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DUGONGS

See **MARINE MAMMAL OVERVIEW**

DYNAMICS OF EXPLOITED MARINE FISH POPULATIONS

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Introduction

The development of sustainable harvesting strategies for exploited marine species addresses a critically important societal problem. Understanding the sources of variability in exploited marine species and separating the effects of human impacts through harvesting from natural variability is essential in devising effective management approaches. Population dynamics is the study of the continuously changing abundance of plants and animals in space and time. For exploited marine species, population dynamics studies provide the foundation for evaluation of their resilience to exploitation, the determination of optimal harvesting strategies, and the specification of the probable outcomes of alternative management actions.

In the following, a 'population' is defined as a group of interacting and interbreeding individuals of the same species. A closed population is one in which immigration and emigration are negligible; an open population is one in which dispersal processes do affect abundance levels. A 'stock' is a management unit defined on the basis of fishery and/or distinct biological characteristics. 'Recruitment' is the number of individuals surviving to the age or size of vulnerability to the fishery. A 'cohort' is defined as the individuals born in a specified time interval; a cohort born in a particular year is also referred to as a 'year class'.

Other articles in this encyclopedia focus on population dynamics in the context of multispecies assemblages, climate-related factors, and the ecosystem effects of fishing. Here, the primary emphasis will be on the effects of harvesting at the population level with the recognition that a full understanding of human impacts on exploited marine species can only be attained with a more holistic view incorporating the ecosystem perspective. The conceptual basis for the development of models of exploited populations and the information requirements for these models and an example of an application of these tools in a fishery assessment and management setting is provided.

Production of Marine Populations

The relative balance between increases in biomass due to recruitment and individual growth and losses from mortality due to natural causes and fishing defines the dynamics of exploited populations (**Figure 1**). The change in biomass of a population over time due to variation in these factors is called net production. For an open population, factors affecting immigration and emigration must also be considered in any evaluation of population change. The integration of information on these fundamental biological and ecological processes is a central focus of population dynamics studies. Prediction of the effects of alternative management regulations or changes in the production characteristics of an exploited population depends on a synthesis of fundamental biological and ecological processes in the form of mathematical models of varying degrees of complexity.

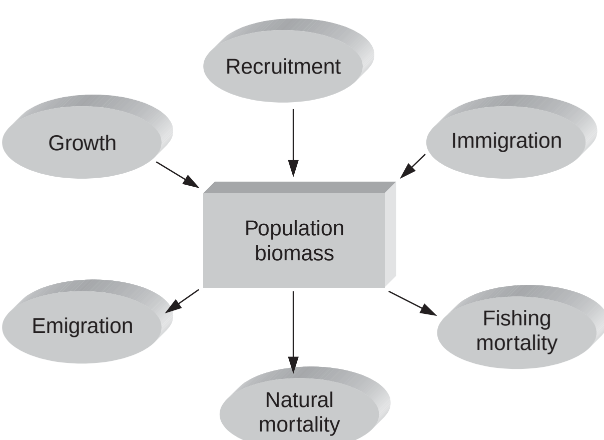

Figure 1 Components of production and dispersal affecting the biomass of exploited marine populations.

Recruitment is often the most variable component of production in many marine populations. Recruitment varies in response to changing environmental conditions as fluctuations in food supply, the activity of predators, and physical conditions affect the growth and survival of the early life stages. The relationship between the reproducing adult population in a given season or year and the resulting recruitment is of particular importance. For a renewable resource, it is of course essential that the replenishment of the population through reproduction should not be adversely affected by exploitation.

With respect to the other elements of production, the natural mortality component reflects the effects of biological factors such as predation and disease as well as adverse physical conditions. The increase in size and weight as an individual grows is an important contributor to change in biomass of a cohort over time. Finally, dispersal among populations or subpopulations through immigration and emigration can have important consequences for the persistence of a population and its resilience to exploitation. For example, a harvested population that receives members from an adjacent unexploited subpopulation in effect receives a subsidy that can contribute to its persistence under exploitation.

