus puntazzo* *Diplodus sargus* *Diplodus vulgaris*	Mediterranean coast off Spain, France and Italy. 8 protected, 13 unprotected sites located where settlement occurs; different habitat types	3yr study—3 settlement / post-settlement events; visual census (counts)	Mortality rates of juveniles in reserves did not differ sig. from unprotected areas after settlement (density-dependent mortality)
McClanahan 1994	Species grouped into eight families of common fish	Malindi, Watamu, Kirstie and Mombasa MNPs (Kenya); shallow fringing reef lagoons on hard substrate along southern coastline	Comparison of 4 protected and 4 unprotected reefs; visual census using transects, quadrats and DGS method	Fish density 380/500m² in protected sites (170/500m² outside); diversity 40spp/500m² in reserve (20 outside)
McClanahan 1997a	Reef biota – *Chelinus trilobatus, Balistapus undulatus, Echinothrix diadema, Diadema savignyi*	2 reserve and 4 unreserved areas in Kenya consisting of fringing and patch reef types	Comparison of 2 protected and two unprotected reefs sampled once by visual census; tethering experiment on sea urchin–plots; transects (benthic and fish) and DGS method (fish)	Total wet fish weight inside reserves 730 to 1100kg/ha (80–150kg/ha in non-reserve areas)

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
McClanahan 1997b	Coral reef community e.g. *Balsitapus undulatus* *Chelinus trilobatus* *Echinothrix diadema* *Diadema savignyi*	Mombasa Marine Park (Kenya); coral reef	Combines monitoring studies on sites in reserve and experimental reduction of sea urchins in 2 sites within reserve; data compared with older protected reefs and unprotected reefs; sampled annually using visual census transects and plots; changes over 1 yr of study	Fish recovery evident in some places within reserve but in others the abundance of sea urchins prevented full recovery; 5 fold increase in total fish wet weight (averaged 1700 kg/ha in protected reefs, 150 in unprotected); sea urchin population in reserve reduced by 60% through predation; coral cover increased from 8% to 45% over 7 yrs; coral 40% cover in protected reefs (18% cover in unprotected)
McClanahan *et al.* 1999	Macrobenthic and reef fish communities.	2 protected reefs in Southern Kenya (protected since 1974—10km²) and northern Tanzania (protected since 1991—500m long); coral surveys conducted in reefs off Dar es Salaam; back-reef sites on patch and rock island reefs	Comparison of reserves with unprotected areas; visual census using line transects (benthic), search sample technique (coral), plots (urchins), transects and DGS method (fish); tethering experiment on urchins	Coral cover 20% higher in protected reefs but not sig.; total fish wet weight estimates 3.5x higher in reserve than unprotected reefs; 25% decrease trend in spp. density between protected and unprotected reefs at 500m² scale; predation 2x lower on tethered urchins in unprotected reefs than reserves
McClanahan & Mangi 2000	Reef fish species	Mombasa Marine Park and Reserve (Kenya); coral reef	Research fishing over 4-month period with baited traps adjacent to Park; supported by measurements of seagrass leaf bite patterns; analysis of 7 years of landings at a local beach (12d/mo)	Spillover from the Park detected for exploitable species of rabbitfish, emperors, and surgeon-fish, and stocks adjacent to the Park were consid-ered to be increased; this was influenced by extent of management controls, and by reef morphology and tides. Variability of fish catch was reduced by Park creation, although overall catch was maintained at levels lower than those pre-reservation. Reduction in area of reserve increased fish catch in adjacent areas, suggesting an optimum reserve size of about 10 to 15% of the inshore potential fishing grounds.

