

MARINE RESERVES FOR THE NORTHERN COD

by

SYLVIE GUÉNETTE

B.Sc. Université de Montréal, 1979

M. Sc. Université du Québec à Montréal, 1991

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR of PHILOSOPHY
in
THE FACULTY OF GRADUATE STUDIES

Resource Management and Environmental Studies
and the Fisheries Centre

We accept this thesis as conforming to the ~~required~~ standard

THE UNIVERSITY OF BRITISH COLUMBIA

June 2000

© Sylvie Guénette, 2000

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of RMEs

The University of British Columbia
Vancouver, Canada

Date June 15th 2000

Abstract

In the midst of several management failures, marine reserves are seen as a potential management tool to control overexploitation. In the literature, both modelling and empirical work have demonstrated that closing an area to fishing would lead to an increase in biomass and mean body size within the reserve. Benefits, in the form of increased catch, outside the reserves are sometimes shown using modelling, but the assessment of such benefits in nature is more difficult. Home range and migration rate of the targeted species are important factors to consider in the establishment of a reserve. A few cases convincingly point at the importance of the source of larvae and the direction and rate of dispersal. Reserves could also be used as a hedge against uncertainty and management mistakes by limiting fishing mortality. This study is intended to evaluate the possibility of using marine reserves to control fishing mortality for northern cod, a migrating fish. A simple dynamic pool model emphasized the importance of including stock recruitment relationship to properly assess reserves benefits. By protecting a part of the spawners, the system containing a reserve was more resilient than the control (no-reserve). However, these results were probably overly optimistic because the proportion of fish staying within the reserve was overestimated. An age- and spatially-structured model was then built to mimic the historical evolution of fishing and stock collapse of the northern cod, offshore Newfoundland. The model included four stocks, migrations, and range dynamics. Fishers were assumed to show hunting behaviour to various degree depending on the gear used. In the first version of the model had to increase catchability as cod biomass decreased. The second model used effort profiles based on documented qualitative and quantitative changes in fishing capacity and effort. In both cases, results showed that very large marine reserves (80%) by themselves could have hedge against mismanagement, while a 50% reserve would have only slowed the decrease of the cod population. The results also suggest that adding seasonal closures could help control fishing mortality although possible temporal effort displacement was not investigated. The principal benefits of seasonal closures would be to protect the spawning aggregations rather than controlling fishing mortality. Every management scenario that was efficient at controlling fishing mortality implied decreasing the catch before the stock started rebuilding. Marine reserves could be used as an additional management tool along with other measures limiting the range of action of the fishery. For example, banishment or severe restrictions on gears allowed in the fishery could limit the geographical range of the fishery and help control fishing mortality.

Table of contents

Abstract	ii
Table of contents	iii
List of tables	v
List of figures	vi
Acknowledgements	viii
Chapter 1. Fisheries management and marine reserves, an overview	1
Introduction	1
Objectives	1
The northern cod, <i>Gadus morhua</i> L.	2
Biology	2
Fishery	2
Thesis outline	4
Chapter 2. Marine reserves: from Beverton and Holt to the present	6
Fisheries and fisheries science are in trouble	6
Beverton and Holt's model of marine reserves	6
Current modelling of marine reserves	8
Population	8
Adult migration	11
Larvae export	11
Yield	12
Protection against overexploitation	12
Increasing recruitment age	13
Uncertainty	13
Habitat degradation	14
Design of reserves	15
Permanent closures	15
Temporal closures	16
Mixture of approaches	17
Social aspects	17
Discussion	18
Chapter 3. An age-structured model showing the benefits of marine reserves in controlling overexploitation	19
Introduction	19
Methods	19
Results	23
Discussion	23
Chapter 4. Catch and effort data	28
Observer data	29
Description	29
Analysis of variance on CPUE	29
Statistics from commercial data	33
Newfoundland landings	33
Yield per gear type	33
Effort data	34
Catch per unit effort	35

Spatial distribution of the catch	39
Total landings (NAFO data)	39
Comparison of Newfoundland and NAFO data set for 1980-1991	39
Period 1960-1980	44
Origin of vessels, their catch and gear used	44
Target species and effort	44
Resulting catch and effort	48
Conclusion	50
Chapter 5. Could marine reserves have prevented the collapse of the northern cod in 1984?	52
Introduction	52
Material and methods	52
Study area	52
Data	52
Model	57
Movement patterns	57
Population parameters	59
Fishing	60
Simulations	61
Results	61
Discussion	70
Data	70
Migrations	72
Fishing capacity and restrictions	72
Conclusion	73
Chapter 6. Could marine reserves have prevented the collapse of the northern cod in 1960?	75
Introduction	75
Material and methods	75
Construction of effort scenarios	75
Gillnet effort scenario	75
Trap effort scenario	79
Trawl effort scenario	79
Model	79
Modifications made to the model	80
Quota calculation	81
Results	83
Discussion	88
Chapter 7. The usefulness of marine reserves, a discussion	90
References	93
Appendix 3.1 Parameter calculations for stock-recruitment relationships	104
Appendix 4.1 Analysis of observer data	105
Appendix 4.2 Analysis of NAFO data	106
Appendix 5.1 Building the stock-recruitment relationship	108
Appendix 6.1 Additional evidence of increase in effort	109
Appendix 6.2 List of modifications attempted	111

List of tables

Table 2.1	Species, population model type, closure type and specific features of the models cited in this paper.	9
Table 3.1	Mean weight, maturity and vulnerability schedules used in the model (adapted from Polacheck 1990).	21
Table 4.1	Spatial and temporal distribution of the total cod catch included in observer data and the percentage of the commercial catch covered for trawlers of size 3 to 7 (1) and gillnetters of size 4 to 6 (2).	30
Table 4.2	Distribution of the cumulative catch in observer data arranged by vessel gross tonnage class, NAFO divisions, and the respective percentage of commercial catch.	30
Table 4.3	Parameters estimated from the generalised linear model used to standardise CPUE by vessel size class, divisions, period, and season.	32
Table 4.4	Total yield landed in Newfoundland per NAFO division and percentage reported for each gear. "3 gears" refers to gillnet, trap and trawl.	33
Table 4.5	Proportion of the catch for which effort was reported by year and by gear for Newfoundland vessels between 1980-1991.	36
Table 4.6	Total catch and proportion of the catch for which effort was reported for vessels with and without logbook by gear and vessel length (Newfoundland vessels).	36
Table 4.7	Declared landings for Newfoundland (Nfld), other provinces (Mari) and foreign countries for regions 2J3KL between 1980-1991, as compiled by NAFO for all gears (gillnet, trap, trawl and others).	44
Table 4.8	Number of months for which the average monthly CPUE was present in the data (Original) compared to CPUE substituted from other period and seasons.	48
Table 4.9	Percentage of boats smaller than 20 m built at each period in Newfoundland, as determined in 1991 (Program Coordination and Economics Branch, 1993).	50
Table 5.1	Mean weight, maturity and vulnerability schedules used in the model.	59
Table 5.2	Number of nursery cells attributed to each cod group in the model.	59
Table 6.1	Number of gillnets and traps reported in Templeman (1966).	76
Table 6.2	Evolution of the number of gear per fisher obtained from Hutchings and Ferguson (2000).	76
Table 6.3	Rationale for the effort scenario constructed for gillnets.	77
Table 6.4	Rationale for the effort scenario constructed for traps.	77
Table 6.5	Weight, vulnerability and maturity at age used in the model (adapted from Shelton <i>et al.</i> 1996)	79
Table 6.6	Vulnerability schedules for the two levels of biomass used in the model.	82

List of figures

Figure 1.1	Study area (shaded) on the coast of Newfoundland and NAFO divisions.	3
Figure 2.1	Yield per recruit for different size of unfishable areas (U) as a function of the fishing mortality on the harvested grounds	7
Figure 3.1.	Organisation of the model.	20
Figure 3.2	Beverton and Ricker eggs-recruitment curves used in the model.	20
Figure 3.3	Behaviour of the transfer rates as a function of the size of the reserves.	22
Figure 3.4	Effect of exploitation rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate and reserve size.	24
Figure 3.5	Effect of transfer rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate and reserve size.	25
Figure 3.6	Effect of increasing the minimum size and exploitation rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate using the Beverton recruitment curve and a transfer rate of 0.3.	26
Figure 4.1	Distribution of the trawl catch within the observer program for divisions 2J, 3K and 3L.	28
Figure 4.2	CPUE for trawlers by season for each vessel size class, as found in the observer data set.	31
Figure 4.3	Average monthly distribution of the catch for years 1980-1991 by NAFO divisions, as found in the Newfoundland data set.	34
Figure 4.4	Catch declared for each size class of trawlers as found in the Newfoundland data set. ..	35
Figure 4.5	Catch, effort and cpue as obtained from Newfoundland data set for year 1980-1991.	37
Figure 4.6	Catch per unit effort by vessel size, division and season as calculated from the Newfoundland data. V1, p1 means vessels of gross tonnage class 1 in period 1 (years 1980-1985).	38
Figure 4.7	Spatial distribution of trawlers's cumulative catches by vessel size, period and unit area, as found in the Newfoundland data set.	40
Figure 4.8	Spatial distribution of tows sampled by class size of trawlers as found in the observer program.	42
Figure 4.9	Total annual catch per gear in NAFO data set. Miscellaneous gear is probably a mixture of gillnet and trap catches (see text).	45
Figure 4.10	Proportion of the catch and effort directed towards cod for each trawler gross tonnage class from the NAFO data set.	46
Figure 4.11.	Catch and effort by gear and species targeted in the NAFO data set for years 1960-1991.	47
Figure 4.12	Catch, effort and CPUE for trawlers, gillnets and traps as extracted from NAFO data. ..	49
Figure 5.1	Study area (shaded) showing NAFO divisions (2J, 3K, 3L), their subdivisions (unit areas) used for statistics purposes, and the size of a cell which is the spatial unit of the model.	53
Figure 5.2	Fishing grounds for each gear used in the model, as derived from the catch statistics and the observer data.	54
Figure 5.3	Monthly proportion of average catch and effort for the three gears between 1980-1991 used in the simulations.	55
Figure 5.4	Catch per unit effort (CPUE) and catchability as a function of the population biomass observed during the period 1980-1991.	56

Figure 5.5	Location of the monthly target cells (numbers in geometric symbols) for 5 yr-old cod used to generate seasonal migration for the four cod groups: Labrador coast (diamond), Belle Isle Bank (triangle), southern Newfoundland (ellipse) and northern Grand Bank (parallelogram).	58
Figure 5.6	Location of marine reserves (black) covering 5, 10, 50 and 80% of the study area (hatched).	62
Figure 5.7	Comparison of observed and simulated population size and catch for trawl, trap and gillnet using historical monthly effort for years 1984-1991.	63
Figure 5.8	Population size, total catch and catch per unit effort for trawl (February and July), trap and gillnet (July) for three scenarios: without and with marine reserves covering 20, 50 and 80% of the fishing ground.	65
Figure 5.9	Population size and total catches for trawl closure (TC) and gillnet closure (GC) used alone, in conjunction with marine reserves, or direct halving of trap and gillnet effort (Effort/2).	66
Figure 5.10	Impact of increasing effort by 10 or 20% when seasonal closures for trawl and gillnet are accompanied by a 20% marine reserve.	67
Figure 5.11	Three different locations for a 20% marine reserve.	68
Figure 5.12	Population sizes and total catches for three different locations for 20% marine reserves as illustrated in Figure 5.11	69
Figure 5.13	Offshore and corridor locations of marine reserves (black) covering 50% of the shelf (hatched).	70
Figure 5.14	Population sizes and total catches for three reserve designs (see Figure 5.13).	70
Figure 6.1	Effort and CPUE for each gear type following the scenarios of effort for years 1960-1991.	78
Figure 6.2	Potential (number of eggs) and realised (number of 2 years old two years later) recruitment and recruitment anomalies over the period 1964-1991.	80
Figure 6.3	Vulnerability of selected years as obtained from a Virtual Population Analysis (R. Ahrens, UBC, pers. comm), and the two vulnerability schedules used in the model.	82
Figure 6.4	Population biomass, total catch and exploitation rate as observed and simulated using one vulnerability schedule (one schedule), and two schedules changing with biomass (two schedules, see text).	84
Figure 6.5	Catch per gear as observed and simulated using one vulnerability schedule (one schedule), and two schedules changing with biomass (two schedules, see text).	85
Figure 6.6	Population size, total catch, catch for each gear, and annual quota calculated for a conservative (0.2) and a large (0.4) exploitation rates.	86
Figure 6.7	Population, catch size and exploitation rate in the case of overestimated quota (exploitation rate of 0.4) used in conjunction with 50 and 80% marine reserves.	87

Acknowledgements

I express my gratitude to Dr Tony Pitcher, my supervisor, for his support and helpful discussions in shaping my project and keeping it focussed. Also, Dr Pitcher gave me several enriching opportunities to present my results and interact with researchers on the international scene. I also thank the members of my scientific committee, Drs Daniel Pauly, Max Stocker and Carl Walters for their helpful advice. I thank Carl Walters especially for being so generous with his ideas and the spatially-explicit model he developed.

I also want to thank my colleagues at the Fisheries Centre, Rashid Sumaila, Marcelo Vasconcellos, Leonardo Huato and Trevor Hutton for helping me with technical problems. I am indebted to David Preikshot, Ying Chuenpagdee, Melanie Power and several other colleagues for their help with my written English.

I thank Dr Bruce Atkinson from the Department of Fisheries and Oceans for the permission to access the data bases. I am especially thankful to Peter Shelton and Eugene Murphy for their help with the survey and catch data, David Kulka with the observer data, and Anne Marie Russell and Sandra Savoy for the detailed catch statistics data base. I would like to express my gratitude to several researchers for their comments and generosity in discussions on cod and cod fisheries, namely: Drs Jeffrey Hutchings, Jon Lien, John Anderson, George Lilly, Richard Haedrich, David Schneider, Bob Gregory, George Rose, Paul Fanning and Bob Mohn.

This long project would not have been possible without the funding provided by diverse scholarships, NSERC, FCAR (Fonds pour la Formation de Chercheurs et l'Aide à la Recherche, Québec), and the University of British Columbia Graduate Fellowship.

Finally, I would like to thank Jean Lamontagne, my life companion, for his persisting support and encouragement through the long learning process in which long hours, nervousness, self-doubt and tight budgets were recurrent. My parents and their deep belief in me were helpful in a lot of different ways. Merci de tout coeur.

Chapter 1.

Fisheries management and marine reserves, an overview

INTRODUCTION

Even in countries where large financial resources have been used for fisheries stock assessment and science, management has often failed to prevent overexploitation for an array of reasons. Although various management reference points have been developed (Deriso, 1987; Sissenwine and Shepherd, 1987; Patterson, 1992; Mace and Sissenwine, 1993; Smith *et al.*, 1993; Mace, 1994; Myers *et al.*, 1994), they mostly rely on accurate estimation of the stocks and adequate models, as well as efficient control of effort and catch. These strategies typically underestimate the importance of uncertainties in stock assessments, population dynamics and environmental processes, which often result in overfishing (Hilborn and Walters, 1992; Ludwig *et al.*, 1993; Rose, 1997; Lauck *et al.*, 1998). In addition, management schemes achieve only partial success in controlling effort and/or catch, in some cases inciting fishers to cheat by misreporting, discarding and upgrading (FRCC, 1996; Munro *et al.*, 1998). Finally, reducing effective fishing effort is almost impossible in the face of improving technology (Hilborn and Walters, 1992; Parsons, 1992; Ludwig *et al.*, 1993; see also Pitcher, in press).

In human history, the solution to local depletion has been to explore the sea a little further, using increasingly sophisticated gear (Pitcher and Pauly, 1998). This behaviour led to the shrinkage of historical fish refuges. Local fisheries have often survived a stock collapse by switching species, resulting in serial collapses (see for example Dugan and Davis, 1993a; Orensaz *et al.*, 1998). Serial spatial depletion is also frequent and a good example is provided by the fishery on sea mounts of the Chatham Rise that, during the 1980s, depleted one seamount after another (Clark, in press). The development of a new technique to fish tuna in very deep water south of Tahiti, a resource previously unknown in the area (Bard, 1999) is another good example. Although useful to local fishers, this innovation has the effect of opening, one more time, a de facto refuge to fishing.

In the light of widespread fisheries management failures, a growing number of scientists are looking for management schemes that do not depend on an accurate knowledge of the stock and fishing processes (Walters, 1998). It is believed that marine reserves, the areas closed to exploitation, would allow better resilience to management errors such as overestimation of stocks, lack of control of fishing effort and inaccurate catch statistics. The idea of using marine reserves in fisheries management is not new. It was first formally considered by Beverton and Holt (1957) who were, for marine reserves as for other aspects of fisheries science, ahead of their time. But they rejected the use of reserves in favour of traditional management techniques such as fleet and gear control. The latter were thought to be simpler to implement and less detrimental to fishers. The authors also felt that detailed knowledge of movement patterns would be required in order to assess benefits properly. Since that analysis many fisheries have collapsed worldwide, illustrating the vulnerability of fishery resources and the ineffectiveness of traditional management techniques.

OBJECTIVES

The present study aims at evaluating the efficiency of marine reserves to protect a migrating and shoaling fish. More specifically the objectives are:

- Assess whether the use of marine reserves could prevent a collapse
- Compare different designs of marine reserves;
 - determine optimal size, shape and location of marine reserve
- Compare marine reserves with other types of management measures;
 - compare with seasonal closures, quotas and direct decrease in effort;
 - assess how marine reserves would protect the stocks if effort increased.

The evaluation of management scenarios uses models based on a case study to add a sense of reality to the exercise. Because its demise was mainly due to overexploitation (Hutchings and Myers, 1994; Myers *et al.*, 1996; Myers *et al.*, 1997a), the northern cod (*Gadus morhua*) off Newfoundland constitutes an excellent case study.

THE NORTHERN COD, *GADUS MORHUA* L.

Biology

Northern cod live about 20 years, although old individuals of 26 years have been found. Under recent exploitation, cod older than 12 were rare. Age at maturity for the northern cod of NAFO regions 2J, 3K, and 3L (Figure 1.1) is about 5-7 years old. Trawl surveys conducted between 1946 and 1991 show a drastic decline of the proportion of older (15-20 yr) relative to younger (7-9 yr) spawners in the cod population and a 85% decrease of the former's contribution to total fecundity (Hutchings and Myers, 1993; Trippel, 1995). These factors are likely to cause an increased variability in recruitment in two ways. Older females spawn over a longer period each year which may enhance probabilities for emerging larvae to encounter favourable environment (Hutchings and Myers, 1993). Also, the older and larger females have larger eggs which lead to larger larvae, which may have a better chance to survive (Kjesbu, 1989; Kjesbu *et al.*, 1996).