Sustainability

Understanding how marine species will respond to exploitation and the appropriate levels of fishing pressure to ensure continued harvest is an essential component of population dynamics studies. More specifically, the extraction of a yield that is optimal in some defined biological or economic sense is a broadly accepted goal in resource management. In order for a long-term sustainable harvest to be possible, the population must have some capacity to compensate for reductions in population biomass through increased recruitment and growth and/or decreased mortality at one or more life history stages. Mechanisms that underlie such compensatory responses include cannibalism and competition for critical resources. If the population exhibits some form of density dependence in critical processes affecting vital rates, different equilibrium levels of population biomass will exist, corresponding to different levels of fishing pressure. Fluctuations in the physical and biological environment and their effects on the population will result in variation about the equilibrium level.

For a population governed by density-dependent feedback processes, harvesting can reduce intraspecific competition or other interactions by reducing density and overall abundance. This results in an increase in the overall productivity of the stock. In the unexploited case, the stock is dominated by larger, older individuals; harvesting shifts the population state to one with a higher proportion of younger, faster-growing (and therefore more productive) individuals. The production generated in this way is called surplus production and, in principle, this production can be taken as yield.

The relationship between surplus production and biomass for a species governed by a simple form of compensatory dynamic is dome-shaped, with a peak at some intermediate level of population biomass. In this simple conceptual model, production is expected to be zero when the biomass is at its highest level (the unexploited state) because of intraspecific interactions such as competition or cannibalism. The production–biomass relationship can be readily translated to one linking yield (surplus production) to fishing intensity. Again, a domed-shaped relationship is expected (**Figure 2**). At relatively low levels of fishing pressure, the yield is lower than the maximum because some correspondingly low fraction of the population is removed. Conversely, at higher levels of fishing pressure, the productivity of the stock is reduced by removing too high a fraction of the population. The point where yield is the highest is the maximum sustainable yield. All of the points on the curve except where yield is zero are considered to be sustainable yield levels. However, as the population is reduced to low levels, its viability is jeopardized, particularly under variable environmental conditions. It is therefore important not only to specify sustainability as a broad goal of fishery management but to consider optimum harvesting policies that also minimize risk to the population.

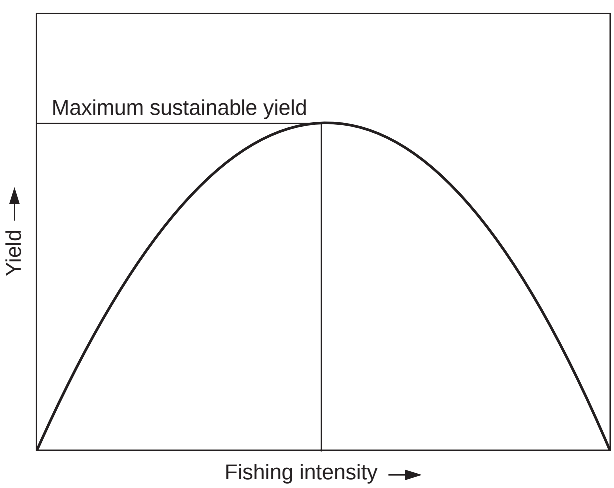

Figure 2 Relationship between yield (surplus production) and fishing intensity (measured as fishing mortality or fishing effort) under a simple conceptual model incorporating density-dependent feedback processes.

Assessing Population Status

The development of management strategies involves several components including the determination of the current biomass relative to 'desired' levels and projections of how alternative management actions will affect the population in the future. The reconstruction of past and present population levels typically involves a synthesis of information derived from fishery-dependent and fishery-independent sources. Fishery-dependent information includes factors such as the catch removed from the population and either marketed or discarded at sea, the age and/or size composition of the catch, and the amount of fishing effort and its spatial distribution. Fishery-independent information includes studies to determine the relative abundance of fish though the use of scientific surveys aimed at estimating population levels at different life stages. For example, surveys are often conducted to determine abundance of juvenile and adult fish using modified fishing gears, and others to determine the distribution and abundance of the eggs and larvae of marine species. A careful attempt is made to standardize the methods and gear used over time to ensure that the changes measured from one survey to the next reflect true changes in relative abundance. Other special studies such as mark and recapture experiments are also employed to determine population size and mortality rates.