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Murawski *et al.* 2000	*Placopecten megellanicus* *Gadus morhua* *Melanogrammus aeglefinus*	3 areas on Georges Bank and in Southern New England totalling 5 000m² closed year-round to any gears capable of retaining groundfish; gravel-cobble pavement	Benthic surveys using standardised dredge surveys; sampled before reservation and yearly for 4yrs after	Spawning stock biomasses increased for groundfishes, sea scallop (14-fold); abundance of scallop increased after 4yrs protection; relative and absolute abundance of groundfishes increased
Nardi *et al.* manuscript	Baldchin groper (wrasse —*Choerodon rubescens)* coral trout (Serranidae *Plectropomus leopardus)*	Coral reef areas; survey of reef slope and back reef habitats	2 reserve sites and 2 control sites; back reef and reef slope habitats at each site; 4–5 replicate visual census surveys at each habitat; sampled before reserve creation and 3 times subsequently over 6 year period	Higher abundance of all size classes of *P. leopardus* in reserves; increase at final sampling of larger *C. rubescens*.
Paddack & Estes 2000	Kelp forest fishes—mainly *Sebastes* spp. Also, *Ophiodon elongatus Hexagrammos decagrammus, Semicossyphus pulcher, Scopaenichthys marmoratus.*	Three reserves in Central California; kelp forest	2yr study in 3 reserves and at least 2 sites next to each reserve; visual census using transects and quadrats (habitat)	No sig. differences in density in reserves, although positive trend observed; average length of *Sebastes* was greater in 2 of 3 reserves; more larger sized fish and greater reproductive potential in reserves; 1yr old reserve showed no sig. increases in density or biomass
Palsson 1997	*Ophiodon elongatus* *Sebastes caurinus* *Sebastes maliger*	Edmonds Underwater Park (Puget Sound) protected fish and shellfish from harvest since 1970	4 harvested sites and a reserve were compared over a 4yr period; visual census using transects	Larger individuals of all 3 spp. observed in reserve (*Sebastes* spp. <40cm in reserve, rare in harvested areas); egg production 100x greater for *S. caurinus*, 10x greater for *O. elongatus*
Rakitin & Kramer 1996	89 species belonging to 36 families were recorded	2.2km long coastal reserve (West Indies) comprising 5 fringing reefs	Five reserve sites and 8 adjacent non-reserve sites surveyed 10 yrs after area reservation	Species abundance average 66% higher inside reserve; actual sizes and statistical significance very low
Roberts & Hawkins 1997	*Lutjanus analis* *Haemulon macrostomum* *Anisotremus surinamensis*	2.6ha coral reef reserve (St Lucia) surrounded by heavily fished reef habitat	One reserve and several nearby non-reserve sites sampled two years after establishment	Fish biomass 4kg/count inside reserve (2kg/count outside); predator biomass 2kg/count (0.5kg/count outside)

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Roberts & Polunin 1992	*Variola louti* *Acanthurus nigrofuscus*	Sinai coast of Egypt, reserve protected since the early 1970s	Comparative census of 9 sites subjected to 3 fishing intensities – unfished, recreational, commercial	Grouper mean 14cm longer and 3 times heavier within reserve; surgeonfish (prey) more abundant outside reserve
Roberts & Polunin 1994	*Mycteropera bonaci* *Lutjanus griseus* Serranidae spp.	Hol Chan Marine Reserve (Belize); 2.6km² reef	Not specified	Biomass of commercial fish 77g/m² at edge of reserve and 340g/m² at centre (elsewhere reported ~45g/m²)
Russ & Alcala 1996a	Serranidae spp Lutjanidae spp Lethrinidae spp	10ha Apo Reserve & 22.5ha Sumillon Reserve (Philippines) on fringing coral reef slope protected intermittently since 1975	Two reserved and two unreserved sites ranging from -2 years to 9 years of protection, visually censused using transects	Overall abundance increased from 1.1 to 9 fish/1000m2 at (Apo); density increased from 1 to 10kg/1000m² (Sumillon)
Russ & Alcala 1998a	Reef fish community – 178 spp. in 18 families censused.	10ha Apo Reserve & 22.5ha Sumillon Reserve (Philippines) protected intermittently since 1975; fringing coral reef slope	Compared protection with natural fishing within 2 reserves over 10-year period; visual census using transects	Fish community biomass sig. affected by fishing, but not density; species richness increased by 1.31 during non-fishing at Sumilon; large predators (caesionids, pomacentrids, chaetodontids) recovered in density when protected for 5yrs in Sumilon, labrids declined; increase in density by factor of 1.43 after 6yrs of protection at Sumilon; biomass rose at Sumilon by factor of 1.6 after 6yrs; biomass at Apo rose by factor of 1.53 (after 6yrs of protection) and 1.55 (after 9yrs)
Russell 1997	*Plectropomus leopardus*	Differing complexity of hard and soft coral, sand and bare substratum (Great Barrier Reef)	Visual census (transect) data on coral trout collected annually at 1 test and 3 control sites for - 1 yr, 3.5 yr reservation, 1 yr re-opening	Abundance of large fish (<38cm) increased in density (9.5 to 49/ha) in reserve; average outside density of 28fish/ha