Although stock assessment has treated northern cod as a single stock, it is widely recognized as a stock complex (Alverson *et al.*, 1987; deYoung and Rose, 1993) with possibly distinct inshore (stay inshore all year long), offshore (remaining in the offshore areas) and migrating stocks. Fishers' description of different groups of cod caught inshore at different period of the year (Lear and Parsons, 1993; Lilly, 1996; Neis *et al.*, 1996) and, to a lesser degree, recent genetic studies (Ruzzante *et al.*, 1996) suggest that inshore and offshore wintering cod are distinct groups. During winter and early spring, cod are aggregated in large shoals, along the slopes of the continental shelf, where they are very vulnerable to trawl fishing. They migrate to spawning grounds and coastal feeding areas in springtime. Spawning occurs in late winter and early summer on the continental shelf (Rose, 1993; Taggart *et al.*, 1994), and inshore (Hutchings *et al.*, 1993; Anderson *et al.*, 1995). They disperse along the coast following capelin. In the fall, cod migrate to their wintering grounds, the warmer ($>2^{\circ}\text{C}$) waters of the margins of the continental slopes.

Fishery

The northern cod has been the principal fishery on the east coast of Canada for centuries (Hutchings and Myers, 1995). Declining catches of cod were observed as early as the 18th and 19th centuries. In response, fishers expanded their activity to the coast of Labrador and to the banks (Hutchings and Myers, 1995). The introduction of European factory trawlers in the 1950s led to a large increase in catch followed by a sharp decrease in the cod population in the 1970s. The extension of Canada's jurisdiction in 1977 was accompanied by an air of optimism that the cod population would rebuild rapidly and that the bounty would

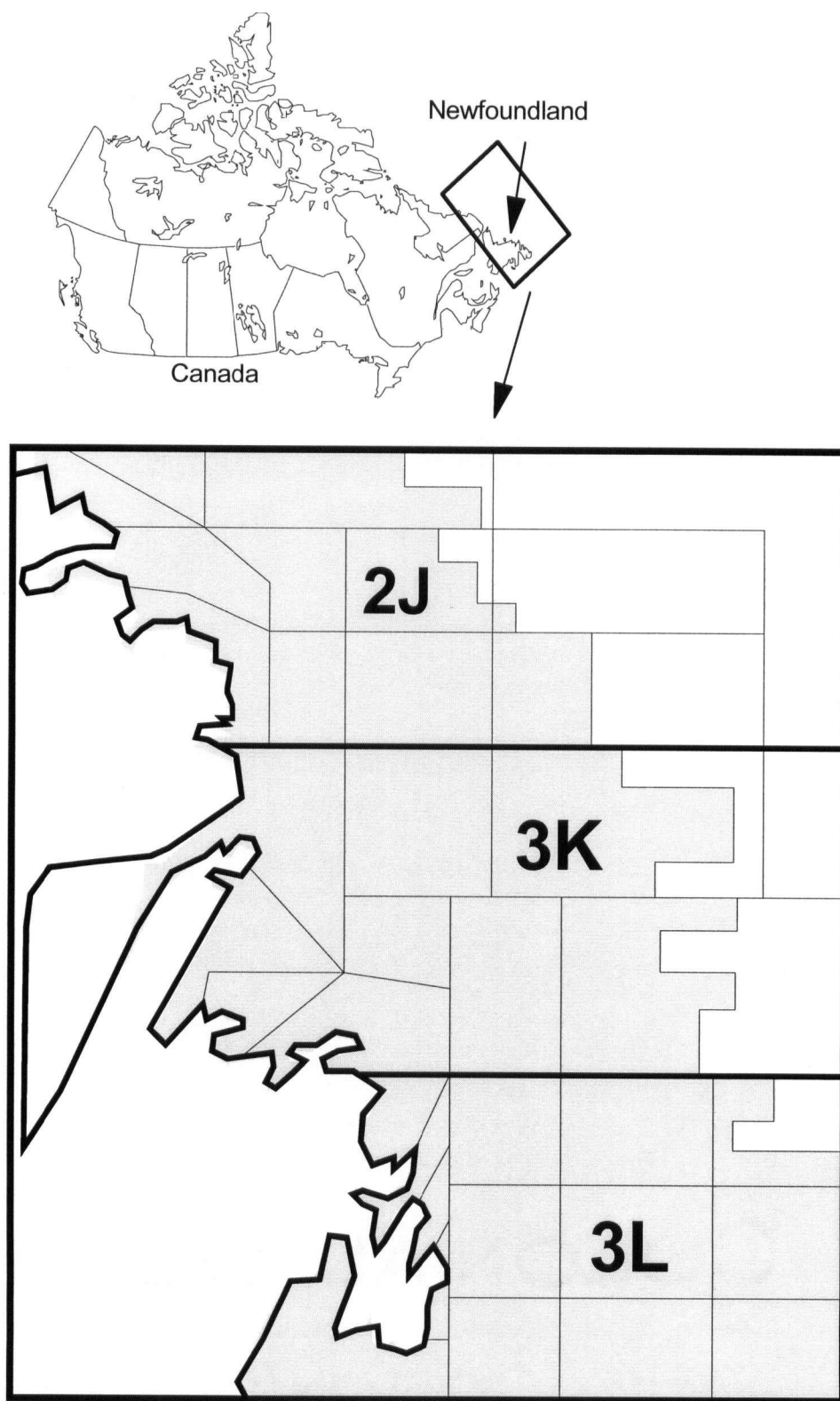


Figure 1.1 Study area (shaded) on the coast of Newfoundland and NAFO divisions.

subsequently be accessible to Canadian fishers (Lear and Parsons, 1993). Instead, the cod never fully rebuilt, and finally collapsed under increased fishing pressure. In 1992, the Government of Canada had to close the cod fishery and about 30,000 people lost their livelihood (Lear and Parsons, 1993; Hutchings and Myers, 1995; Harris, 1998).

This catastrophe gave rise to numerous analyses and critiques underlining the failures of the science and the management. It is generally recognized that the collapse was mainly caused by overexploitation. The cod population and sustainable exploitation rate were systematically overestimated entailing overestimation of the quotas (Lear and Parsons, 1993; Walters and Maguire, 1996). Although the target fishing mortality was set to a maximum of 0.2 ($F_{0.1}$) as early as 1977 (Hutchings and Myers, 1995), tagging data show that F was equal to 0.5 or higher in the 1960s and increased in the late 1980s and early 1990s reached or exceeded 1.0 (Myers *et al.*, 1996)! In the meantime, widespread catch misreporting and discarding occurred in both the inshore and offshore fleets due to the lack of larger cod (Hutchings, 1996). Facing declining catches, inshore fishers increased effort, using rapidly improving technology (Neis, 1992; Hutchings and Myers, 1995; Neis *et al.*, 1999). The mobility of the trawl fleet, its efficiency at finding fish aggregations and the tendency of the cod to form large aggregations, even when abundance decreases (Hutchings, 1996), are factors that often lead to fishery collapses (Hilborn and Walters, 1992; Pitcher, 1995). Since the trawl fishery targeted the pre-spawning and spawning aggregations (Hutchings, 1995; Hutchings, 1996; Younger *et al.*, 1996), CPUE remained stable in an apparent hyperstability often encountered in pelagic fisheries (Hilborn and Walters, 1992). Shoaling behaviour along with the non-random search has often been an important cause of collapses (Saville, 1980; Saville and Bailey, 1980; Pitcher, 1995).

In addition, Atkinson *et al.* (1997) showed that the geographical range distribution of cod decreased with its abundance. Similar range variation has been observed for Japanese sardine (Kondo, 1980), Peruvian anchoveta (Arenas, 1992), Atlantic herring (Winters and Wheeler, 1985), Norwegian spring spawning herring (Dragesund *et al.*, 1980) and many other species of aquatic and non-aquatic animals (Arenas, 1992). As stock abundance and their geographic distribution decrease their catchability increases rapidly leading to stock collapse (Pitcher, 1995). This has been found in several species such as the Californian sardine fishery from 1932-1950 (MacCall, 1976), the Atlantic cod (Rose and Leggett, 1991), Norwegian spring-spawning herring (Ulltang, 1980) the Georges Bank haddock (Crecco and Overholtz, 1990) and the Pacific salmon sport fishery (Peterman and Steer, 1981).

THESIS OUTLINE

Chapter 2 reviews the literature on the use marine reserves as a fisheries management tool. It was published in *Reviews in Fish Biology and Fisheries* in 1998. I was the first author of a team of three; thus, I played a major role in setting the goals, elaborating the plan, and writing the paper. Chapter 3 describes an age-structured dynamic pool model based on cod that included reproductive factors. The model, based on Dr Tony Pitcher's original idea, has been published in *Fisheries Research* in 1999. I am responsible for all the modelling and the writing. The next step was to build a realistic spatially and temporally structured model based on data regarding fish biology and the cod fishery characteristics in Newfoundland. Chapter 4 describes the temporal and spatial distribution of the catch and effort for the period 1960-1991 which provides the basic information for the models developed in Chapter 5 and 6.

The spatially-explicit model (Chapter 5) includes fish migrations, geographical range collapse and fishing behaviour (spatial redistribution of fishing effort in response to cod abundance). It is intended to test the usefulness of marine reserves in the case of a migrating fish, to compare reserves to closed seasons and

reduction of effort. The model is also used to compare various reserve designs. The model was first developed by Dr Carl Walters and used for lobster and shrimps and sharks. I modified it to suit cod life history and the fishery characteristics. I am also responsible for the data gathering and writing the paper which is in press in *Bulletin of Marine Science*. Chapter 6 describes a modified version of the model used in Chapter 5 that starts in 1960, when the population was larger. The model also includes recruitment anomalies. The chapter is intended to evaluate marine reserves acting as insurance policies against assessment and management errors. It also evaluates whether the fishery would have been sustainable in the absence of trawlers.

The complete references are:

- Guénette, S., Lauck, T., and Clark, C., 1998. Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries*, 8:251-272.
- Guénette, S., and Pitcher, T. J., 1999. An age-structured model showing the benefits of marine reserves against overexploitation. *Fisheries Research*, 39:295-303.
- Guénette, S., Pitcher, T. J., and Walters, C. J., in press. The potential of marine reserves for the management of northern cod in Newfoundland., *Essential Fish Habitat and Marine Reserves*, William R. and Lenore Mote International Symposium in Fisheries Ecology, Sarasota, Florida, *Bulletin of Marine Science*.

Chapter 2.

Marine reserves: from Beverton and Holt to the present ¹

FISHERIES AND FISHERIES SCIENCE ARE IN TROUBLE

Despite intensive management effort, fish stocks have been dwindling worldwide, bringing fisheries science to a crossroad. Uncertainties in stock assessments, population dynamics, underlying physical processes and their variability have interacted to mask the real trends of many fisheries (Hilborn and Walters, 1992; Ludwig *et al.*, 1993). Fisheries' statistics, though widely available, have usually been highly inaccurate (Larkin, 1977) and misrepresented fishers' behaviour. Further, the use of misleading or inadequate models has led to overfishing (Larkin, 1977; Bohnsack, 1993; Walters and Maguire, 1996). Also, in the past, uncertainty in fisheries management has not received sufficient attention (Hilborn and Walters, 1992; Walters and Punt, 1994; Frederick and Peterman, 1995; Lauck *et al.*, 1998) and policy suggestions may not always have been implemented. Lastly, economic, social and politically motivated decisions often resulted in overfishing, stock collapse and loss of substocks (Larkin, 1977; Ludwig *et al.*, 1993). These factors coupled with increasing pressure on natural populations have made protection of fish stocks even more crucial. Therefore marine reserves, areas completely closed to fishing, are receiving renewed attention for protecting populations from overexploitation (Bohnsack, 1996).

Beverton and Holt (1957) extended their yield per recruit model to examine the effect of spatial variation in fishing mortality, caused by unfishable areas, on plaice (*Pleuronectes platessa*) in the North Sea. Unfishable zones were identified as nurseries (not much fished but likely to contain some adults), areas naturally unsuitable to trawling or out of range of the fleet, and the mine fields extant after World War II that prevented use of otherwise good fishing grounds. This led them to consider closed areas as a possible management tool, then a novel concept. After four decades, it would be worthwhile examining whether subsequent modelling and empirical data modify Beverton and Holt's conclusions. In so doing, it would also be worthwhile to consider management objectives that go beyond the question of simply increasing yield.

This paper focuses on marine reserves as a management tool and on modelling efforts that have been carried out so far. We review only briefly the evidence in support of marine reserves, using a representative subset of the available literature, because comprehensive reviews have been published by Plan Development Team (1990), Roberts and Polunin (1991), Dugan and Davis (1993a), Rowley (1994) and Bohnsack (1996).

BEVERTON AND HOLT'S MODEL OF MARINE RESERVES

A simplifying assumption, that has received some attention in later models, was that the transfer of fish between exploited and unfished areas was governed by uniform random diffusion, independent of location or age. The yield per recruit (Y/R), in weight, was given as a function of fishing mortality (F) in the exploited region for different values of unfishable areas (U ; Figure 2.1). The yield per recruit curve did not change much when the unfishable area was smaller than 25% (Figure 2.1). The three curves reached F_{max} , F at which the yield per recruit is maximal, at similar values, and yields decreased as fishing mortality passed F_{max} . However, as the unfished area increased, the curve changed shape considerably and F_{max}

¹ Published as: Gu  nette, S., T. Lauck and C. Clark 1998. Marine reserves: from Beverton and Holt to the present. Reviews in Fish Biology and Fisheries 8:251-272

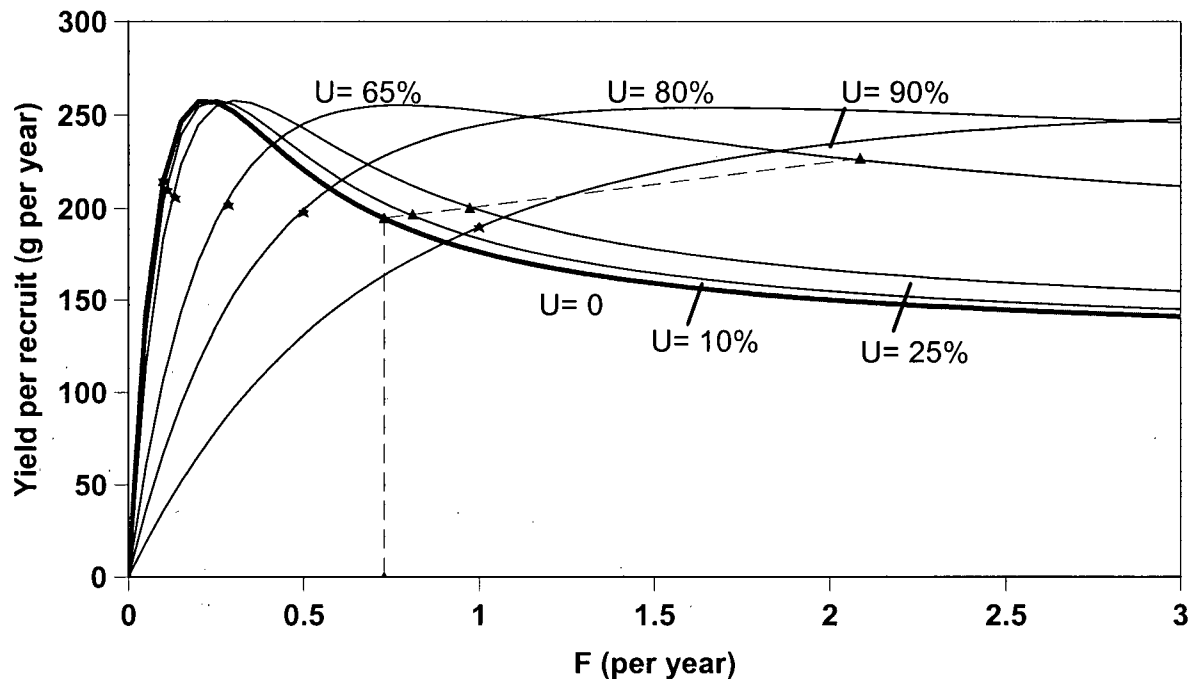


Figure 2.1 Yield per recruit for different size of unfishable areas (U) as a function of the fishing mortality on the harvested grounds (Redrawn from Beverton and Holt 1957). In order to evaluate marine reserves as a management tool the effort has been assumed to be concentrated on the harvested grounds, increasing F in fished areas. The broken line connects the yields for different reserve size corresponding to $F_{\infty} = 0.73$, while the stars corresponds to $F_{\infty} = 0.1$. See text for details.

increased. It is worth noting that these larger *de facto* reserves maintain higher yields when the population is overfished ($F > 0.5$) (this and all subsequent instantaneous rates are understood to be annual).

To examine the effect of using reserves as a management tool, Beverton and Holt assumed that fishing effort, originally applied to the entire area in absence of a reserve, would be concentrated in a smaller area, increasing the fishing mortality such that $F_{MR} = F_{\infty} / (1 - MR)$. F_{∞} is the fishing mortality applied to the total area in the absence of a reserve and MR is the reserve size expressed as a proportion of the total area. Here we used MR instead of U to emphasize that establishment of reserves implied redistribution of fishing effort. Beverton and Holt (1957) assumed a constant effort generating a pre-war value of $F_{\infty} = 0.73$. When the reserve size was 25%, for example, the resulting fishing mortality F_{MR} was 0.97. The resulting yield was found at the intersection of F_{MR} and the $U=25\%$ curve. The broken line joined these new estimates of yield and showed that the theoretical yield per recruit would increase gradually as the size of the reserve increased (Figure 2.1). Note that reserve sizes of 80 and 90% resulted in very high fishing mortalities in the fished area, F_{MR} of 3.65 and 7.3 respectively, which are outside the graph range. The authors noted that the closed area would have to be large to produce any marked increase in yield even at high fishing mortality. Under the same procedure with a low fishing mortality ($F = 0.1$), the yield per recruit decreased slightly in the presence of a reserve (stars; Figure 2.1).