If accurate information on catch levels is available, coupled with information on the size or age composition of the catch, estimates can be made of both population size and mortality rates. The number in the catch removed in a specified time interval, if accurately known, provides an initial minimum estimate of the population size in the sea because at least that many individuals had to have been present to account for the catch. If the fraction of the population removed by harvesting and the fraction dying due to natural sources such as disease and predation can be determined, it is possible to derive an estimate of the actual population size. Knowing the age or size composition of the catch is critical in determining the overall mortality rates. By tracking the changes in the numbers of a cohort over time as it progresses through the fishery, it is possible to estimate the survival rates from one age class to the next and therefore to generate estimates of the population size-at-age. If size but not age composition of the catch is known but we do know the growth rates and the time required to grow from one size class to the next, we can also determine the population size and survival rates.

In some cases, the catch adjusted by the amount of fishing effort to obtain that catch can be used as an index of relative abundance. The utility of this index depends on the accuracy of the catch statistics and on the validity of the measure of fishing effort. The latter can be complicated by the fact that several different types of gear may be employed in a single fishery and it will necessary to standardize among the gear types. Similarly, fishing vessels of different sizes have differing fishing power characteristics that require adjustment factors. Finally, technological developments such as advanced navigation and mapping systems, satellite imagery of oceanographic conditions and increasingly sophisticated echosounders used to locate concentrations of target species result in continual increases in the realized fishing power of vessels. Most importantly, it is essential to recognize that fishers are not striving to attain unbiased estimates of overall population size but rather are attempting to maximize their catch rates using all of the experience and tools at their disposal. This must be considered in any attempt to use catch-per-unit-effort as an index of abundance.

Scientific surveys are an attempt to provide an independent check on information derived from the fishery itself. Such surveys have proven to be invaluable tools in determining the status of marine populations and the communities and ecosystems within which they are embedded. Typically, fishery-independent surveys are employed to collect information not only on economically important species but all species that can be adequately sampled by the survey gear, thus providing a broader perspective on changes in the system. In addition, key oceanographic and meteorological measurements are routinely made to index changes in the physical environment.

The information noted above is integrated into mathematical models that describe, for example, the decay of a cohort over time under losses due to fishing and other sources. The information from fishery-independent sources can be used to calibrate models operating on fishery-derived data sources in an integrated analysis. In turn, the estimates of population size derived from these models and estimation procedures can be used in models designed to assess alternative harvesting strategies.

An example of the application of this overall research approach is provided below for the Icelandic cod population. Estimates of cod recruitment at age 3 years based on applications of models to catch-at-age information from the fishery and fishery-independent survey information are provided in **Figure 3**. Estimates of the number of recruits over a 50-year period show fluctuations about a relatively stable level. Estimates of the adult population size for this period are also available and show overall declines during this period as exploitation increased. The relationship between adult biomass and the resulting recruitment for Icelandic cod is provided in **Figure 4** along with the predicted fit from a simple model for this relationship. Note that there are substantial deviations from the deterministic curve, reflecting the effects of variable environmental

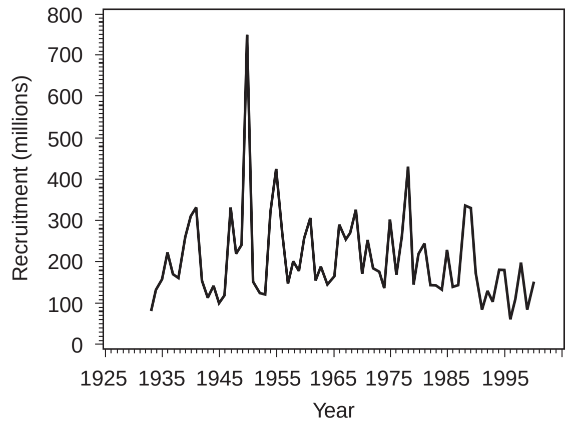

Figure 3 Estimates of recruitment at age 3 years (millions) for the Icelandic cod population over a 50-year period based on stock assessments conducted under the auspices of the International Council for Exploration of the Sea.

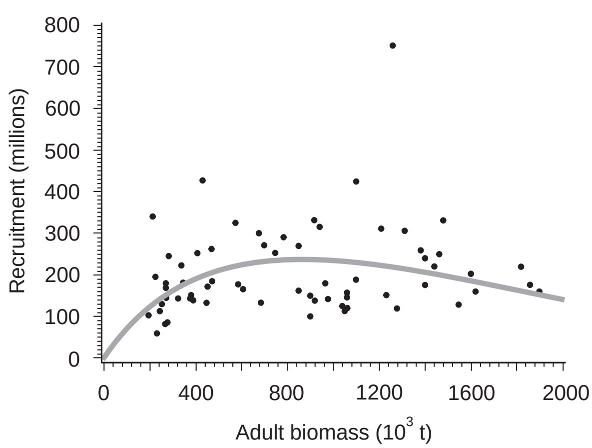

Figure 4 Relationship between recruitment and adult (spawning) biomass of Icelandic cod based on stock assessments conducted under the auspices of the International Council for Exploration of the Sea.