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Samoilys 1988	Coral reef fish—188 spp Chaetodontidae and Serranidae.	Kenyan coast, between Simambya and Mwamba Midjira reefs; seaward reef slopes; reef degradation is evident in some reserves; illegal fishing	Visual censuses using transects carried out over 4 mths at 19 sites, which were protected, semi-protected, and unprotected	Species richness higher in reserve; lowest spp. richness at dynamited unprotected reef; biomass not different except for serranids (16x higher in reserve than unprotected reef); abundance similar in reserve and fished areas; density of serranids at lightly fished site 13x greater than heavily fished site
Sasal *et al.* 1996	*Gobius bucchichii*	Cerbere-Banyuls Marine Reserve (Mediterranean), mainly sandy habitat	Three area types – protected, partially and unprotected—sampled irregularly between March and June 1994	Mean length of male and female fish 87.5 and 78mm inside reserve; (77 and 74.5mm in unprotected area)
Sluka *et al.* 1997	*Epinephelus striatus*	Exuma Cays Land and Sea Park 456km² (Bahamas); sites in patch reef, channel reef, fringing reef, windward hard-bottom	Data on Nassau grouper collected at 75 sites within and up to 10km outside reserve; visual census using transects	Mean grouper size inside park 42cm (32cm outside); biomass 574g/100m2 inside reserve (137/100m² outside); 8.61M eggs/ha inside (1.4M outside)
Stoner & Ray 1996	*Strombus gigas*	Exuma Cays Land and Sea Park (Bahamas); sand, coral rubble, seagrass <15m; sand coral ridges <15m	Fished and unfished areas sampled in 1991 and 1994 (surveys confirmed inter-annual population stability)	Conch density inside reserve 70.1/ha (13.3 outside); mean larval density 20.7/m3 inside reserve (1.3 outside); larger specimens in reserve due to protection by depth (conchs unable to be collected by divers)
Tupper & Juanes 1999	Haemulidae – 3spp.	Nine fringing reefs (Bahamas), 7km section of coast; 3 sites in reserve, 3 north of reserve, 3 south of reserve; distance separating adjacent study reefs 780m	Visual census using transects and mark recapture techniques (subcutaneous injections) comparing reserve and non-reserve sites	Predator density sig. higher in reserve than exploited reefs, mean predator size sig. higher in reserve; density of adults grunts sig. higher in reserve; mean size of older juvenile grunts did not differ; density of early juveniles grunts much lower in reserve (predator density); mean settlement of grunts was higher on exploited reefs

Summary of the Empirical Evidence for Reserve Effects

Reference	Scientific name	Reserve details	Type of study	Specific effects
Wallace 1997	*Haliotis kamtschatkana*	William Head, south coast of Vancouver Island (British Columbia)	2 control areas (CPUE data based on commercial fishers' logbooks); historical data compared with a restricted area; length-fecundity model applied	Abalone 16mm larger and 8 yrs older 1.2x and 1.4x as fecund as 2 unprotected sites; not self-recruiting, however
Wallace 1999	*Haliotis kamtschatkana*	Juan de fuca Strait (British Columbia); 2 reserves (one protected since 1958 and other since 1980); coast-wide closure of abalone harvesting (1990); sloping bedrock at 3–7m	Comparison of sites with differing protection status; visual census using transects and surveys	1958 reserve abalone sig. larger (16mm larger) than other sites; 26.5% of abalone <130mm and on average 30yrs old at oldest reserve; 1/3 of specimens <100mm in 1958 reserve, ~55% of specimens <100mm in other reserves; 1958 reserve had highest reproductive output
Wantiez *et al.* 1997	205 species from 9 common commercially important families	Five coralline lagoonal island reserves 1.5–18km off Noumea coastline (protected since 1989); 27km² in total area	5 reserves visually censused using transects prior to protection and 5 years after; compared with six non-reserve sites	Species richness increased 67%, density 160%, biomass 246% inside reserve after 5yrs; density and biomass of 9 families increased sig. after reservation; density in reserve increased by 89% over 4yrs; density of Chaetodontidae and Labridae increased in reserve over 5yrs; decrease in mean size of fishes (influx of small fishes—recruitment)
Zeller & Russ 1996	*Plectropomus leopardus*	Lizard Island, Great Barrier Reef, area closed to fishing 0.42km²; fringing and patch reefs	Visual census, recapture & ultrasonic telemetry (tagging) sampling undertaken contrasting inside and outside reserve 12 years after closure	Density of coral trout inside reserve 5.5/m² (outside density 4.6/m²)

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"A truly precautionary approach … would make use of large protected marine reserves as a hedge against the combined effects of irreducible uncertainty, uncontrollability, and economic shortsightedness that are associated with virtually every marine fishery" (Clark 1966)