It should be noted that the yield per recruit model gave an incomplete picture of the impact of fishing as it assumed that the population reached a steady state and that recruitment was adequate. In fact, a high level

of fishing mortality may reduce spawning biomass and thus negatively affect recruitment. Even worse yield per recruit curves usually show a positive yield per recruit, even when collapse is imminent. Comparing management strategies using theoretical yield per recruit curves is still useful, but considerations of spawning biomass and possible recruitment failures must be kept in mind.

Though a potential increase in yield was noted, Beverton and Holt were not convinced of the usefulness of marine reserves as a management tool. They felt that detailed knowledge of fish movements would be required, making benefits difficult to assess. Also, both very fast and very slow interchanges between areas would negate increases in yield. In the first half of the 20th century traditional management tools were easier to understand and were thought sufficient to control fishing effort. It was thought that the cost of finding fish would likely increase if fishers were arbitrarily restricted, so effort control became a popular management strategy.

On the other hand, Beverton and Holt (1957) cautioned that any fishery would become the victim of its own financial success. They recommended that regulatory measures be combined with control of fishing intensity lest immediate profits from the fishery create an incentive towards excess fishing power. Since then it has been found that regulatory measures such as gear selectivity, catch size regulation, control of fleet size and power and catch reduction, often provided inadequate protection for fish stocks. Trip limits and by-catch regulations have been found to encourage misreporting and dumping at sea (Halliday, 1988; Richards, 1994). Roy (1996) concluded that quota management failed to control overfishing in the Northwest Atlantic groundfish fishery and failed to prevent a stock collapse by not accounting for the large uncertainties inherent to fisheries management. As early as the 1970s, most pelagic fisheries were recognized as being in a critical state (Saville, 1980). Commercial landings had either declined or were being sustained by shifting species or sectors which in turn declined successively (Ballantine, 1991a; Dugan and Davis, 1993a). All of these gave incentives to reconsider the idea of marine reserves to control fishing effort more efficiently.

CURRENT MODELLING OF MARINE RESERVES

Many investigators (Table 1) have enhanced the yield per recruit model to assess the impact of a reserve and fish movements between it and adjacent fishing grounds, on yield and reproductive capacity as indicated by spawning stock biomass, number of recruits or quantity of eggs produced. Simulations covered a wide range of species such as Atlantic cod (*Gadus morhua*) (Polacheck, 1990; Daan, 1993; Mohn, 1996; Sumaila, 1998), penaeid shrimps (Die and Watson, 1992b; Watson *et al.*, 1993), red sea urchins (Quinn *et al.*, 1993), endemic surf-zone South African fish (Attwood and Bennett, 1995) and reef fishes (Russ *et al.*, 1992; DeMartini, 1993; Man *et al.*, 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997).

Population

In the absence of fishing mortality, abundance and biomass of fish are expected to increase within reserves, which protect both fish and habitat (Polunin and Roberts, 1993; Rowley, 1994). Reserves may then support surrounding fisheries by adult emigration (spillover) or exportation of larvae (Rowley, 1994). Empirical data have provided evidence of the capacity of marine reserves to rebuild populations. Within reserves, density and average size of sedentary animals such as molluscs and reef fish have been found to increase: see comprehensive reviews by Plan Development Team (1990), Roberts and Polunin (1991), Dugan and Davis (1993a), Rowley (1994) and Bohnsack (1996) and recent papers such as those of Bennett and Attwood (1991; 1993), Branch and Moreno (1994), Francour (1994), Ramos-Espla and McNeill (1994), Davis (1995), Ferreira and Russ (1995), Roberts (1995), Rakitin and Kramer (1996), Russ and Alcala (1996b),

Table 2.1 Species, population model type, closure type and specific features of the models cited in this paper.

Species	Population	Model type	Characteristics of model			Sources
			closure	F adjusted ⁽¹⁾	others features included	
Atlantic cod	Georges Bank data	Y/R ⁽²⁾	areas	yes	—	Polacheck (1990)
Atlantic cod	Fictitious	Dynamic pool ⁽³⁾	areas and season	no	catchability adjusted for change in abundance; protection of aggregations	Mohn (1996)
Atlantic cod	Barent Sea	Dynamic pool	areas	NA	no overexploitation; population subjected to series of recruitment failures; bioeconomics	Sumaila (1998)
Penaeid shrimps	Australia	Y/R	areas	no	migration; uncertainty on F	Die and Watson (1992b)
Penaeid shrimps	Australia	Y/R	season	yes	fleet dynamics (redistribution of effort)	Watson <i>et al.</i> (1993)
3 species of reef fishes	Pacific	Y/R	areas	yes	comparison of life histories and SLOSS ⁽⁴⁾	DeMartini (1993)
reef fish	Philippines	Y/R	areas	NA	prediction of mechanisms for observed higher yields around Sumilon reserves	Russ <i>et al.</i> (1992)
reef fish	Fictitious	Metapopulation	areas	no	larval dispersal; density-dependence	Man <i>et al.</i> (1995)
reef fish	Caribbean	Dynamic pool	areas	no	Larval dispersal; assess long-term benefits of reserves	Sladek Nowlis and Roberts (1997)
Red Sea urchins	West Coast USA	Logistic	areas	yes	density-dependence; space and age structured	Quinn <i>et al.</i> (1993)

Species	Population	Model type	Characteristics of model			Sources
			closure	F adjusted ⁽¹⁾	others features included	
3 species of surf zone fish	South Africa	Dynamic	areas	no	Larval and adult dispersal; space, time and age structured; test for potential increase in yield for sport fishery	Attwood and Bennett (1995)
cod-like	North Sea	Short-term dispersion of adults	areas	yes	sub-units scattered or contiguous (SLOSS) ⁽⁴⁾	Daan (1993)
red snapper	Gulf Mexico	Leslie dynamics	areas	yes	density-dependent growth, survival and transfer; uniform dispersal of larvae	Holland and Brazee(1996)
Fictitious	Fictitious	Discrete logistic growth	areas	yes	large uncertainty in attainment of harvest targets	Lauck <i>et al.</i> (1998)

⁽¹⁾ Assume concentration of effort in the fished area and thus increase exploitation rate.

⁽²⁾ Yield per recruit.

⁽³⁾ Age structured model including stock-recruitment function.

⁽⁴⁾ Single Large or Small and Scattered reserves debate

Stoner and Ray (1996), and Vincent and Pajaro (1997). Given the expected increase in individual size, reserves could be a hedge against recruitment failures for sex changing species threatened by size-selective fishing (Buxton, 1993). Adult migration would result from a density gradient while increase in fecundity and dispersion by ocean currents would result in export of larvae. Although hard to test, larval dispersal is likely to play an important role in enhancing recruitment in surrounding fishing areas (Bohnsack, 1996).

Adult migration

Most models showed that the reproductive potential (spawning stock biomass (SSB/R) or eggs per recruit) for the whole population improved when closed areas were considered. However, faster transfer rates of adult fish from the reserve to the fishing grounds diminished the increase in spawner biomass. In non-migratory species, it is easy to understand why the spawning stock biomass could increase with a reserve: lower transfer rates allow better survival in a part of the population, which in turn improves the reproductive capacity because the age structure includes more mature individuals. Closed seasons worked similarly for shrimp (Die and Watson, 1992b) by protecting the spawning stock of some cohorts until they reached sexual maturity and spawned, increasing eggs per recruit (Die and Watson 1992b). As expected, results were dependent on the length of closure, due to the pulse of effort at the beginning of all fishing seasons, and the variation of recruitment patterns. Holland and Brazee (1996) showed that optimal reserve size increased when transfer and growth rates were changed from density dependent to density independent. Mohn (1996) found that closed seasons increased the biomass and yield of a stock when the spawning aggregation was protected. Besides increasing density and biomass, reserves may protect against stochastic events such as recruitment failures, even at moderate fishing mortalities (Sumaila, 1998). Also, marine reserves would decrease the risk of management failure when the uncertainty of actual harvest is large (Lauck *et al.*, 1998).

Daan (1993) examined the impact of fish movements for a short period of time (1 year) without including any population dynamics (growth, mortality, recruitment). He divided up the North Sea into cells in which cod-like fish were homogeneously distributed and dispersed on a weekly time step. Alternately modelling the reserve with either a collection of scattered or contiguous cells, he showed a significant increase in survival with contiguous cells. De Martini (1993) obtained similar results, finding that longer boundaries increased the transfer rate. He also found that the efficiency of marine reserves varied among the three species considered and depended on their natural and fishing mortalities and, to lesser extent, on their rate of transfer from the reserve. In order to protect the spawning biomass, reserves could be smaller (MR= 10%) for short-lived fast-growing species than for long-lived slow-growing ones (>30%). However this result may be linked to transfer rates, because the long lived species also had the highest transfer rates in DeMartini's model. The recruitment of juveniles to the fishery before they reach maturity has been shown to diminish the benefits of a reserve (DeMartini, 1993). Thus a reserve alone may not provide sufficient protection for a population and should not be considered in isolation from other management measures.

Larvae export

A few models accounted explicitly for eggs or larvae exports (Quinn *et al.*, 1993; Attwood and Bennett, 1995; Man *et al.*, 1995; Sladek Nowlis and Roberts, 1997). Man *et al.* (1995) used a metapopulation approach. If fish were distributed in patches, the rate at which they occupied new patches would be dependent upon the proportion of occupied versus unoccupied patches. This raised the question of what proportion of the population, or patches, should be included in a reserve when the fishing mortality is not controlled. At high exploitation rates, optimum yield was obtained when the proportion of area held in the reserve was just below 50%. Also, at optimal reserve size, maximum yield was obtained when half of the patches had new recruits. Quinn *et al.* (1993) constructed an age- and space- structured which included larval dispersal and a depressed survivorship per capita as abundance diminishes, for both spawning and abundance of the larvae. They then showed that the number of larvae remaining in the reserve and the

strength of the density-dependant effects both influenced the rate of replenishment of the fished area and concluded that the distance between reserves should be less than the dispersal distance of the larvae. This conclusion emphasized the importance of reserve location with respect to seeding populations. For example, a network of small reserves with proper distance from each other would better protect red sea urchins than a single large reserve. However, if exploited grounds are fished down below a critical density, recruit settlement will not be successful, retarding or jeopardizing the rebuilding of populations of fishing grounds (Quinn *et al.*, 1993).

Yield

Most models have confirmed Beverton and Holt's main results, that marine reserves would decrease yields at low fishing mortality but may increase it slightly at high F . The level of increase depends on reserve size and transfer rate from the closed area (Russ *et al.*, 1992; DeMartini, 1993; Quinn *et al.*, 1993; Attwood and Bennett, 1995). Considering directed migration of adults with a yield per recruit model, Die and Watson (1992b) also found a decrease in yield per recruit which depended on the residence time in a closed area. They also found an increase in the value of the catch owing to increased individual size. The model developed by Attwood and Bennett (1995) included larval and adult dispersal based on a model of larval dispersal in the Benguela current and tag-recovery data. They showed a potential increase in yield for two of three species of fish considered, all subjected to high sport fishing pressure. The optimal size of a reserve is highly dependent on the distance travelled by the fish it has been created for. In the case of a sedentary fish (*Diplodus sargus capensis*) small closely distributed reserves protected fish and improved yields, which was attributed to "reserve-edge" effect. In contrast, a highly mobile and long-lived fish (*Dichistius capensis*) responded to the total area protected not the size of individual reserves. The authors assumed constant recruitment for the third species, white steenbras (*Lithognathus lithognathus*). They found that the spawning biomass per recruit, actually below 12% of the unexploited biomass (B_0), could be maintained at 20% using a reserve. Although the three species have different life histories and movement patterns, it was possible to find network properties that met all their requirements. After an initial drop, yield increased to the original level or higher within 10-30 years in Sladek Nowlis and Roberts' model (1997) and 6-9 years in Holland and Brazee's model (1996). Sumaila (1998) assumed that fishing fleets would exploit rationally, that is no risk of overexploitation, and found a decrease in yield are mitigated only where high transfer rate can be assumed.

Protection against overexploitation

The above results may lead to the conclusion that reserves would not be very useful as management tools. However, a growing body of evidence shows that most fisheries are heavily fished or overexploited (Ludwig *et al.*, 1993; Safina, 1995; Botsford *et al.*, 1997). In this sense the most important finding, brought to light by the use of dynamic models, is that reserves could increase resilience against overexploitation (Quinn *et al.*, 1993; Man *et al.*, 1995; Holland and Brazee, 1996; Mohn, 1996; Sladek Nowlis and Roberts, 1997; Lauck *et al.*, 1998) and disasters (Sumaila, 1998). As fishing mortality increased over MSY, yield remained constant in the presence of a reserve. Without a reserve, yield and population crashed.

As for other conservation measures, the initial establishment of reserves may result in short term losses for fishers (Brander, 1996; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997). Russ *et al.* (1992) pointed out that despite the negative effect on yield there could still be advantages because of the maintenance of the spawning biomass in the reserve. Daan (1993) contends that in fisheries management for the North Sea, any measure that would reduce exploitation rates is worth considering. In some cases however, loss of fishing grounds may increase competition among fishers, resulting in an incentive for investing in new technologies, thus increasing fishing mortality (Walters and Pearse, 1996).

Evidence that marine reserves may support a fishery has been less complete, owing to problems such as fish behaviour, poor sampling design, and recruitment variation (Dugan and Davis, 1993a) and variation in habitat quality (Roberts and Polunin, 1993b). Moreover, most existing marine reserves are small and were not necessarily designed for fisheries management purposes (Roberts and Polunin, 1993a; Alder *et al.*, 1994). Marine reserves are often exceptionally productive habitats difficult to monitor without comparative baseline data (Russ, 1985; Roberts and Polunin, 1993a). Finally, we have no general baseline studies telling us what an undisturbed and unfished area is like (Pauly, 1995). Still, many studies have demonstrated increased yields in surrounding fishing areas. For example, Ramos-Espla and McNeill (1994) reported an increase of 50-85% for the catches of *Sparus aurata*, *Epinephelus guaza* and *Dentex dentex* around the Tabarca Reserve in Spain, two years after it was created. Russ *et al.* (1992) suggested that the observed increase in yield around the Sumilon Reserve (Philippines) could not be accounted for by an increase in individual fish size and random dispersion alone. They believed it could be explained partly by a strong density gradient and the active emigration of adults from the reserve to the fished area. Subsequent evidence enforced that hypothesis. Following the breakdown of the Sumilon reserve in the Philippines, catch per unit effort in the 'unprotected' area fell by 50% within a year, suggesting that the biomass in the unfished area had been enhanced by the reserve (Alcala and Russ, 1990). Despite the probable increase of fishing effort around the Apo Reserve in the Philippines, densities of large predators increased in the fished area (Russ and Alcala, 1996a). After a 9 year delay, the effect was detected to a distance of 500m from the reserve boundary.

Increased CPUE, or persistent fishing, has been noted for Zuwai crab *Chionoecetes opilio*, in Japan (Yamasaki and Kuwahara, 1989), pink shrimps *Penaeus duorarum*, in Florida (Roberts, 1986) and spiny lobster *Panulirus argus* of Florida Bay (Davis and Dodrill, 1989). For pink shrimps, the lack of a spectacular increase in abundance was attributed to illegal fishing and large variations in recruitment (Roberts, 1986). Rowley (1994) mentioned anecdotal reports of changes in the behaviour of fishers, who concentrated their effort around the reserve, suggesting that some spillover occurs outside the reserve. This is probably the reason for the increased fishers' support for reserves.

INCREASING RECRUITMENT AGE

Regulating mesh and catch minimum size has been thought to be equivalent to spatial closures for delaying the age of recruitment into a fishery (Beverton and Holt, 1957; Die and Watson, 1992b). However, since the final vulnerability schedule of fish is the result of the selectivity of the gear, as well as the spatial distribution of smaller fish, closing nurseries would reduce the massive mortality from discarding juveniles. Garcia and Demetropoulos (1986) reported an increase in yield ranging from 2 tonnes to 3.5 tonnes per square nautical mile when Cyprus extended a closed season, thus preventing fishers from trawling too close to the littoral nursery grounds for red mullet and resulting in diminished juvenile mortality. Caddy (1990) reported that similar regulations on the Adriatic coast of Italy resulted in increased landings in both Italy and Yugoslavia. He attributed these results to an increased number of recruits coupled with additional growth.

UNCERTAINTY

Uncertainty confounds virtually every aspect of fisheries management, leading towards overfishing and stock collapse. A major contribution of reserves would be their function as an insurance policy against stochasticity and unforeseeable events (Ballantine, 1991a; Walters and Parma, 1996; Lauck *et al.*, 1998). An additional benefit would be protection against our lack of knowledge (Ballantine, 1991a). We need to acknowledge that no matter how much we have learned or understood, a large part will remain unknown, thus rendering complete control impossible. Our lack of knowledge covers specific items such as the

accurate estimate of population biomass and allowable quotas, to broader ones such as the adequate fisheries strategies to adopt, the functioning of marine environment and the impact of long-term environmental changes.

Most management strategies in temperate waters have been based on estimations of stock biomass and setting appropriate catch levels and exploitation rates. Even involuntarily, these rates are often exceeded several years in a row and sometimes systematically (e.g. Myers *et al.*, 1996; Nakken, 1998). Reserves would diminish our dependence on such precise and real-time information by shielding a part of the population from overharvesting (Botsford *et al.*, 1997; Roberts, 1997). Most fisheries should be exploited at very low levels to avoid removing older more fecund females (Pauly, 1997). However, history shows that we are not able to keep exploitation at low levels and decreasing fishing effort is the most difficult thing to do (Hilborn and Walters, 1992). Moreover, decreasing the effort and creating a reserve are not equivalent strategies because of the large uncertainty confounding fisheries management (Clark, 1996). Closing a significant part of the fishing grounds decreases the proportion of the population that is vulnerable (Walters and Parma, 1996; Lauck *et al.*, 1998). Thus extreme fishing mortality would be less likely, as long as there is no poaching.

Beverton *et al.* (1984) examined 10 exploited marine species with varying life histories. They noted that the absence of habitat refuge, along with features of life history like shoaling behaviour and aggregation at certain stages of life may decrease both robustness and reliability of fisheries. Indeed, natural refuges have disappeared because of improved technology, increased effort (Dugan and Davis, 1993a; Hutchings, 1995; Bohnsack, 1996) or erosion of traditional conservation methods (Johannes, 1978). Because they have worked in the past, we may assert that marine reserves would benefit the fishery (Shackell and Lien, 1995).