conditions (and variation attributable to estimation errors). Despite this variability, it is evident that this relationship is nonlinear — recruitment does not increase continuously with increasing adult biomass but rather levels off and even declines at quite high levels of spawning population size. This reflects a form of compensatory response in the adult–recruit relationship. For Atlantic cod populations in general, it is known that cannibalism can be an important regulatory factor that limits recruitment at higher population levels. The model used to develop the predicted relationship between adult biomass and recruitment in **Figure 4** is in fact one that incorporates the effect of predation by adults on their progeny. Recall that some form of compensatory capacity is essential if a sustainable harvest is to be possible. An illustration of how this information can be combined with other key aspects of the production of cod to predict yield at different levels of fishing pressure is described later.

Management Targets and Limits to Exploitation

Effective management requires a clear specification of goals and objectives to be achieved. Without an appropriate and pre-agreed target for management, the many conflicting and entrenched interests in the fishery management arena cannot be reconciled. The development of biological and economic reference points has played an integral role in fishery management. In the following, the emphasis will be on biologically based targets for management and on the determination of the resilience of the population to exploitation on the basis of models of the dynamics of exploited populations. One important reference point has already been encountered — the maximum sustainable yield (MSY). The corresponding level of fishing pressure resulting in MSY is also of direct interest. Although the concept of MSY has endured a somewhat controversial history, it remains a cornerstone in many national and international fishery policy statements. For example, in the United States, the Magnuson–Stevens Fishery Management Act of 1996 defines the optimum yield as 'equal to maximum sustainable yield as reduced by economic, social, or other factors.' This statement includes an important change in the specification of optimum yield relative to the original legislation introduced in 1976 in which optimum yield was defined as 'equal to maximum sustainable yield as modified by economic, social, or other factors.' In the more recent version, MSY and the corresponding fishing mortality rate is taken as a limit to exploitation.

Other important biological reference points for management are based on consideration of the effect of harvesting on a cohort once it enters or is recruited to the fishery. By tracking the growth and the fishing and natural mortality over the lifespan of the cohort, it is possible to determine the effects of harvesting on yield and the adult biomass as the level of fishing pressure is changed and/or as we modify the age or size of vulnerability to the fishery. The fishing mortality rate at which yield is maximized (denoted $F_{\max}$) is one such reference point (assuming a maximum does in fact exist). An alternative reference point that has been widely applied is defined by the point on the yield-per-recruit curve where the rate of change in yield is one-tenth of the rate at the origin (denoted $F_{0.1}$). An advantage of this reference point is that it always exists (unlike $F_{\max}$); further, in cases where $F_{\max}$ does exist, $F_{0.1}$ is always lower and therefore leads to more conservative management. An example for Icelandic cod is provided in **Figure 5**; in this case, $F_{\max} \sim 0.35$ and $F_{0.1} \sim 0.2$.

The advantage of this overall approach is that it does not require specific information on the incoming recruitment. Rather, it is possible to express the yield on a per-unit-recruitment basis. A disadvantage of this approach if it is taken alone is that it does not provide direct information on how fishing pressure might affect the replenishment of the population through recruitment.

To fully evaluate the effects of fishing on the population, it is possible to combine information from the yield and adult biomass per recruit analysis with the data on recruitment as a function of adult

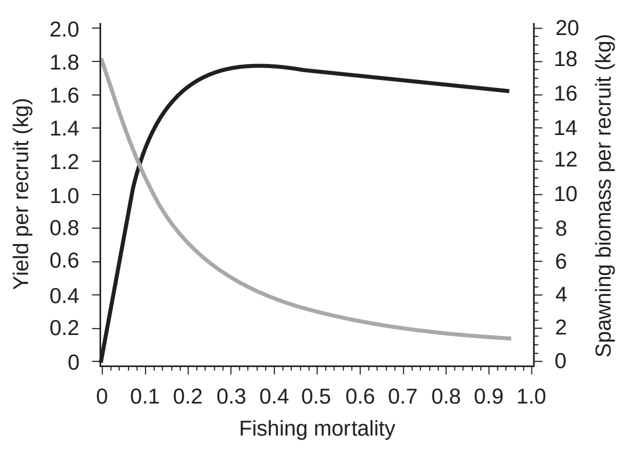

Figure 5 Yield per recruit (peaked curve) and adult (spawning) biomass per recruit (decaying exponential curve) as a function of fishing mortality for Icelandic cod based on stock assessments conducted under the auspices of the International Council for Exploration of the Sea.