"Fishing exerts a profound effect on almost all components of associated communities and ecosystems" (Dayton *et al.* 1995)

"We must acknowledge realistic limitations and expectations, and not present the MPAs as a general panacea. …It is important to step away from the euphoria or momentum verging on political correctness that this issue [MFRs enhancing fisheries] has acquired and attempt to define the real objectives of multiple–use management of MPAs" (Dayton *et al.* 2000)

"Marine fisheries refugia have the potential to protect coastal stocks from recruitment and ecosystem overfishing and thus enhance, restore, or stabilize fishery yields" (Dugan & Davis 1993)

"Fishing is banned within only 36 square miles (0.2%) of all Sanctuary waters, amounting to about 0.001% … of U.S. territorial waters" (Fujita *et al.* 1998b)

"Managing most marine finfisheries to achieve optimum yields is an unattainable dream. Protecting these resources from serious depletion through precautionary management seems the only practical option" (Johannes 1998a)

"…even very low rates of fishing mortality are unsustainable in demersal stocks unless a sizeable fraction of their spawning adults are completely inaccessible, owing to some natural refuge …[or] new refuges—marine reserve area …" (Pauly *et al.* 1988a)

"…marine fisheries are in a global crisis, mainly due to open access polices and subsidy–driven overcapitalization" (Pauly *et al.* 1998a)

"Reserves can simultaneously allow the build up and maintenance of spawning stock biomass of many commercial species, protect habitat, restore biodiversity and reduce losses of genetic diversity by fishing. They are probably the only way of maintaining some of the most valuable but vulnerable species in a fishery" (Roberts 1997b)

"… marine reserves represent a promising approach to fisheries management but, at present, many of their perceived benefits remain untested" (Roberts & Polunin 1991)

"…the export of larvae from reserves to augment regional fisheries has great potential and appears to be logically feasible, but is almost entirely unproven." (Rowley 1994)

"Given the critical levels of over–exploitation of coral reef resources in many parts of the world, marine reserves may be the ***only*** [retained emphasis] viable option available to maintain levels of spawning stock biomass necessary to sustain reef fisheries" (Russ *et al.* 1992)

"Management actions that might have prevented the disastrous collapse of fisheries, but which carried a price unacceptable to industry, have been scrupulously avoided. Society has simply lacked the political will to forestall the fishing industry's tendency to use up its living capital and thereby destroy itself" (Sutton 1997)

"It is a sad comment on the state of world fisheries that we can now develop fairly elaborate taxonomies for the causes of collapse" (Walters 1998)

"Instead of treating the seas as open to fishing with small exceptions (marine refugia), we will only safely limit harvest rates if we reverse this view and treat the seas as closed to fishing with small exceptions (limited fishing areas and times)." (Walters 1998)

Around the world many fisheries have collapsed, including some in Australia. Consequently marine fisheries are under increasing pressure to adopt more precautionary management approaches. Although Australia's fisheries are generally in good shape—few are overfished—many are fully exploited.

Overseas experience tells us that even the best fisheries management systems have not always been able to protect against overfishing. This review examines the extent to which 'no-take' marine reserves can benefit fisheries and provide support for fisheries management. It aims to inform people with an interest in Australian fisheries about modern ecological experience with reserves, and the benefits that can be derived from them.

Marine fisheries sanctuaries, where exploitation is not permitted, appear to offer many benefits, including improved stability of catches, reduced cost to fisheries management, protection from overfishing and conservation of a range of non-fished species that live within the sanctuaries. Although there is a body of ecological theory and some empirical evidence that support the beneficial role of sanctuaries for fisheries management purposes, global experience with such reserves is limited, and there are few cases where sanctuaries have been clearly demonstrated as providing a benefit to fisheries. However, many fisheries appear to have benefited from *de facto* sanctuaries, where some of the stock is out of the reach of the fishery, such as in water too deep for fishing.

Fisheries that are over-exploited or heavily exploited stand to gain most from sanctuary implementation: sanctuaries can contribute to achieving ecologically sustainable fisheries by reducing the risk of overfishing and by providing refuges for non-fished species that might otherwise be severely affected. Fishery sanctuaries can also make an important contribution to regional biodiversity conservation goals and provide reference sites where global changes in marine ecosystems can be studied and evaluated.

Despite some costs and risks, marine sanctuaries appear to offer our fisheries an important and cost-effective option for the implementation of precautionary fisheries management, while simultaneously improving the protection of Australia's marine ecosystems.

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