Marine reserves are not a panacea for all fisheries management problems although in cases like coral reefs where information and management options are unavailable they may be the only viable solution (Williams and Russ, 1995). In most cases, reserves should be seen as an additional management tool that would hedge against the risk of collapse (Bohnsack, 1993) and not as the ultimate management tool that would replace all other conventional measures.

HABITAT DEGRADATION

Lindeboom (1995) reported that each square metre of the Dutch sector of the North Sea is trawled at least once a year and several ICES (International Council for the Exploration of the Sea) rectangles are trawled up to 7 times a year by large Dutch fishing vessels. Therefore the benthic community never remains undisturbed for long, and has consequently changed from a system of large long-lived species to an assemblage of smaller faster-growing species such as worms. Such changes must have had an effect on fish populations. Lindeboom (1995) emphasized the need for undisturbed grounds to be used for studies on the effects of fishing as well as benthic ecological studies. Even at low exploitation rates, fishing activities may have profound effects on the habitat of demersal species by modifying the habitat and/or catching non-targeted species (Auster and Malatesta, 1995; Ballantine, 1995; Shackell and Lien, 1995; Jennings and Lock, 1996; Pauly, 1997) and modifying relationships between species (Branch and Moreno, 1994; Jennings and Lock, 1996). Fishing techniques such as dynamite, poison and *muro-ami* are particularly destructive to habitats and may impoverish marine resources and fish stocks (Jennings and Lock, 1996; Vincent and Pajaro, 1997). Other authors have emphasized the need of unfished areas to provide baseline data for studies which look at long-term environmental change (Ballantine, 1991b; Bohnsack, 1993; Dye *et al.*, 1994).

DESIGN OF RESERVES

Many authors have suggested that networks of representative habitats would insure that most marine species are protected against extractive use (Plan Development Team, 1990; Dye *et al.*, 1994; Shackell and Lien, 1995; Bohnsack, 1996) providing that they amount to a significant proportion of the total habitat. A network would increase reserves' buffer function against environmental variation and catastrophes by keeping a large spawning stock biomass and by supplying other areas with recruits. The Plan Development Team (1990) recommended that a minimum of 20% of the southern Atlantic coast of the United States be included in marine reserves on the basis that it would protect 20% of the spawning biomass at equilibrium, a threshold below which stocks are likely to collapse. Modelling results, using several species, suggest that a large proportion (up to 50%) of the total habitat be included in reserves (Attwood and Bennett, 1995; Man *et al.*, 1995; Sladek Nowlis and Roberts, 1997).

When the objective of reserves is to control fishing effort, protect specific exploited species and/or sustain the fishery then reserve design should account for life history strategies. Most work on marine reserves has been oriented towards relatively sedentary animals with widely broadcast larvae. In such cases, the spatial structure of populations, the relationships between patches and their dispersal capabilities, have been determined as crucial to the design of protected areas (Fairweather, 1991; Carr and Reed, 1993). This finding emphasizes the importance of protecting seeding populations organized in networks. Reserve design for more mobile animals should consider migration patterns and critical habitats (Plan Development Team, 1990; Shackell and Willison, 1995; Bohnsack, 1996). Numerous authors besides Beverton and Holt have noted that increased migration out of the reserve would diminish stock protection (Polacheck, 1990; Bohnsack, 1993; DeMartini, 1993). However, it may be possible to design reserves that would help protect the stock when they are used along with other management measures.

Permanent closures

Permanent closures would have the advantage of protecting the stock and the habitat from direct and indirect effects of harvesting. Reefs have provided the most numerous examples of successful reserves. Sedentary animals would be better protected by permanent closures that are adequately located, especially when the density of adults is an important factor for successful reproduction. For example, Rogers-Bennett *et al.* (1995) suggested that seed populations of red sea urchins, located in generally unfished shallow waters, be formally protected from exploitation to replenish fishing grounds. McGarvey and Willison (1995) proposed a closed area for scallops on the Georges Bank (Canadian and United States) where larvae are generally retained because of currents. Shepherd and Brown (1993) advocated using the metapopulation concept to deal with similar issues for greenlip and blacklip abalone (*Haliotis laevis*, *H. rubra*). Tegner (1992) showed that larval dispersal is rather limited for green abalone (*Haliotis fulgens*) on the Californian coast, preventing disturbed and overfished areas from being recolonised by other populations. Brood stock transplant experiments in 1981-1983, in sites where the probability of larvae retention was high, were successful in repopulating depleted areas (Tegner, 1993). Based on relative higher densities of larvae of Queen conch (*Strombus gigas*) in protected areas and on dominant currents in the Bahamas, Stoner and Ray (1996) attributed the source of larvae to the presence of large adults in the reserve and in unfishable sections of the unprotected area. They suggested that additional reserves should be located upstream of the extant reserve and that critical habitat such as migration paths be considered in the creation of a reserve.

Protecting critical habitat of migratory species has been shown to be a successful strategy. For example, Zuwai crab (Yamasaki and Kuwahara, 1989), pink shrimps (Roberts, 1986) and spiny lobster (Davis and Dodrill, 1989) have been protected with some success by closing specific habitats for juveniles, spawning females and pre-recruits. Failure to protect critical breeding and hatching grounds as well as juvenile habitat

were the suggested reasons for unclear results in the closed area for the red king crab (*Paralithodes camtschaticus*) in the Bering Sea (Armstrong *et al.*, 1993).

The idea of closing critical habitat may also be worthwhile in the management of groundfish fisheries. Walsh *et al.* (1995) proposed closing fishing grounds on the east coast of Canada located in nurseries for groundfish such as American plaice, *Hippoglossides platessoides*, yellowtail flounder, *Pleuronectes ferruginea*, and Atlantic cod. Closures could be used to reduce juvenile mortality from discarding off the Grand Banks on the East coast of Canada (NAFO Divisions 3L, 3N and 3O). It is believed that such a closure would be more effective than mesh regulations as it would reduce mortality and the indirect impacts of bottom trawling. Lastly, the complexity of habitat structure, used as cover by many species, could be a factor to protect and rebuild stocks (Auster and Malatesta, 1995; Gregory and Anderson, 1997).

Temporal closures

Cod, small pelagics and other highly migratory species have often proven to be highly vulnerable at certain times of the year. Along with permanent closures discussed earlier, protecting aggregations, core populations and migration paths on a temporal basis may be key components of proper management. Seasonal closures have been present in fisheries regulations for a long time (Hilborn and Walters, 1992). They were generally aimed at controlling effort and had the advantage of being easy to enforce. Although they often produced variable results depending upon changes in migration dispersal patterns as well as timing (Hilborn and Walters, 1992), these measures may grant protection at vulnerable periods of a species' life. Ultimately, where the area of distribution is shown to have been too large and variable, the fishing activity might best be confined to a limited area by a series of windows in time and space (Walters and Parma, 1996). This strategy has been used with success for Pacific salmon (Walters and Pearse, 1996). The Cyprus closed season mentioned earlier (Garcia and Demetropoulos, 1986) provided further evidence in support of this strategy. After analysing the historical catch data for cod, Hutchings (1995) proposed a ban on trawling during the pre-spawning and spawning aggregation period which would restore the spatial and temporal refuges that existed before the introduction of factory trawlers in the 1950s.

This idea could be developed further by acknowledging the vulnerability of species throughout different life history stages. The concept of protecting critical habitats, as part of an international network, is currently used for migratory birds (Myers *et al.*, 1987). Such networks have been designed to account for nesting, wintering and stop-over areas along migration paths. The protection of habitat has come to be seen as part of a series of management tools including hunting control and habitat improvement (Williams and Nichols, 1990). Apart from the fishery ban imposed to rebuild most whale populations, the protection of core habitats has been considered to be crucial (Brown *et al.*, 1995; Faucher and Whitehead, 1995). In Canada, for example, heavy ship traffic has been reduced and rerouted outside of whales' feeding and nursery areas.

As pelagic stocks aggregate when abundance declines, their catchability can increase rapidly, which can lead to stock collapse. Shoaling behaviour along with increased capability of finding fish exacerbates this phenomenon (Saville, 1980; Pitcher, 1995). MacCall (1990) modelled the expansion and contraction of the geographic distribution of fishes in relation to abundance and a theoretical index of spawning habitat quality. Protection should occur at locations, and times of high population concentration in a species' core habitat. Migration routes, spawning aggregations and/or nurseries should therefore be part of reserves. Such reserves should also be large enough to include the habitat used when the abundance is low. This information is available for many stocks that have been driven to collapse. As populations increase and spread out they would become available to fishing. For such a reserve to be effective, the spatial distribution of populations would need to be monitored to make sure the reserve includes a substantial portion of the population. Because we have not been able to predict fine scale-migrations, a protected area should not be

established within a rigid framework. In other words, marine reserves should also be used as a learning tool (Ballantine, 1991a).

Mixture of approaches

Three haddock (*Melanogrammus aeglefinus*) spawning grounds off the eastern coast of Canada and the United States have been closed each spawning season since 1970, along with further regulations such as TAC (total allowable catch), maximum by-catch (1%) and exclusion of certain gears in closed areas (Halliday, 1988). The spawning time (March-April) closure, the highest catch rate period, was implemented to reduce total catch by 20% and spread the catch throughout the year. Fishers supported the closures because they believed these would have a direct impact on recruitment. Indeed, biologists found that the closure was more effective at lowering mortality than various catch quotas and by-catch limits. Similarly, seasonal closures have been introduced in the North Sea to protect nurseries of vulnerable stocks of cod, plaice and haddock (Symes, 1990). Results within and around closed areas have suggested that reserves would be beneficial for these species (Lindeboom, 1995). The plaice box, in the North Sea, had been closed for half of the year from 1989 to 1994 to protect juveniles (ICES, 1994). However the expected benefits of the closure were lessened because the small vessels, allowed to fish in the box, increased their activity and investments starting in 1989.

When fishing grounds could be depleted below a critical density, additional measures are necessary. Botsford *et al.* (1993), using a yield per recruit model, suggested rotating harvesting grounds to control effort. Providing that the minimum size limit was respected, yield and spawners' biomass were found to increase linearly as the period between harvest was increased from 1 to 5 years. The authors pointed out that more work should be done on fishers' response to that policy and to the possible increase in cost. The expected increase in catch give fishers incentives to increase their effort at the onset of the fishing season (Watson *et al.*, 1993). Dye *et al.* (1994) suggested that this strategy would be applicable when the species concerned are fast growing and access to them restricted. They cited an example in Chile where a restricted number of persons were given the right to harvest alternately seaweeds and grazers. A second example, in southern Africa, involved cropping of fast growing kelp for which recruitment is better in the absence of mature plants. However, reopened areas are submitted to very high harvesting pressure and depleted rapidly (Plan Development Team, 1990; Roberts and Polunin, 1991; Bohnsack, 1993).

SOCIAL ASPECTS

Including fishers early in the decision making process has been argued to be essential to specify the reserve correctly in biological terms using their knowledge, and to gain their support by elaborating designs that take their concerns into account (Fiske, 1992; Alder *et al.*, 1994; Neis, 1995; Vincent and Pajaro, 1997). The closure of spawning grounds for haddock on the east coasts of Canada and United States was effective because fishers were convinced of its legitimacy and usefulness. The Apo and Pamilacan reserves in the Philippines were managed and supported by the local people because they believed in the potential benefits of protecting these areas (Russ and Alcala 1994). Although positive effects of the Sumilon reserve in the Philippines were acknowledged, the perception that the reserve was imposed by external powers, drove the fishermen to contest the legitimacy of the reserve (Russ and Alcala, 1994). Effective coastal management requires local participation because it promotes social equity and makes management more responsive to environmental and social changes (McManus 1996). Finally, the impact of possible changes in fishers' behaviour and their degree of compliance should also be evaluated to foster successful reserve design and implementation (Die and Watson, 1992a; Goodridge *et al.*, 1997; Hart, 1997).

DISCUSSION

Despite finding a small increase in yield per recruit with the use of a reserve, Beverton and Holt did not recommend their use. They reasoned that understanding the detailed movement of fish, although necessary, would be difficult to achieve. They thought that restricting access would create an unnecessary rise in the cost of fishing when alternative strategies, such as fleet reduction and gear restriction, were available and easier to implement. However, they were careful to recommend a mixture of these regulations to control fishing intensity.

Beverton and Holt's concern about the possible loss of yield following the creation of a reserve has become overshadowed by the need to control fishing mortality, rebuild stocks and prevent stock collapses. Using marine reserves may address these concerns and could be a way to formally take into account uncertainty. In combination with traditional control measures, marine reserves may help promote stock recovery, increase spawning stocks, provide a hedge against stock collapse and provide areas for the study of natural history and population dynamics. Marine reserves may also be easier to enforce than quotas and minimum size of fish, and may help resolve conflicting single-species regulations (Dye *et al.*, 1994; Ballantine, 1995). Used in combination with other management strategies, marine reserves would make exact knowledge of catch and population abundance less critical.

To date, Beverton and Holt's doubts about the potential benefits of marine reserves for fisheries, which arose from the complexity inherent in accounting for fish movement, has not yet been resolved. In fact, there has been little information forthcoming on the real relation between marine reserves and fish movement. Recent models have attempted to include relevant features that Beverton and Holt did not such as reproductive success, larvae dispersal, fish migrations and reserve geometry. Protection of crucial life history events such as spawning and juvenile development have been included as well. Also, including stock-recruitment relationship has introduced the notion of resilience to exploitation. Although equilibrium models have allowed us to examine the basic mechanism behind marine reserves, i.e. transfer rate and population dynamics, most of them still suppose homogenous distribution. In reality, aggregation or larvae production sites would play a crucial role in the design of a reserve. The most informative models published so far have included somewhat realistic spatial structure within which adult fish or larvae are moving according to probable speeds drawn from field study (Quinn *et al.*, 1993; Attwood and Bennett, 1995).

The next stage may be to integrate formally fish behaviour such as schooling and homing which could address many of Beverton and Holt's original concerns. Also, fish movement patterns in relation to their habitat should be investigated as they are essential to understanding vulnerability to fishing outside the reserve. Designing networks of reserves with proper size, shape and location presupposes a knowledge of critical habitat requirements in relation to selecting areas to protect, especially for migratory species. Similarly, for sedentary species, information about critical densities and the location of seed populations is crucial. Also the effectiveness of spatial closures should be evaluated and compared to effort control and other traditional management measures. Finally, determining the size, shape and location of a reserve should be considered a learning experience and modifications must be made as new information becomes available (Ballantine, 1991a). Monitoring the spatial distribution of keystone species must also become part of the learning process and would aid in the prevention of poor reserve design.

Chapter 3.

An age-structured model showing the benefits of marine reserves in controlling overexploitation ²

INTRODUCTION

In the face of continuously high pressure on fish stocks, marine reserves (areas closed to fishing) are emerging as an effective tool to protect populations from exploitation by putting a part of a population out of the reach of fishers (Polacheck, 1990; Dugan and Davis, 1993b; Rowley, 1994; Bohnsack, 1996; Lauck *et al.*, 1998). Beverton and Holt (1957) first considered the usefulness of closed areas for plaice in the North Sea using yield-per-recruit modelling but despite a potential increase in yield, they advised against the use of marine reserves because such a restriction on fishers was likely to increase the cost of finding fish. Also the importance of detailed analysis of spatial dispersion of fish was thought to be essential to assess the usefulness of marine reserves. Therefore Beverton and Holt recommended other regulatory measures for fisheries such as fleet reduction, catch reduction and minimum length of fish caught. Using an equilibrium model, Polacheck (1990) reconsidered closed areas with the goal of controlling fishing mortality. He showed that a marine reserve would cause an increase in spawning biomass but that the size needed for an effective reserve depends on the mobility of the fish. Subsequent modelling of no-take marine reserves has generally continued to employ equilibrium models assuming random fish movements. These models predict decreasing yield and benefits with increased fish movement. Most do not include biological factors, such as stock-recruitment relations and the higher fecundity of larger fish. Equilibrium models, such as the yield-per-recruit model, underestimate the impact of fishing on a population by assuming that recruitment remains adequate at any level of fishing mortality. Worse, even when collapse is imminent, yield-per-recruit curves will still show positive values.

In the present paper we use a non-equilibrium dynamic pool model to explore the advantages of marine reserves for recruitment and resilience against exploitation. This age-structured model, based loosely on Atlantic cod (*Gadus morhua*), includes stock-recruitment and weight-fecundity relationships.

METHODS

We compared a **Reserve** regime, that included an area closed to fishing, and a **No-reserve** regime in which only the usual fishery management rules are applied (Figure 3.1). Reserve size was expressed as a proportion of the total area. Each sector had its own age-structured dynamic pool that covered ages 1 to 15. The population was assumed to have equal numbers of both sexes at all ages and an instantaneous natural mortality (M) of 0.2 year⁻¹. Based roughly on values for cod, the age-specific weight, vulnerability (partial recruitment), and maturity schedules for ages 1-15 were based on Polacheck (1990) (Table 3.1) and the weight-fecundity relation of Buzeta and Waiwood (1982):

$$F = 110 * W^{1.14}$$

² Published as: Guénette, S. and T. J. Pitcher. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research 39:295-303

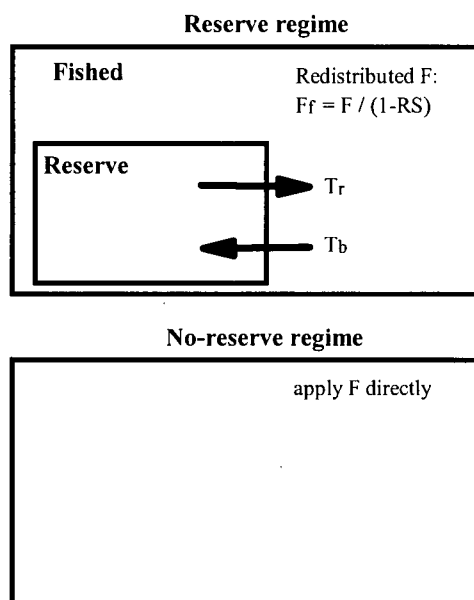


Figure 3.1. Organisation of the model. RS = reserve size as a proportion of the total area, F = instantaneous fishing mortality, F_f = redistributed F , T_r = transfer rate of fish from the reserve, T_b = transfer rate of fish from the fished area to the reserve, ref = reference reserve size (0.1), N_r and N_f = number of fish in the reserve and the fished area respectively.