population size to generate a complete life-cycle representation. Fishing reduces the adult biomass and it is possible to estimate the predicted recruitment for each level of fishing as a function of the spawning population (see **Figure 4** for the case of Icelandic cod). Multiplying the yield per recruit at each of these fishing rates by the predicted recruitment then gives the total yield. This process is illustrated for the Icelandic cod example in **Figure 6** where the predicted equilibrium yield is shown as a function of fishing mortality. Superimposed on this curve are the observed (nonequilibrium) yields for Icelandic cod against the estimated fishing mortality rates. The actual catch data reflect variability in the stock–recruitment relationship due to factors not included in the model. The maximum yield is predicted to occur at moderate levels of fishing mortality ($F \sim 0.35$) and the limiting level of fishing mortality is at $F \sim 1.0$. Although estimated fishing mortality rates for Icelandic cod decreased at the very end of the available time series, it is clear that Icelandic cod has been overexploited and that the effects of excessive fishing have adversely affected yields. The limiting level of fishing mortality beyond which the probability of stock collapse is high can be shown to be directly related to the rate of recruitment at low spawning stock sizes. Species characterized by a high rate of recruitment at low adult population size are more resilient to exploitation than those with a lower rate.

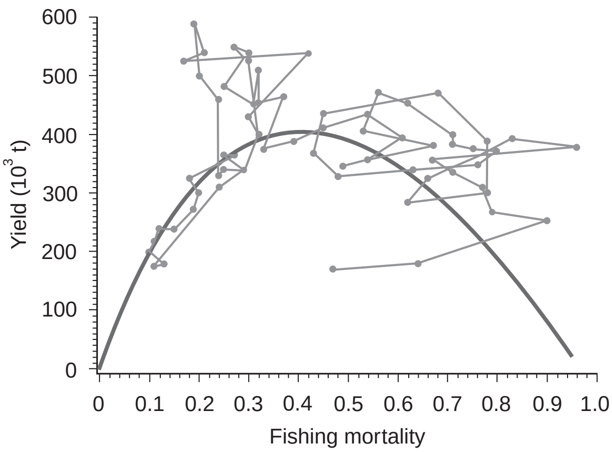

Figure 6 Predicted equilibrium relationship between yield (surplus production) and fishing mortality (solid line) based on an age-structured model for Icelandic cod incorporating information on the adult–recruitment relationship (see **Figure 4**), and yield and adult biomass per recruit analyses (see **Figure 5**). Observed (nonequilibrium) yield and estimated fishing mortality rates for Icelandic cod are shown (dots).

Shifting Environmental States

The discussion has concentrated so far on conditions under which the physical and biological environments affecting the population are relatively stable and do not undergo trends or shifts in state. However, persistent shifts in environmental conditions do occur on decadal timescales with important implications for harvested species. It is useful to distinguish environmental variations in physical factors such as temperature and salinity or biological factors such as prey or predator concentrations that occur on relatively short timescales (seasonal to interannual) from those that occur on longer timescales. The distinction between high-frequency variation on seasonal or annual timescales and low-frequency variation on decadal timescales has important implications for overall levels of productivity of a population and its resilience to exploitation. With low-frequency variation, the potential interaction between changes in the environment and harvesting is of particular concern because persistent shifts in productivity of the population require change in the biological reference points. Exploitation regimes that are sustainable under one set of environmental conditions may not be under another, lower-productivity pattern. An illustration of this in the context of a simple production model is shown in **Figure 7**, where a change in the basic productivity level of the population under changing environmental conditions is reflected in a change not only in the overall yield levels attainable but also in the level of fishing pressure at which yield is maximized and at which a stock collapse is predicted. Under the lower-productivity regime depicted, the stock collapses at a fishing pressure that is sustainable (although