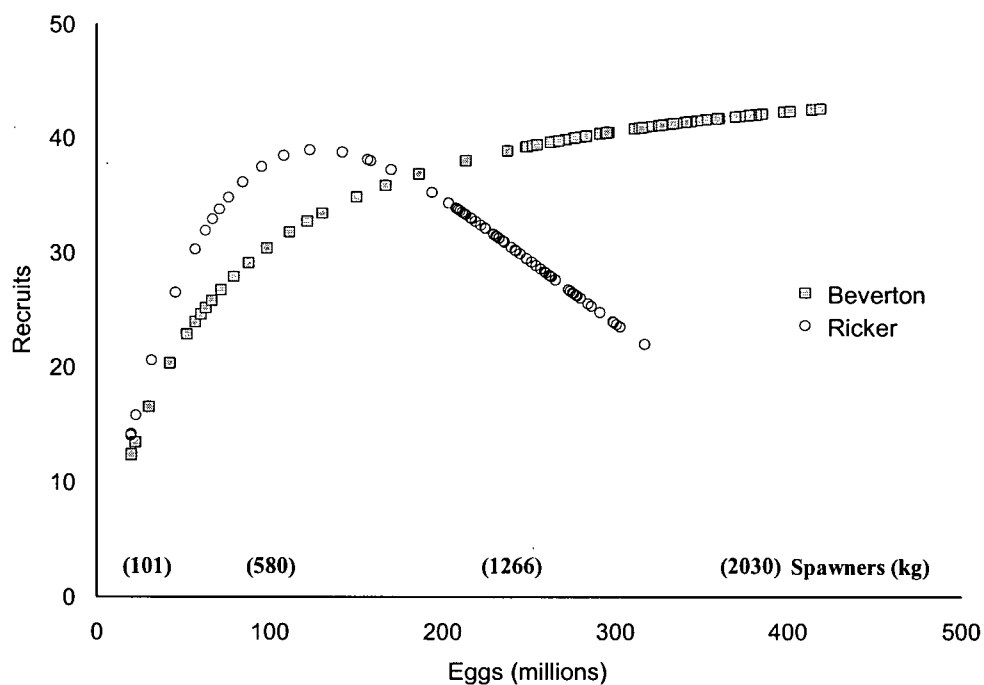


Figure 3.2 Beverton and Ricker eggs-recruitment curves used in the model. Numbers in parenthesis are the corresponding spawner biomass in kg, at low exploitation level ($u=0.1$).

Table 3.1 Mean weight, maturity and vulnerability schedules used in the model (adapted from Polacheck 1990).

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Weight (kg)	0.98	1.52	2.32	3.84	5.35	6.72	8.60	10.2	12.16	13.43	15.16	16.82	18.38	19.85	21.21
Maturity	0.01	0.25	0.71	0.91	0.97	0.99	0.99	1	1	1	1	1	1	1	1
Vulnerability	0.02	0.5	0.92	0.98	1	1	1	1	1	1	1	1	1	1	1

where W is the weight (g) and F the number of eggs. We used the number of eggs as a predictor of recruitment to emphasize the relative importance of large females for their proportionally larger number of eggs (Kjesbu, 1989). In addition large females spawn for a longer period which may lead to higher larval survival (Hutchings and Myers, 1993). The number of recruits (R) was a function of the number of eggs following either the Beverton:

$$R = \text{Eggs} * S_{\max} * (1 + k * \text{Eggs})^{-1} \quad S_{\max} = 8.29 * 10^{-07} k = 1.71 * 10^{-08}$$

or Ricker equations:

$$R = \text{Eggs} * S_{\max} * e^{(-k * \text{Eggs})} \quad S_{\max} = 8.29 * 10^{-07} k = 7.82 * 10^{-09}$$

where S_{\max} is the maximum survival rate of eggs and k is the scaling factor or carrying capacity (Figure 3.2). Parameters were calculated by finding the equilibrium transformation from B_0 and F_{\max} to K and S_{\max} (see Appendix 3.1). The carrying capacity was assumed to be related to the area of the habitat i.e., the number of recruits was proportional to the relative area of each sector of the Reserve regime. Hence, recruitment was scaled for reserve size of the Reserve regime: $K/(RS)$ for reserve and $K*(1-RS)^{-1}$ for the fished sector. White noise was added to recruitment by multiplication with a log-normally distributed random number.

We assumed random dispersion of fish and no directed movements in a uniform habitat so that fish movement is not a consequence of density or habitat quality but of velocity. As fish move out of the reserve, the area close to the boundary will be depleted after a short period (Beverton and Holt, 1957). We assume here that on an annual basis the movement rate of fish is large enough to compensate for the depletion effect along the borders. However, as the reserve size increases the ratio of perimeter over area diminishes and the probability to cross the border decreases. Thus, fish transfer rate out of the reserve (T_r) was a function of the reserve size:

$$T_r = T * (RS * ref^{-1})^{-0.5} \quad (\text{modified from Polacheck, 1990})$$

where the nominal transfer rate T , varies from 0.1 to 0.7 and represents the annual proportion of the population that would move outside the reserve, RS is the relative reserve size and ref is the reference reserve size (10%) used to scale the transfer rate. Thus the highest transfer rate from the reserve (T_r) occurs when the reserve size equals 10% of the total area. Also, the larger the reserve, the smaller the transfer of fish out of the reserve (Figure 3.3). The transfer rate of fish back to the reserve (T_b) is also function of relative size of the fished area:

$$T_b = T_r * RS * (1 - RS)^{-1} \quad (\text{modified from Beverton and Holt 1957})$$

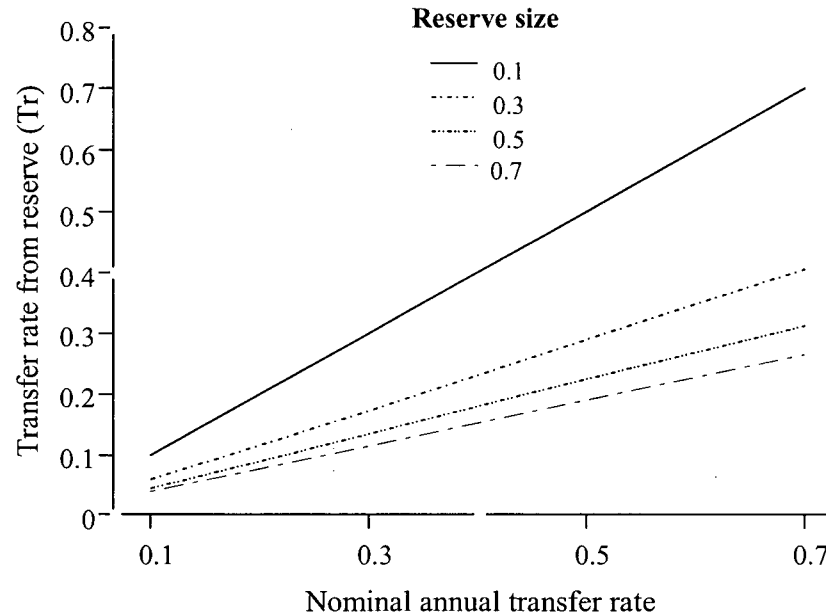


Figure 3.3 Behaviour of the transfer rates as a function of the size of the reserves.

Hence, no net transfer would occur when the mortality rate is equal in both sectors, meaning:

$$T_r N_r = T_b N_f$$

where N_r and N_f are the population size present in the reserve and fished sector respectively. Following the implementation of a reserve the fishing effort, generating an instantaneous fishing mortality (F), is assumed to be redistributed into a smaller area. Hence, the instantaneous fishing mortality in the fished sector (F_f) is increased as a function of the reserve size:

$$F_f = F * (1-RS)^{-1}$$

This implies a linear relationship between fishing effort and fishing mortality although it may not be true for all abundance levels. For convenience, the results were expressed as a function of the annual exploitation rate ($u = 1 - e^{-F}$) occurring in the No-reserve regime. The population abundance at age 1 is equal to the recruitment produced in the precedent year (R_{t-1}) as computed with the eggs-recruitment equations. For subsequent ages, the abundance in the No-reserve regime is described by:

$$N_{C,t,a} = N_{C,t-1,a-1} * S_{a-1} * (1 - v_{a-1} * u)$$

where $N_{C,t,a}$ is the abundance in the No-reserve regime at time t and age a , S is the annual survival rate ($=e^{-M}$), v the vulnerability at age to the fishery (Table 3.1). The abundance in the Reserve is:

$$N_{R,t,a} = (N_{R,t-1,a-1} + N_{F,t-1,a-1} * T_b - N_{R,t-1,a-1} * T_r) * S_{a-1}$$

and in the fished sector:

$$N_{F,t,a} = (N_{F,t-1,a-1} + N_{R,t-1,a-1} * T_r - N_{F,t-1,a-1} * T_b) * S_{a-1} * (1 - v_{a-1}^u)$$

The indicator variables used to monitor performance of the reserve were the number of years of weak recruitment, the spawner biomass and the yield. Recruitment was compared to an arbitrary threshold for each recruitment curve. The spawner biomass is the biomass of older females (7-15 years old) used as an indication of survival rate and draws attention to the importance of large spawners to recruitment. Results were expressed as units per thousand units of the population biomass at carrying capacity. The model was run for 60 simulated years in annual steps. For each combination of transfer rate, reserve size and exploitation rate we used the average result of 3,000 iterations.

RESULTS

The Maximum Sustainable Yield (MSY) was reached at similar exploitation rates using the Ricker recruitment curve (0.18) and the Beverton curve (0.15). Also, the response to exploitation and fish movements followed the same pattern for both recruitment curves (Figures 3.4 and 3.5). At a moderate transfer rate (0.3), the number of years of weak recruitment increased sharply as exploitation rate increased over MSY in the No-reserve regime while the spawners biomass decreased to practical extinction (Figure 3.4). In the Reserve regime with large reserves (≥ 0.3) relative recruitment was more stable and spawners biomass maintained at higher levels even at extreme exploitation rate (Figure 3.4). At an exploitation rate corresponding to the MSY, the yield was 12-50% smaller in the Reserve regime for reserve sizes of 0.3 to 0.7 respectively. Past this point the yield in the No-reserve regime collapsed while yields in the Reserve regimes were kept at 23% of the yield obtainable at MSY.

In order to compare the impact of the transfer rate in both models we used a high exploitation rate where the yield curve of No-reserve and Reserve regimes met, that is 0.35 in both recruitment regimes. The number of years of weak recruitment stayed rather stable at all levels of T . The biomass of older female spawners decreased as transfer rate increased although the biomass was maintained at higher levels than that of the No-reserve regime. As transfer rate increased from 0.1 to 0.4 the yield went up in the Reserve regime reaching or surpassing that of the No-reserve regime (Figure 3.5) and then plateaued.

When the age at which 50 % of fish are vulnerable to the fishery (age at recruitment) was increased from 2 to 4, the shape of the response curve to an increase of exploitation rate remained about the same although the spawners biomass and the yield were generally higher (Figure 3.6). The exploitation rate at which the number of years of weak recruitment increases shifted from 0.2 to 0.4. As the exploitation rate increases, the level of biomass of spawners (age 7-15) decreases and the yield depends increasingly on individuals between 4 and 6 years old. However, the yield does not collapse under the No-reserve regime as it did when the age at recruitment was only 2. Also the yield in the No-reserve regime remained higher than that of the Reserve regime.

DISCUSSION

The use of a dynamic pool model which accounts for the impact of overfishing on recruitment, led to more positive results with marine reserves than has been shown before (Polacheck, 1990). Our dynamic pool model shows that MSY is reached at $u = 0.15-0.18$ ($F = 0.16-0.2 \text{ year}^{-1}$) which is slightly higher than Hutchings and Myers (1994) recommended as a conservative target for Atlantic cod ($F = 0.09-0.13 \text{ year}^{-1}$)

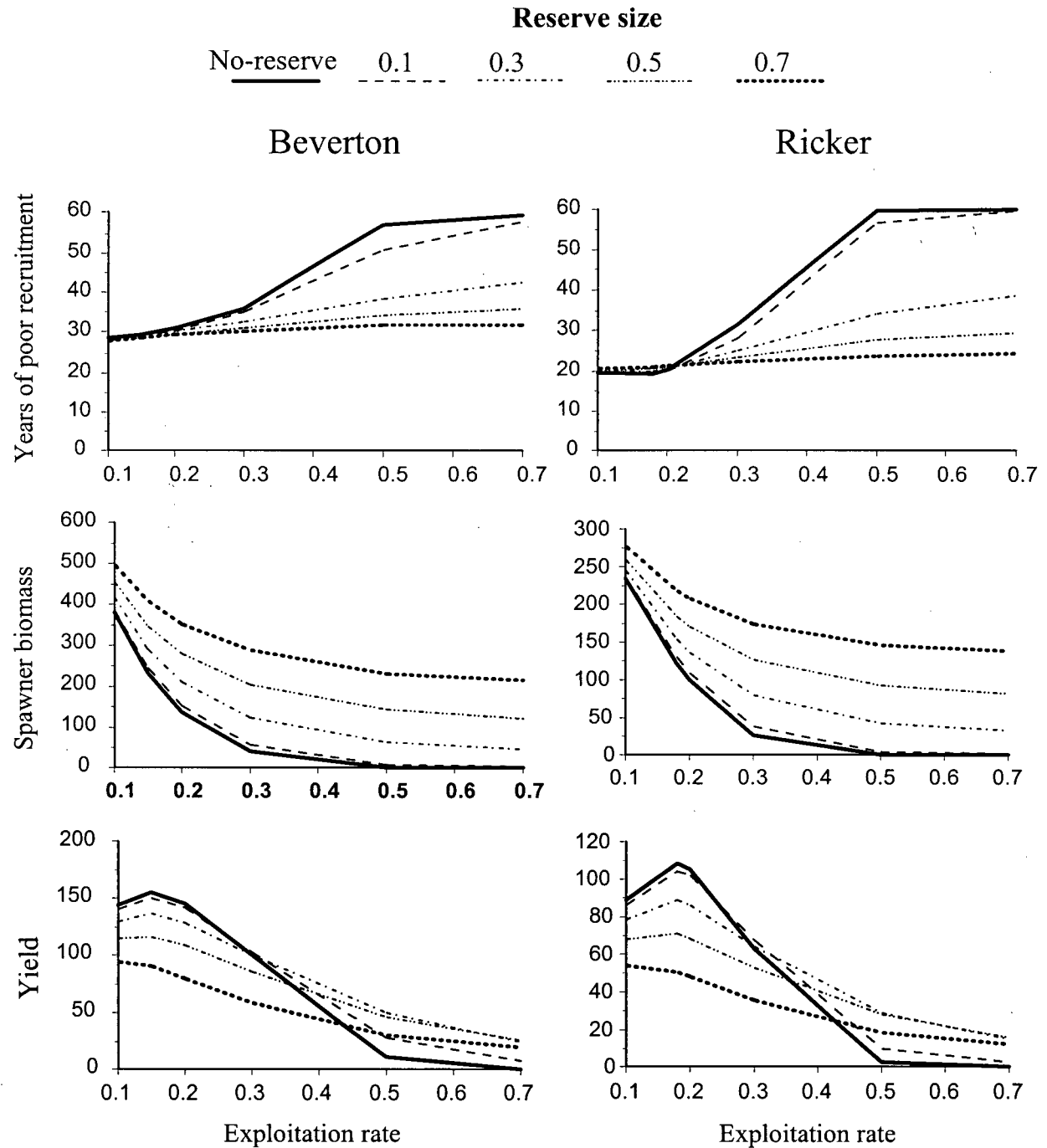


Figure 3.4 Effect of exploitation rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate and reserve size. Ricker and Beverton recruitment curves are compared using a transfer rate of 0.3.

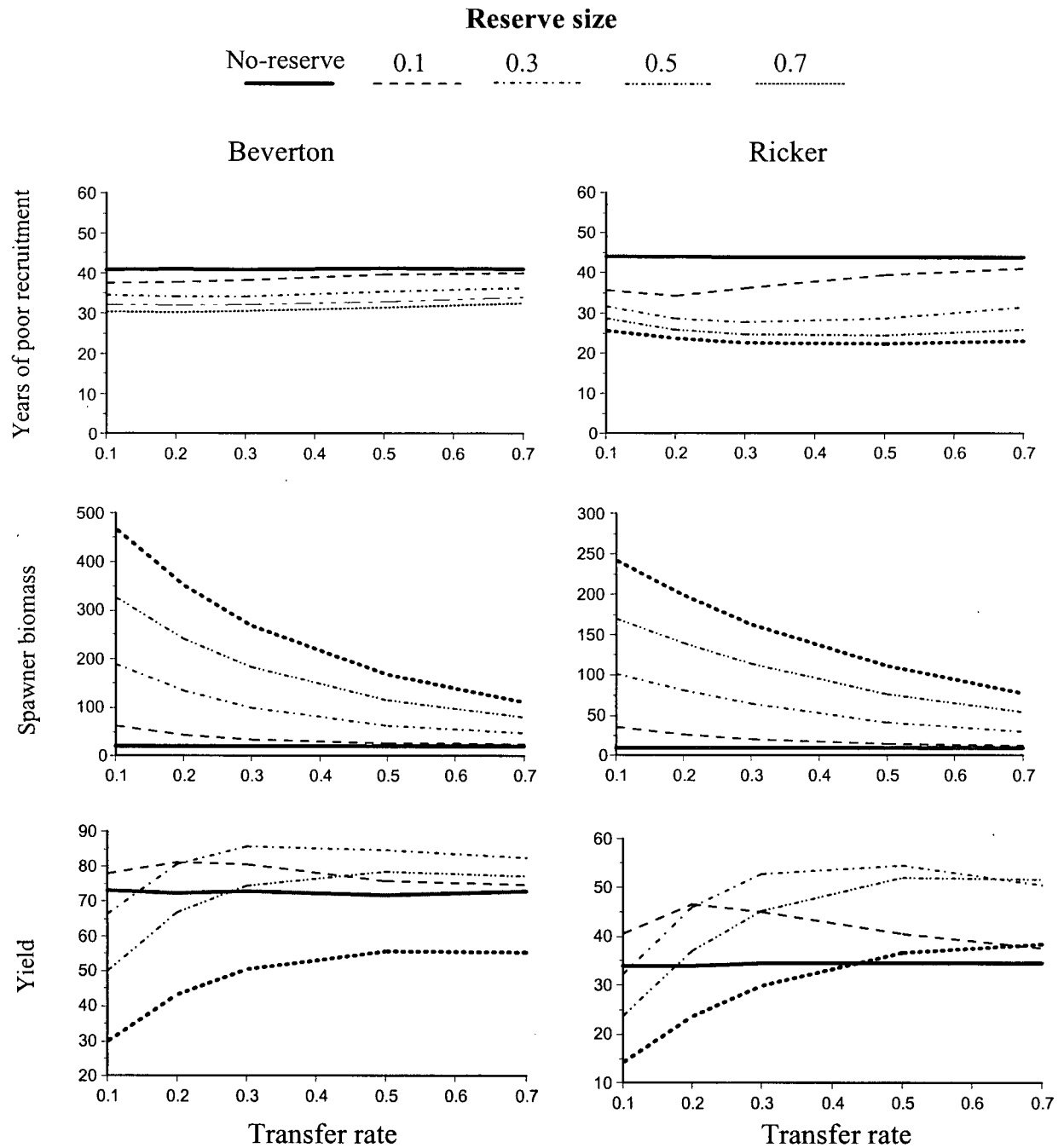


Figure 3.5 Effect of transfer rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate and reserve size. Ricker and Beverton recruitment curves are compared using an exploitation rate of 0.35.

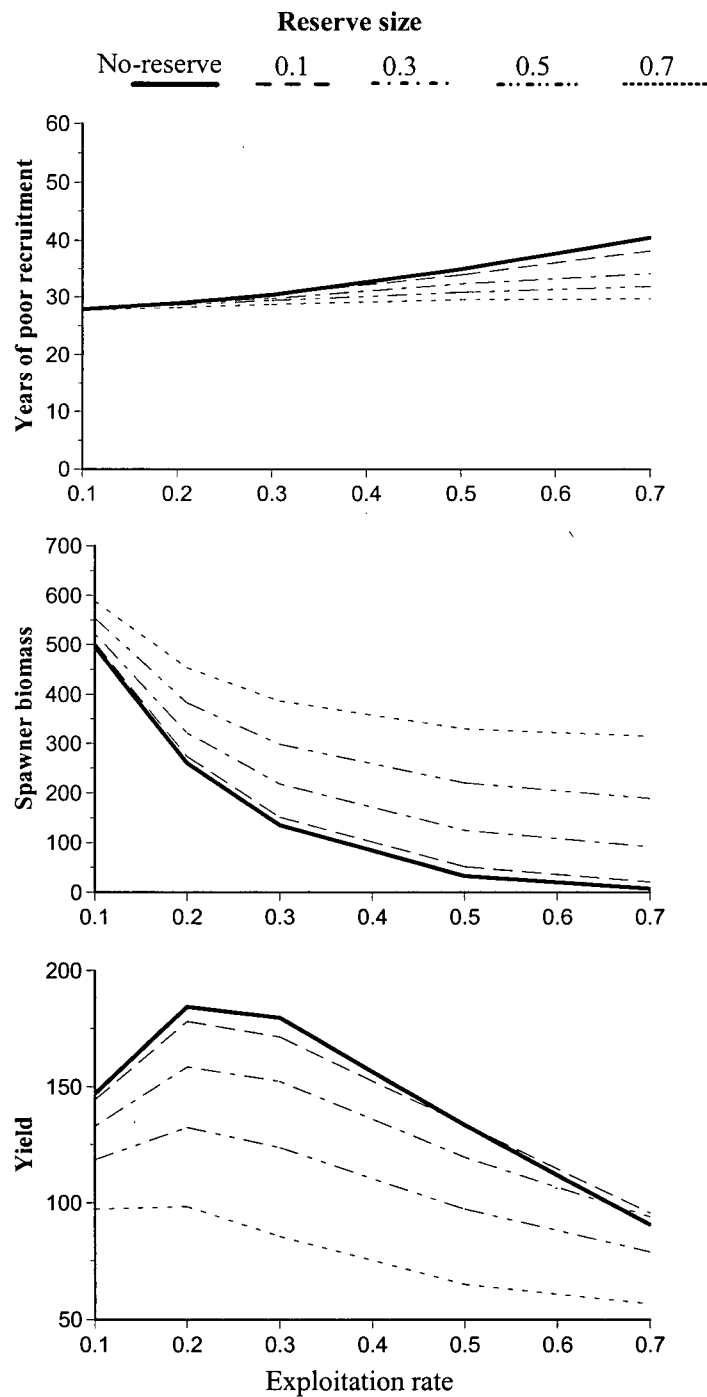


Figure 3.6 Effect of increasing the minimum size and exploitation rate on the number of years of weak recruitment, relative spawner biomass and yield as a function of exploitation rate using the Beverton recruitment curve and a transfer rate of 0.3.

utilising population growth analysis. Our model suggested that marine reserves increase resilience to overexploitation by keeping the spawner biomass and recruitment success at higher levels than in the No-reserve regime. Decrease in yield would occur if management had succeeded in keeping exploitation rates low. However, the real exploitation rate is often higher than the one targeted and this was certainly the case for the Atlantic cod (Myers *et al.*, 1996). Uncertainty about the effective exploitation rate applied to the stock is a good example where marine reserves would be beneficial by acting as a protection against stock collapse. In the past, uncertainties in stock assessments, population dynamics and lack of control over exploitation level have not received sufficient attention (Lauck *et al.*, 1998).

Our results also showed that transfer rates of fish decreased the benefits of marine reserves, confirming results from previous studies (Beverton and Holt, 1957; Polacheck, 1990; DeMartini, 1993). Nevertheless, the biomass of spawners and the level of recruitment would still be higher in the Reserve regime, suggesting that even for fast moving fish a reserve might be beneficial. However, more realistic fish movements would be needed to clarify this point. Dispersion of juvenile plaice towards fishing grounds in the North Sea can be seen as a shift in centre of density of the population (Beverton and Holt, 1957). The overall net movement is directional but it may result from small scale individual random movements. In the present model we used random movements which may be consistent with juvenile cod dispersion. However, adult cod show directed migrations on an annual basis that depart from pure random movements. Adults could be very vulnerable at certain periods of the year (autumn and spring migrations) when most of them would be likely to move outside of a reserve. In fact, further analysis of marine reserves should be spatially and temporally structured to take into account realistic migration and aggregation patterns and other aspects of the life history.

These factors influence both fishing mortality and the effectiveness of marine reserves. Mohn (1996) showed the danger of fishing on aggregations and hinted at the usefulness of closed seasons to avoid overexploitation. Hutchings (1995) suggested closing the offshore cod fishery during pre-spawning aggregations. Such a closure would reduce the overall mortality that is inflicted during that period and return the fishing patterns to the 1950's when these areas were not exploited and hence acted as a temporal refuge. We have not modelled other mooted behavioural advantages of older fish such as site fidelity or enhanced reproductive homing. Although outside the scope of the present model, cannibalism could reduce the benefits of a reserve especially in cases where abundance would likely increase.

The impact of age at recruitment on the spawners biomass and yield in both regimes suggests that increasing the minimum size could be as effective as implementing a reserve. In practice though, marine reserves could be more efficient than mesh size restrictions by protecting juveniles in their habitat (Garcia and Demetropoulos, 1986; Caddy, 1990). Marine reserves should however not be seen as a panacea. The increased fishing mortality that would result from concentrating the effort in the fished sector of the Reserve regime emphasizes the necessity to use marine reserves as complementary to more traditional management techniques aiming at controlling effort.

Chapter 4.

Catch and effort data

In order to build a spatially explicit model for the northern cod (NAFO regions 2J, 3K, and 3L, Figure 4.1) and explore management scenarios, good data on the spatial distribution of effort and catch is necessary. This chapter describes the on-board observers data (Department of Fisheries and Oceans (DFO), St. John's, Newfoundland), and the commercial catch and effort found in the Newfoundland and NAFO (Northwest Atlantic Fisheries Organization, Dartmouth, Nova Scotia) data sets. The observer data provided an independent estimate of catch per unit effort for trawlers and detailed spatial distribution. First, each data set is described. Second, spatial distribution of the catch, by vessel size and by origin (Canadian or foreign) is analysed. Particular attention has been given to detecting inconsistencies in effort and catch per unit effort (CPUE). Landings and catch are used as synonyms since no effort was made to include discards in the statistics.

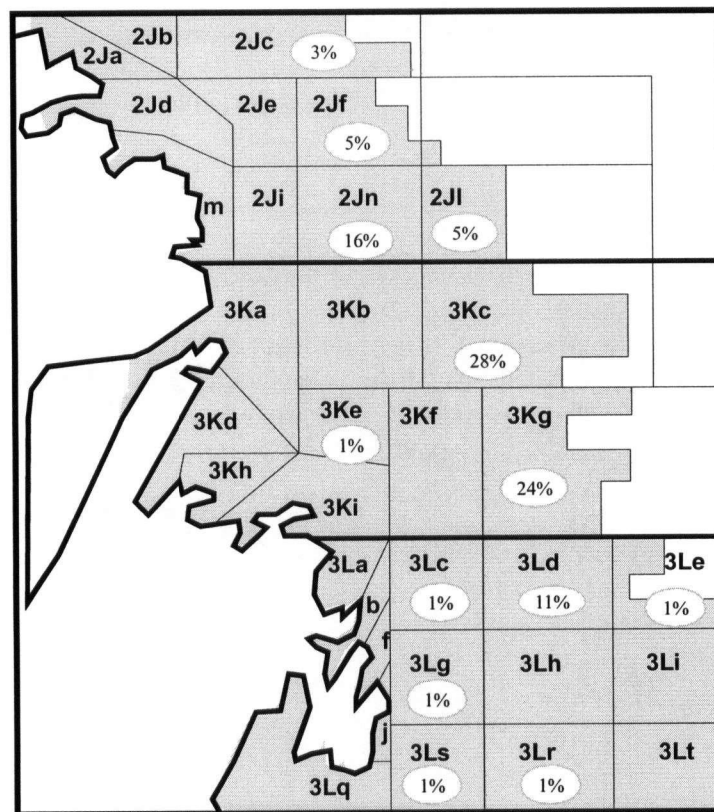


Figure 4.1 Distribution of the trawl catch within the observer program for divisions 2J, 3K and 3L. Only unit areas having catch percentages higher or equal to 1% are represented.

OBSERVER DATA

Description

The on-board observer program started in 1980. Observers stationed on board of a proportion of the offshore trawlers from all countries recorded information on the location fished, hours towed, and catches of all species (Wroblewski *et al.*, 1995). Vessels and trips were not strictly selected randomly as management concerns also influenced the choices. For the cod directed fishery in divisions 2J, 3K and 3L, the observer program covered 20% of January to April fishing activities by the **offshore** trawler fleet from 1980 to 1986, and 100% starting in 1987 (Kulka *et al.*, 1996). Data from the observer program were recorded with detailed information (latitude and longitude) on spatial distribution of effort for trawlers and, to a lesser extent, gillnetters (Table 4.1) (see Kulka *et al.*, 1996). Although data from non-target trips were available, only trips targeting cod were analysed. Most of the observer data were collected in winter (January to April) in regions 2J and 3K (Figure 4.1). In 3L, because it is a multispecies fishery, catch and thus observer data are more evenly distributed throughout the year (David Kulka, DFO, St. John's Nfld, pers. com.). About 98% of the observations have been done in 15 of the 35 unit areas, mainly located offshore (Figure 4.1). Class 5 (500-1000 gross tonnage) trawlers account for 66% of all observed catch (Table 4.2). Catches from offshore gillnetters were covered on vessels of size 4 to 6 which constitute only a small portion of the catch for this gear. In the first few years of the series, the percentage of commercial catch that the observer program is supposed to have covered show some inconsistencies, suggesting under-reporting (Table 4.1).

Analysis of variance on CPUE

Catch per unit effort per year was calculated as

$$\ln CPUE = \left(\sum_{i=1}^I \ln(\text{catch} * \text{effort}^{-1}) \right) * n^{-1}$$

where n is the number of NAFO unit areas, catch is in tonnes and effort is number of hours fished. Using a logarithmic transformation decreases the influence of the extreme CPUE and linearizes the relationship between CPUE and correlating factors. An analysis of variance was used to describe the relationship between trawlers' CPUE and vessel size, season, region fished (NAFO division). Because fishing power may have changed, the data series was cut in two periods (1980-1985 and 1986-1991):

$$\ln CPUE = \mu + \alpha \text{ size class} + \beta \text{ period} + \gamma \text{ season} + \delta \text{ divisions} + \epsilon$$

Results show that vessel size, division, period and season together only explained 23% of total variation ($N=79425$, $p=0.0001$) (Table 4.3). The most important variable in the analysis was the season (mean sum of squares (MS)=4785), followed by period (MS=3409), division (MS=2192) and vessel size (MS=1469). Analysis at smaller spatial scales (unit areas instead of divisions, not shown) did not improve discrimination between vessels. Large inter-annual fluctuations in CPUE (see Appendix 4.1), skipper ability and the grounds visited are additional sources of variance unaccounted for by this analysis. The catch per unit effort was significantly higher in the winter, when cod aggregate along the edge of the shelf, and decreased rapidly after April (Figure 4.2, Table 4.3). According to the variance analysis, winter CPUE is almost three times larger than that of the fall (Table 4.3). Catch per unit effort is slightly lower in 3L than in other regions perhaps because of the multispecies nature of the fishery on the Grand Bank. CPUE was consistently higher in the last part of the 1980s (period 2) than in the first part (period 1), in all regions. CPUE of vessels of tonnage class 6 and 7 were 150 and 200% higher than class 5 vessels respectively (Table 4.3). The CPUE

Table 4.1 Spatial and temporal distribution of the total cod catch included in observer data and the percentage of the commercial catch covered for trawlers of size 3 to 7 (1) and gillnetters of size 4 to 6 (2).

Year	Catch (tonnes)									
	Trawl				% catch (1)	Gillnet				% catch (2)
	2J	3K	3L	Total		2J	3K	3L	Total	
1980	8733	3986	7613	20332	32	368		2257	2625	185
1981	4723	4663	6061	15447	19			2266	2266	88
1982	12889	2751	5153	20793	20			2207	2207	56
1983	9453	3566	4150	17169	15			2558	2558	79
1984	3293	12778	5457	21528	18			3034	3034	79
1985	81	16632	2080	18793	15		7	3969	3976	91
1986	8819	11596	5975	26390	14				0	0
1987	36475	38440	9130	84045	57				0	0
1988	32539	37895	13236	83670	58		539	331	870	16
1989	20628	36140	15805	72573	51		159	343	502	10
1990	10006	27356	15466	52828	55			1	1	0
1991	406	25145	17209	42760	65		39	176	215	8

Table 4.2 Distribution of the cumulative catch in observer data arranged by vessel gross tonnage class, NAFO divisions, and the respective percentage of commercial catch.

Tonnage class	Tonnage range	NAFO regions			Total	% of commercial catch
		2J	3K	3L		
3	50-149.9		724	2728	3452	13
4	150-499.9	623	5759	6204	12586	14
5	500-999.9	97899	147910	57405	303214	31
6	1000-1999.9	18395	25839	25449	69683	37
7	2000 +	24141	34310	13528	71979	83
Unknown		1323	1266	828	3417	
Total					460879	

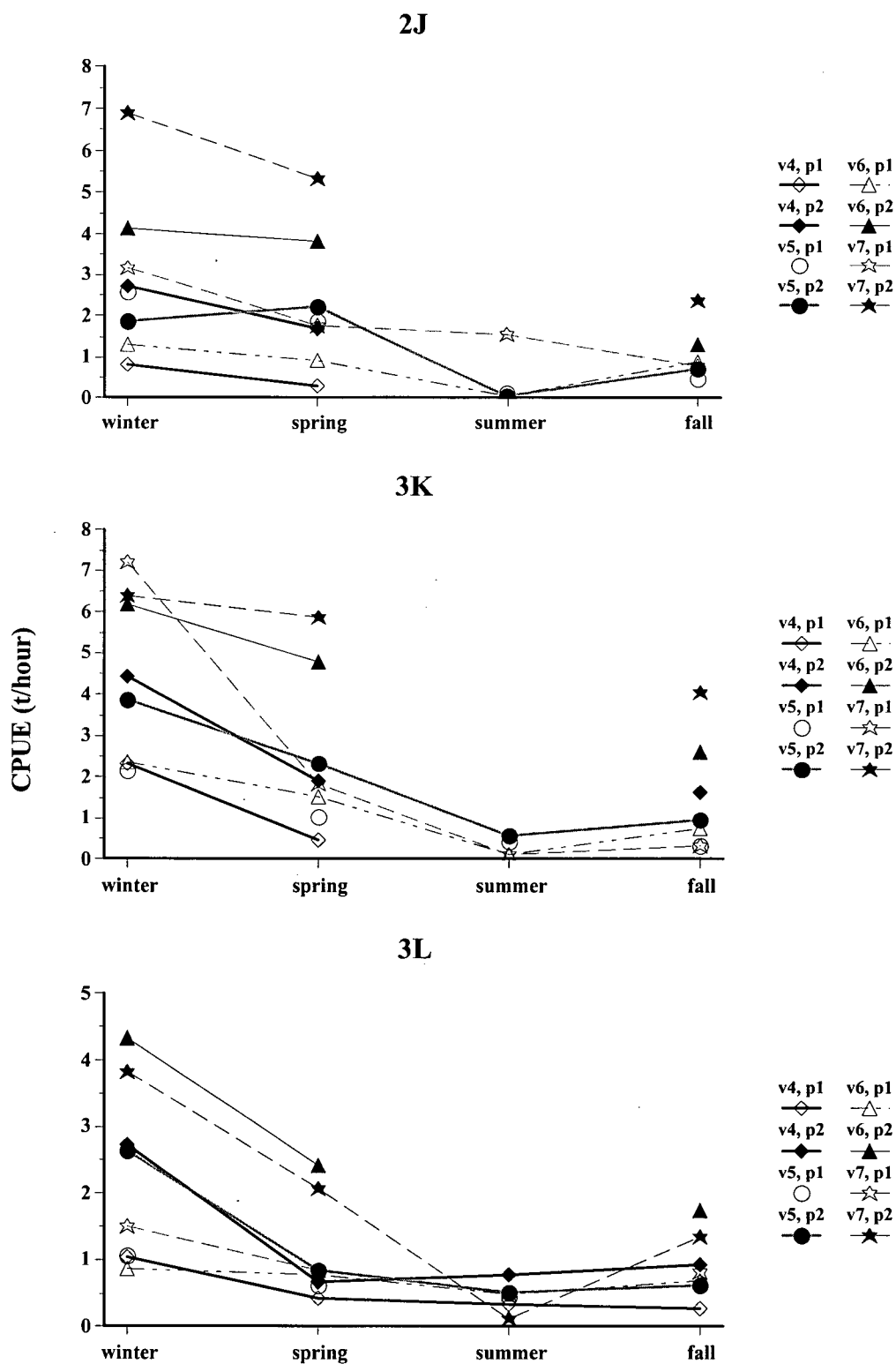


Figure 4.2 CPUE for trawlers by season for each vessel size class, as found in the observer data set. Gross tonnage classes are defined in Table 4.2. v4,p1 refers to vessel size class 4, period 1 (1980-1985).