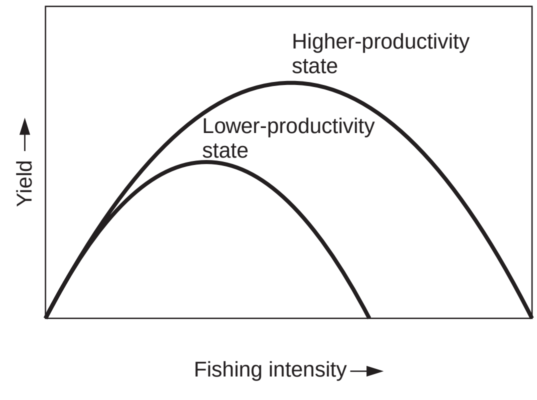

Figure 7 Yield (surplus production) as a function of fishing intensity under two environmental regimes in which the intrinsic rate of increase of the population is affected by changing productivity.

suboptimally) under higher productivity levels. It is clear that a dynamic concept of maximum sustainable yield and other reference points is required that does account for changing conditions in the biological and physical environments experienced by the population. The integration of population dynamics studies with broader ecological investigations and physical oceanographic research is essential if we are to improve understanding of the effects of harvesting on exploited marine species.

Uncertainty, Risk, and the Precautionary Approach

Sustained monitoring of the abundance, demographic characteristics, and productivity of widely distributed marine populations entails special challenges. The precision with which it is possible to measure changes in these key variables depends critically on factors such as funding levels and infrastructure available for both fishery-dependent and fishery-independent programs, and on intrinsic characteristics of the populations themselves such as their degree of heterogeneity in space and time. Some of the principal sources of uncertainty in fishery assessments can be attributed to (a) variability (error) in estimates of population size and demographic characteristics, (b) natural variation in production rates and processes, particularly in recruitment, and (c) lack of complete information on broader ecosystem characteristics that affect the species targeted by harvesting and on the direct and indirect effects of harvesting on the ecosystem. The intrinsic variability of marine populations, communities, and ecosystems contributes substantially to these components of uncertainty.

It is now commonplace to frame issues concerning human health in terms of risk. Considerations of diet, exposure to chemicals, lifestyle choices, etc. affect the probability that an individual will contract certain diseases. Similarly, it is increasingly common in fisheries stock assessments to describe the risk to the population under alternative management scenarios. Although many specifications of risk are possible, an easily understood definition is that risk is the probability that the population will decline and remain below some specified level. Uncertainty in estimates of key parameters and quantities contributes to risk because of the possibility that errors in estimation or in basic model structures may result in overestimates of population size and productivity, inadvertently resulting in overfishing of the resource.

The recognition that many populations of exploited marine species are now fully exploited or overexploited has led to an important reevaluation of management policies. In particular, the need for a more precautionary approach to management has been recognized and integrated into a number of national and international management policy statements. Under the precautionary approach, more conservative management is required in situations where higher levels of uncertainty concerning the stock status and production characteristics exist. The burden of proof that harvesting activities were detrimental to marine populations, communities, and ecosystems has historically (and implicitly) rested with scientists and managers. An important element of the precautionary approach is the recognition that a shift in the burden of proof is required to show that the users of a resource are not adversely impacting the productivity of a population or ecosystem.

Summary

Questions relating to the stability and resilience of marine species under exploitation involve fundamental ecological considerations such as the role of density-dependent processes in population regulation, the importance of interspecific interactions such as predation and competition, and the role of the physical environment in the production dynamics of the system. Studies of the dynamics of exploited species incorporating these considerations provide an essential framework for quantitative consideration of the effects of alternative harvesting policies on these populations. The importance of fisheries in an economic and social context has led to intensive efforts on a global basis to understand the dynamics of exploited marine species on broad spatial and temporal scales. These studies have become increasingly important as it has become clear that we are near or have exceeded the apparent limits to fishery production from marine systems. Widespread problems such as overcapitalization and excess capacity of fishing fleets and the prevalence open-access fisheries, however, remain substantial impediments to effective management. The extensive information base available for exploited marine species and recent advances in understanding of ocean ecosystem dynamics can provide a strong foundation for improvements in resource management.

See also

Ecosystem Effects of Fishing. Fisheries: Multispecies Dynamics. Fishery Management. Fishery Management, Human Dimension. Marine Fishery Resources, Global State of.

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