Table 4.3 Parameters estimated from the generalised linear model used to standardise CPUE by vessel size class, divisions, period, and season.

	ln value	value	parameter
Intercept ¹	-0.4233	0.65 ²	μ
Division			
2J	0.2746	1.31	δ_1
3K	0.6293	1.88	δ_2
3L	0	1	δ_3
Period			
1980-1985	-0.5132	0.6	β_1
1986-1991	0	1	β_2
Season			
winter	1.0860	2.96	γ_1
spring	0.5717	1.77	γ_2
summer	-0.3038	0.74	γ_3
fall	0	1	γ_4
Vessel size class			
3	-0.5814	0.56	α_3
4	-0.1274	0.88	α_4
5	0	1	α_5
6	0.4134	1.5	α_6
7	0.7406	2	α_7

¹ CPUE for vessel size 5, division 3L, period 1986-91 and fall.

² The corresponding value for vessel 6 is $0.65 \times 1.5 = 0.98$

computed in this section and the spatial distribution of the observations will be compared with those from commercial data in the next section.

STATISTICS FROM COMMERCIAL DATA

The catch and effort data for vessels that *landed* their catch in Newfoundland (mainly Newfoundland vessels) for 1980-1991 were obtained from the Department of Fisheries and Ocean (DFO). Summarised catches from all sources, Newfoundland, other provinces and countries, were obtained from NAFO for the period 1960-1991. Data from Newfoundland were analysed separately as they were available in a more detailed spatial scale (NAFO unit areas).

Newfoundland landings

Yield per gear type

Catch statistics for Newfoundland vessels are reported by unit (unit areas of NAFO regions, Figure 4.1) and month. The data did not specify whether the effort was directed towards cod or other species. Although five gears are used to catch cod, we concentrated on the three most important (trap, gillnet and trawl) which constituted an average of 88%. Note that the range over 1980-1991 period was 79-92% of the total catch; trawlers alone accounted for 46% (range: 33-58%) of the total landings (Table 4.4). Traps are used from May to September, although 54% of the landings occur during the month of July (Figure 4.3). Gillnets are used almost all year, but 57% of their landings occur in July and August. For trawls, a large proportion of the catch is taken in the winter (January to March) at the break of the shelf, although the reported effort is relatively low during this period. The trawlers' summer catch comes mainly from the northern Grand Banks (3L). Class 5 trawlers caught the largest part of the total catch (Figure 4.4). It is interesting to note that the contribution of size 6 and 7 vessels was marginal in this data set since they were mainly from other countries, as explained in the NAFO data set section.

Table 4.4 Total yield landed in Newfoundland per NAFO division and percentage reported for each gear. "3 gears" refers to gillnet, trap and trawl. Catches are in tonnes.

Gear\Year	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Trap	30283	18024	4513	40051	38676	39877	34600	27807	44325	38872	46969	35300
Gillnet	36344	34534	4867	39981	36618	21485	25916	37165	39637	44973	45990	17367
Trawl	46720	62258	77202	79936	77184	78567	10272	98483	11267	86238	65977	52673
Other	29948	27705	2093	28107	24504	20177	13614	14319	17077	17624	21940	12263
Grand total	143296	142520	191942	188075	176983	160106	176857	177773	213719	187706	180876	117603
% of Grand total												
3 gears	0.79	0.81	0.89	0.85	0.86	0.87	0.92	0.92	0.92	0.91	0.88	0.90
Trap	0.21	0.13	0.24	0.21	0.22	0.25	0.20	0.16	0.21	0.21	0.26	0.30
Gillnet	0.25	0.24	0.25	0.21	0.21	0.13	0.15	0.21	0.19	0.24	0.25	0.15
Trawl	0.33	0.44	0.40	0.43	0.44	0.49	0.58	0.55	0.53	0.46	0.36	0.45

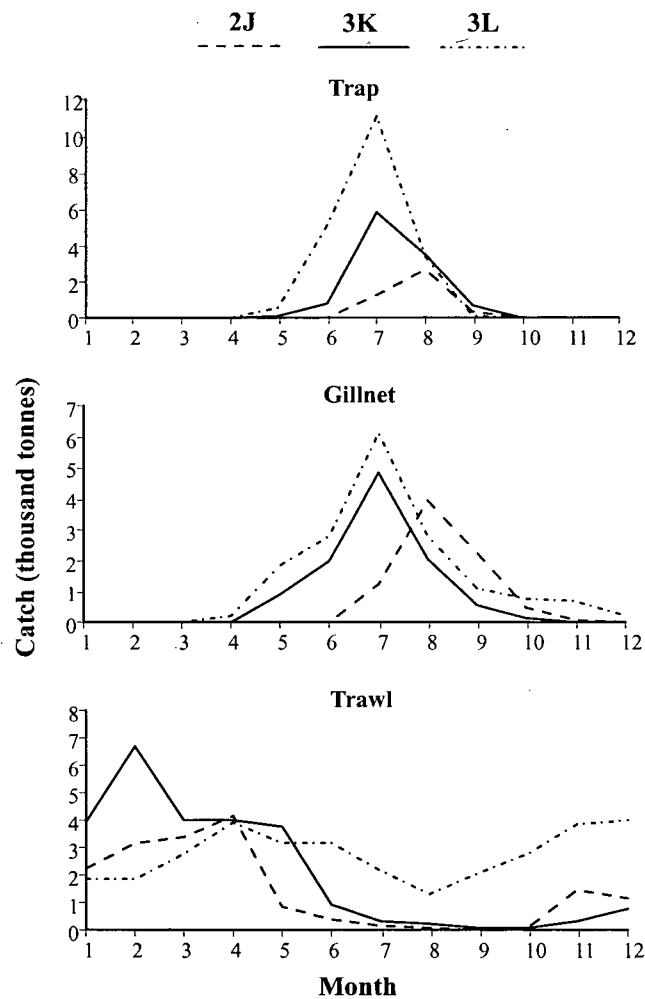


Figure 4.3 Average monthly distribution of the catch for years 1980-1991 by NAFO divisions, as found in the Newfoundland data set.

Effort data

The effort (in hours) is the amount of time during which the trawl was in the water; or the number of hours the trap or gillnet (in 100-metre units) were in the water, multiplied by the number of units. The proportion of the catch for which effort is declared is generally very low, especially for 1982-1986 (Table 4.5). Since vessels smaller than 10 m long (<35 feet) were not compelled to carry logbooks except those carrying a crab license), their fishing effort was largely under reported (Table 4.6). Although landing statistics are considered to be more reliable than effort (Anne Marie Russell, Department of Fisheries and Ocean, St. John's, Newfoundland, pers. comm.), some doubts remain regarding the precision of catch statistics. The statistical branch of DFO aggregated the catch by month, community, and location until 1985-1986. It is impossible to develop an estimate of effort using the number of active fishers since there is no record of how

many fishers were active at any given time. Because a groundfish license gives the right to use any fixed gear, the link between number of fishers and effort per gear is weakened. Although regulations are

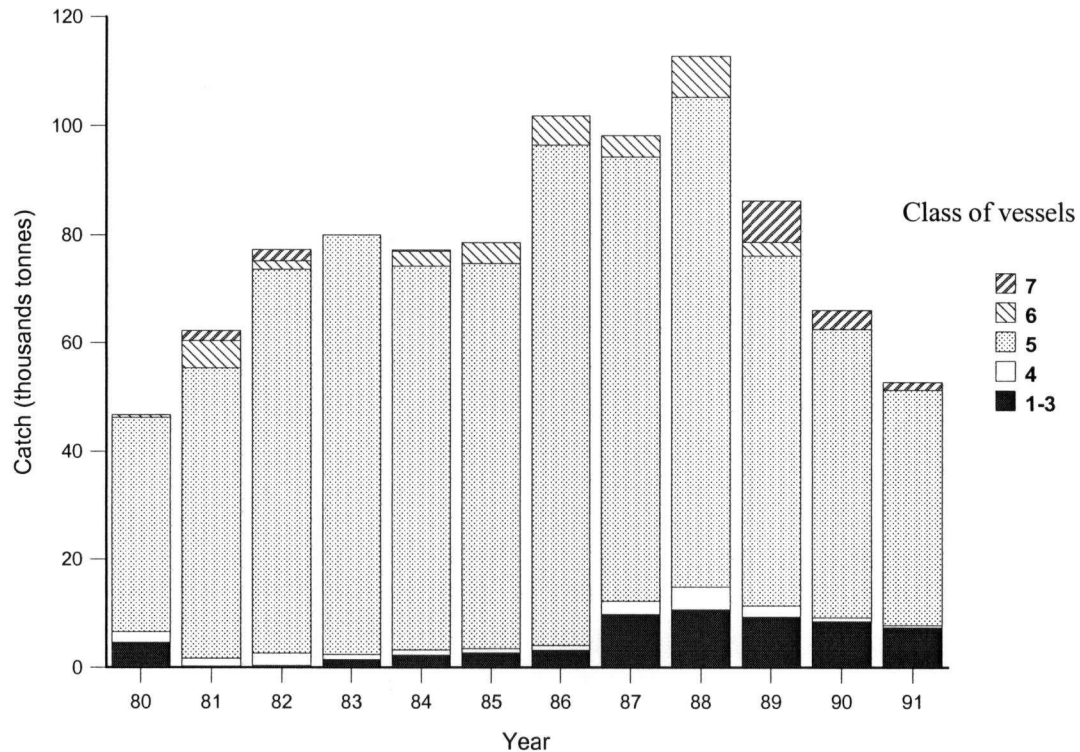


Figure 4.4 Catch declared for each size class of trawlers as found in the Newfoundland data set. Gross tonnage class of trawlers are defined in Table 4.2.

structured by vessel length, gross tonnage has been found to be more closely related to CPUE (Kulka *et al.*, 1995). Thus, vessels were classified according to gross tonnage class as defined in Table 4.1 from now on.

Catch per unit effort

Catch of both gillnets and traps decreased in the mid 1980s, then increased until 1990. Effort was the largest in 1980-81 and data is often missing in the mid 1980s, which led to inconsistent CPUE (Figure 4.5). Therefore, inshore CPUE data was not indicative of the stock biomass. Trawling effort oscillated throughout the 1980s, but CPUE and effort decreased sharply between 1989 and 1991. Data for trawlers was also biased by including boats targeting cod and those targeting other species. This data set did not allow differentiation between the two fisheries.

In an attempt to compensate for the missing effort data, the average catch per unit effort was computed by period (1980-1985 and 1986-1991) and season. The calculations of CPUE per vessel size underlines the extent of the underestimation of effort and the inconsistencies that followed. Although most trawlers reported effort for each trip at sea, the effort was clearly misreported. For example, the winter CPUE computed for vessel class 6 in 3L in the commercial catch data, $11 \text{ t} \cdot \text{hour}^{-1}$ (Figure 4.6), is 3 times higher than the corresponding CPUE computed from the observer data set, $4.2 \text{ t} \cdot \text{hour}^{-1}$ (Figure 4.2). Vessels of size 1 declared an average winter CPUE of 6 to $16 \text{ t} \cdot \text{hour}^{-1}$. The comparison between observer and catch data emphasizes the magnitude of under-reporting of effort. As in the observer data set however, the catch data show consistently higher CPUE in the winter than in other seasons.

Table 4.5 Proportion of the catch for which effort was reported by year and by gear for Newfoundland vessels between 1980-1991.

Year	Trap	Gillnet	Trawl
1980	0.15	0.34	0.63
1981	0.17	0.64	0.96
1982	0.00	0.04	0.97
1983	0.00	0.01	0.99
1984	0.00	0.03	0.97
1985	0.00	0.08	0.94
1986	0.01	0.10	0.96
1987	0.05	0.24	0.99
1988	0.09	0.35	0.99
1989	0.12	0.43	1.00
1990	0.13	0.51	1.00
1991	0.17	0.71	1.00

Table 4.6 Total catch and proportion of the catch for which effort was reported for vessels with and without logbook by gear and vessel length (Newfoundland vessels). Prop.: proportion of the catch that is coupled with effort estimates.

Length class		With logbook				Without logbook			
Feet	Metres	Total catch (t)	Prop.	Effort (hours)	CPUE	Total catch (t)	Prop.	Effort (hours)	CPUE
Trap									
<35	<10	3125	0.183	10318	0.036	356908	0.001	3512	0.032
35-50	10-15	64401	0.271	306535	0.029				
50-65	15-20	16403	0.213	33533	0.054				
65-100	20-31	276	0.199	444	0.069				
Gillnet									
<35	<10	3224	0.279	53680	0.009	194804	0.001	8024	0.010
35-50	10-15	110049	0.305	1116772	0.015				
50-65	15-20	90887	0.466	539083	0.040				
65-100	20-31	10551	0.199	11075	0.138				
> 100	>31	20355	0.478	35686	0.109				
Trawl									
<35	<10	162	0.950	739	0.099	3753	0.816	1048	0.989
35-50	10-15	534	0.423	536	0.288				
50-65	15-20	30251	0.601	17495	0.626				
65-100	20-31	530	0.670	382	0.596				
> 100	>31	916742	0.970	849819	0.584				

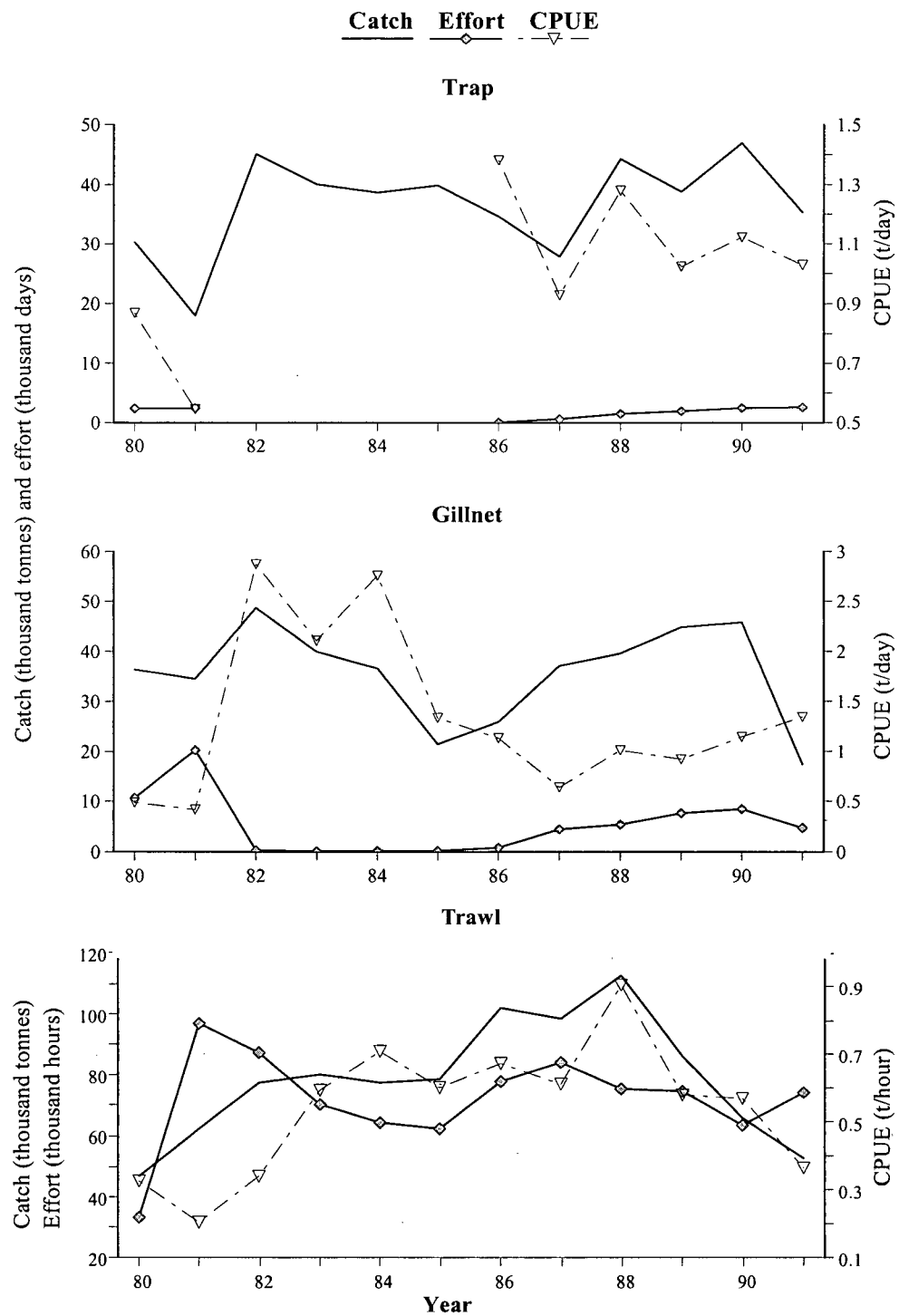


Figure 4.5 Catch, effort and cpue as obtained from Newfoundland data set for year 1980-1991. Note the increased cpue for the second period (1986-1991) for gillnet and trap.

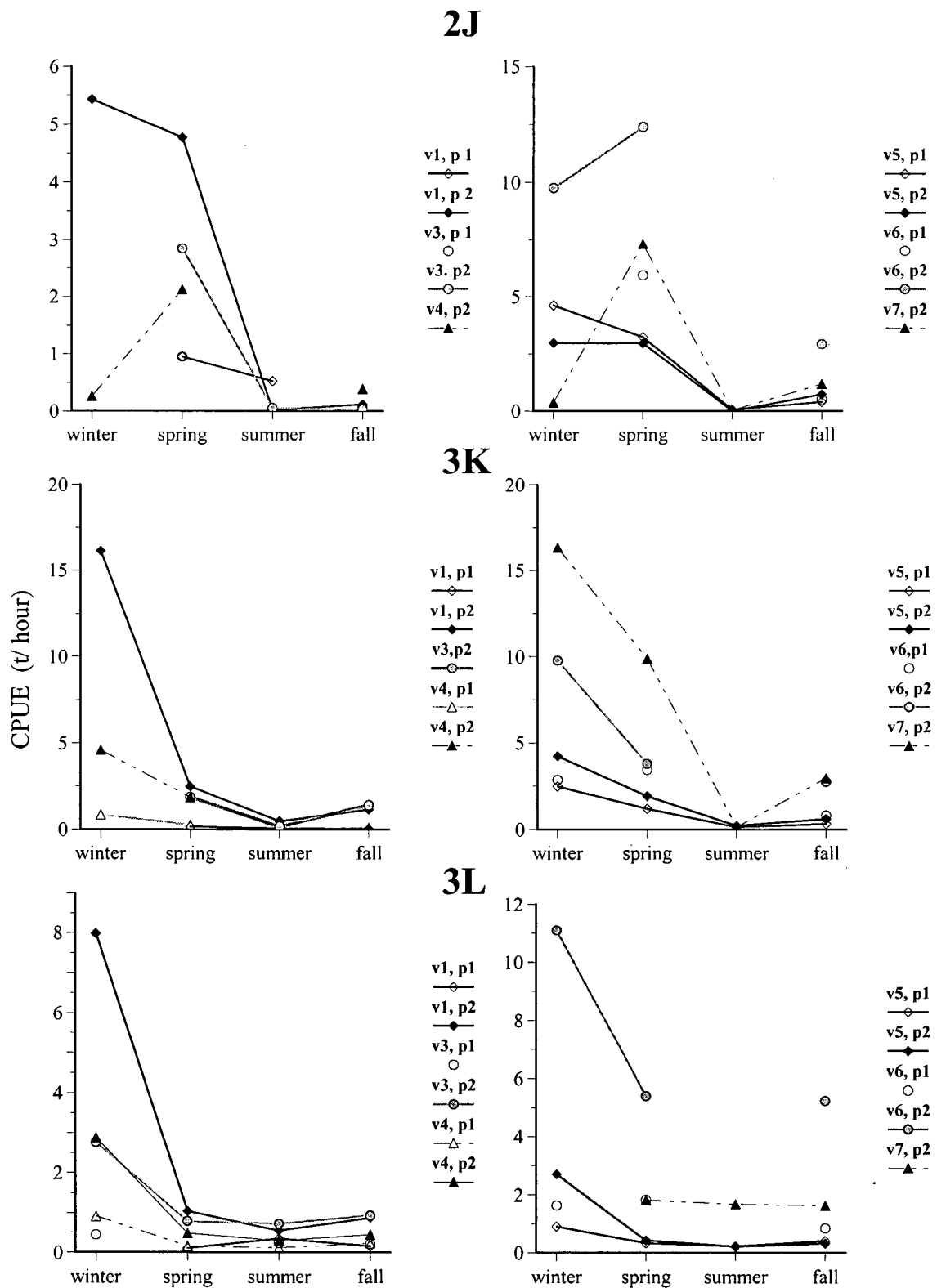


Figure 4.6 Catch per unit effort by vessel size, division and season as calculated from the Newfoundland data. V1, p1 means vessels of gross tonnage class 1 in period 1 (years 1980-1985).

Spatial distribution of the catch

Size class 1 and 2 trawlers were found to fish more in the inshore (2Jm, 3Ka, 3Ki) in the first period than in the second period (Figure 4.7). It was quite surprising to see that small trawlers would risk going so far offshore. However, this is consistent with reports that trawlers working inshore depleted the resource between 1960-1980 (Fischer *et al.*, 1997), which was bound to lead trawlers further offshore. Size 3 trawlers were fishing mainly in 3Lq during the first period but expanded on the Grand Banks (3L d, g, r, s) in the second period. Size 4 trawlers observations became more concentrated to the southern part of the study area during the years 1986-1991. Vessels of class 5 and 6 concentrated in the offshore unit areas of 3L region. It should be kept in mind that vessel 6 and 7 were not well represented in this data set. The spatial distribution of the reported commercial catch seems to have been adequately sampled by the observer data (Figure 4.8), except for the southern unit areas (3Lq, r, s). Gillnets increasingly fished offshore as cod stocks were depleted, starting in the early 1980s (Hutchings and Myers, 1994; Neis *et al.*, 1999). Traps fished inshore in water not deeper than 20m (Rose, 1992).

Total landings (NAFO data)

The NAFO data base includes monthly catch and effort by regions only (2J, 3K, 3L). Distinctions are made for vessel type and species targeted. Effort is compiled both in hours and days fished for trawlers but only in days fished for traps and gillnets. The trends were similar in both units, but the effort was kept in hours to compare with observer data, however, the model in Chapter 6 used fishing effort in days.

Comparison of Newfoundland and NAFO data set for 1980-1991

From 1980 to 1991, NAFO records showed that Newfoundland was responsible for 76% of the total catch in regions 2J3KL, while foreign countries caught an average of 14% (Table 4.7). Foreign vessels were mainly trawlers. Newfoundland was responsible for all the catch with traps and 95% of the gillnet landings. Small trawlers (class 1 to 3) were almost exclusively from Newfoundland. Foreign countries landed 61% of the fish caught by size 4 trawlers, except for years 1982 and 1989 where, unexpectedly, Newfoundland vessels declared 75 and 93% of the catch (Appendix 4.2). This may be due to mistakes in attribution of origin of vessels. Newfoundland and the Maritimes were responsible for an average of 96% (range 89-100%) of the catch recorded for size 5 vessels. Declared catch for large vessels (class 6 and 7) originated mainly from foreign countries and the Maritimes. The latter started using size 6 and 7 trawlers in 1983 and 1987 respectively. Landings declared with Newfoundland size 6 and 7 trawlers began only in 1987 and 1989 respectively. After size 6 trawlers from the Maritimes started fishing, foreign trawlers kept catching an average of 60% of the total catch for that class of vessel. Unfortunately, NAFO and Newfoundland data sets did not coincide completely because of the presence of undetermined size vessels in the former set and undetermined origin of vessels in the latter.

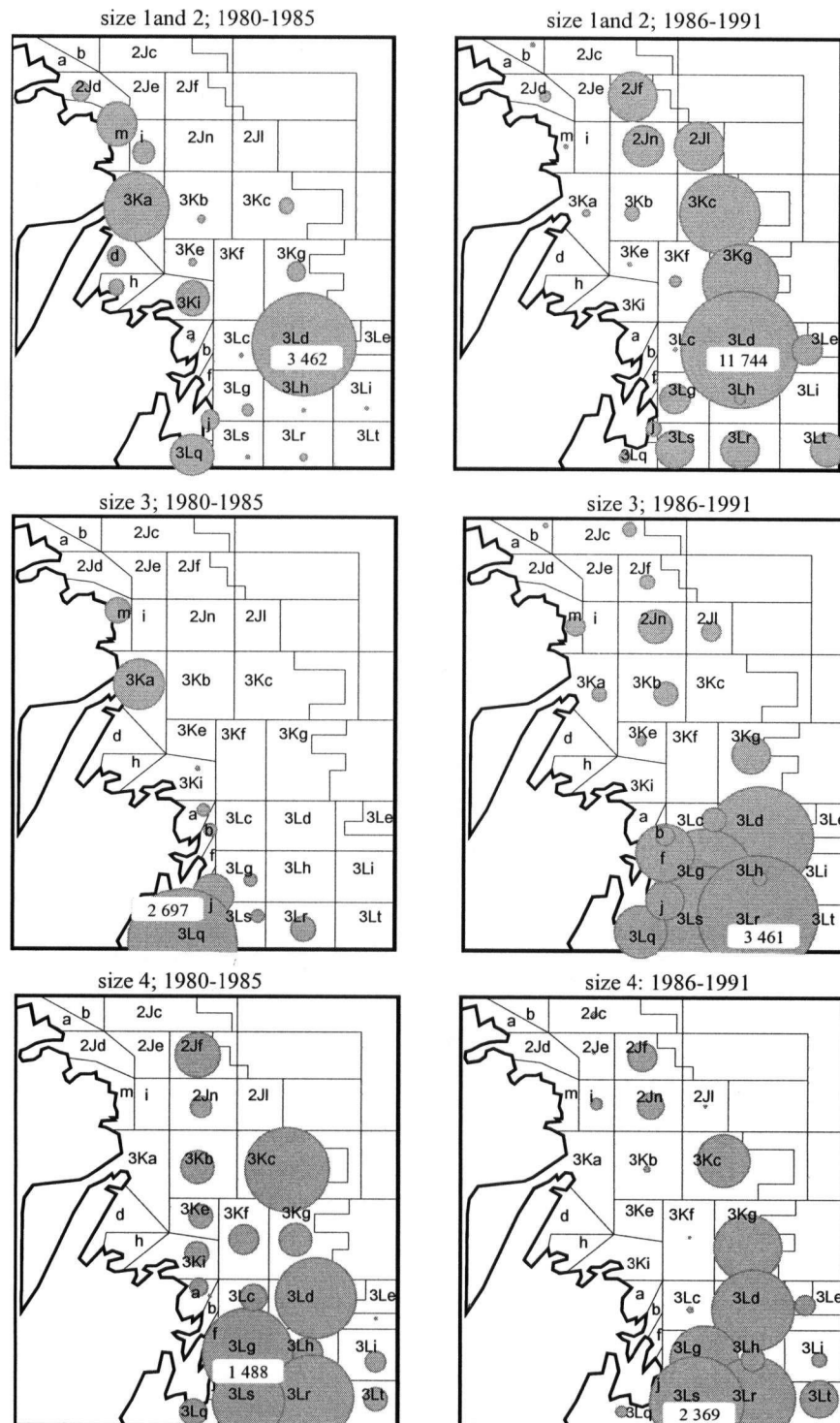


Figure 4.7 Spatial distribution of trawlers' cumulative catches by vessel size, period and unit area, as found in the Newfoundland data set. The bubble diameter is proportional to the maximum cumulative catch of each map. The actual value appears in the largest bubble.

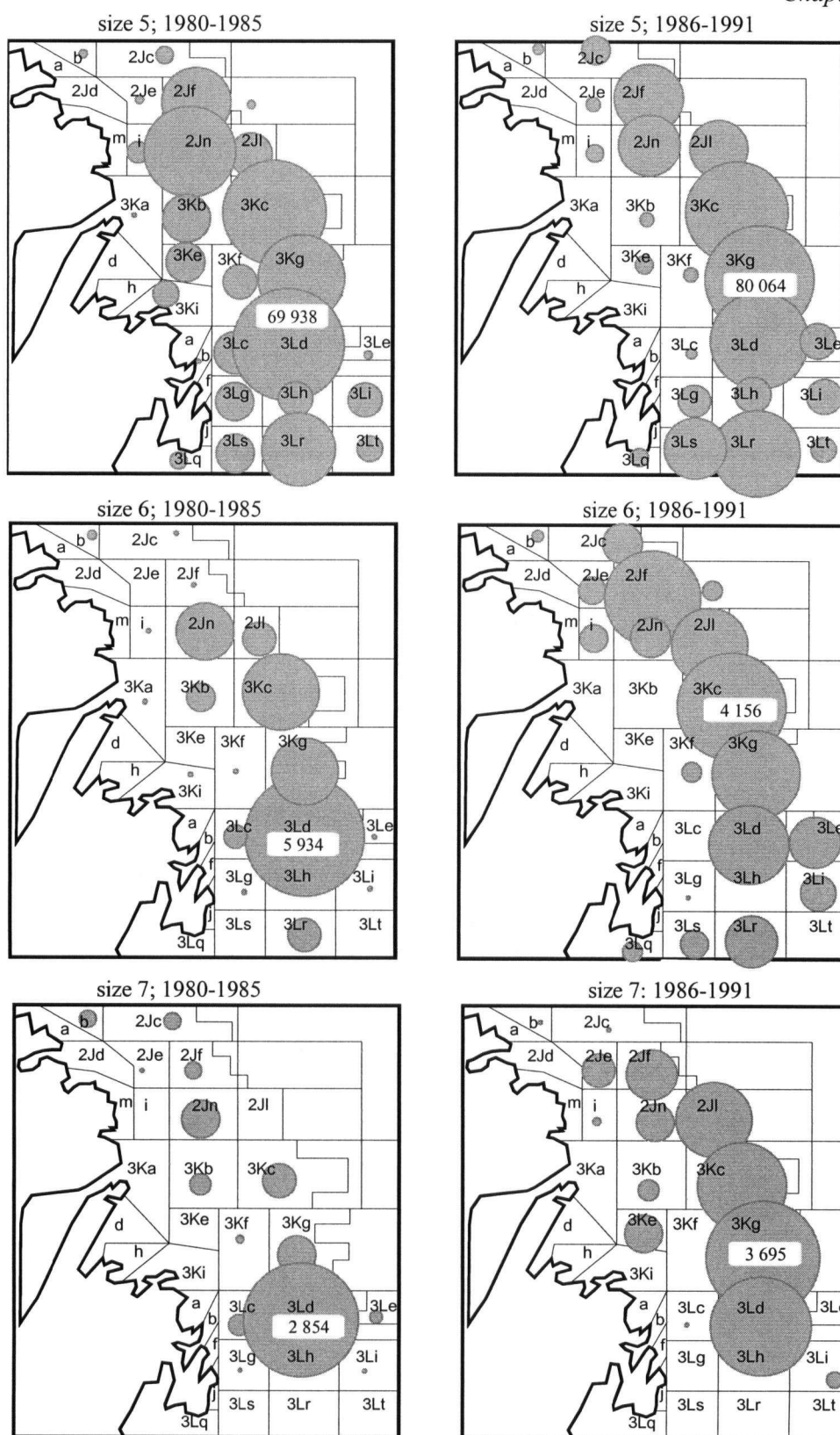


Figure 4.7 continued

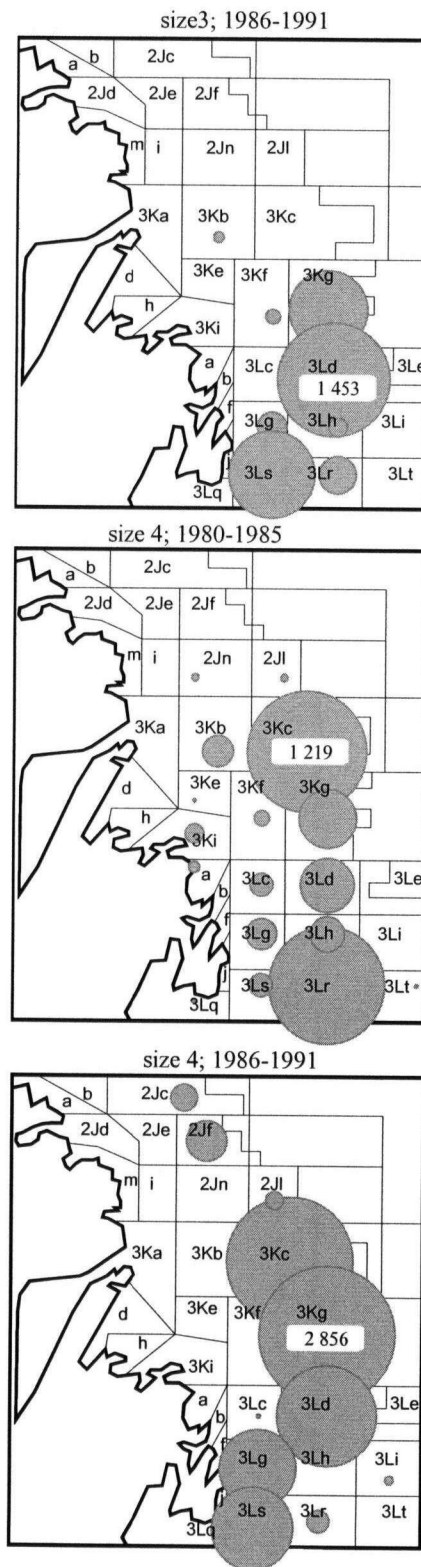


Figure 4.8 Spatial distribution of tows sampled by class size of trawlers as found in the observer program. Bubbles are relative to the largest, the actual value of which can be seen in the white rectangles.



Figure 4.8 continued

Table 4.7 Declared landings for Newfoundland (Nfld), other provinces (Mari) and foreign countries for regions 2J3KL between 1980-1991, as compiled by NAFO for all gears (gillnet, trap, trawl and others).

Year	Nfld	Mari	Foreign	Total	%Nfld	%Foreign
1980	139228	8330	28224	175782	0.79	0.16
1981	135425	11646	23677	170748	0.79	0.14
1982	186676	20830	22268	229774	0.81	0.10
1983	186369	28083	17888	232340	0.80	0.08
1984	171817	30840	29814	232471	0.74	0.13
1985	154494	32600	44199	231293	0.67	0.19
1986	170915	28212	67586	266713	0.64	0.25
1987	177324	26525	36075	239924	0.74	0.15
1988	213719	28151	26807	268677	0.80	0.10
1989	187707	27475	35761	250943	0.75	0.14
1990	180870	12407	26175	219452	0.82	0.12
1991	117537	8422	24067	150026	0.78	0.16
Average					0.76	0.14

Period 1960-1980

Origin of vessels, their catch and gear used

The proportion of the catch landed by trawlers decreased from 80% in 1960-1976 to 60% in the 1980s (Figure 4.9). In the 1960s-70s, vessels of class 6 and 7 were taking most of the trawler catch (Figure 4.10). In comparison, throughout the 1980s, class 5 vessels were responsible for most of the catch. Oddly, there were no records for traps and gillnets until 1969, which had likely been included in the category miscellaneous (Figure 4.9). Examination of the monthly distribution of the catch showed that the catch declared under 'miscellaneous' was probably from both gillnets and traps. Thus catch for the months of January to April and October to December was attributed to gillnets while the catch for the months of May to September was equally apportioned between gillnets and traps.

Target species and effort

The cod per unit effort is expected to be lower when cod is not the targeted species. Therefore any calculation of CPUE should account for the type of fishery. However, the declaration of species targeted by fishers has varied quite noticeably over the years. Often, fishing trips targeting cod and those targeting mixed species have been used interchangeably. See for example, the catch declared trap and gillnet in the early 1960s (Figure 4.11). Typically, for traps and gillnets, large landings from mixed species fisheries are not associated with any effort. For trawl, mixed fisheries were more important in the 1970s and contributed a proportionally larger amount of effort than the fishery targeting just cod. In all cases, the fishery targeting other species contributed little to total catch but resulted in a large constituent of total effort, resulting in smaller CPUE.

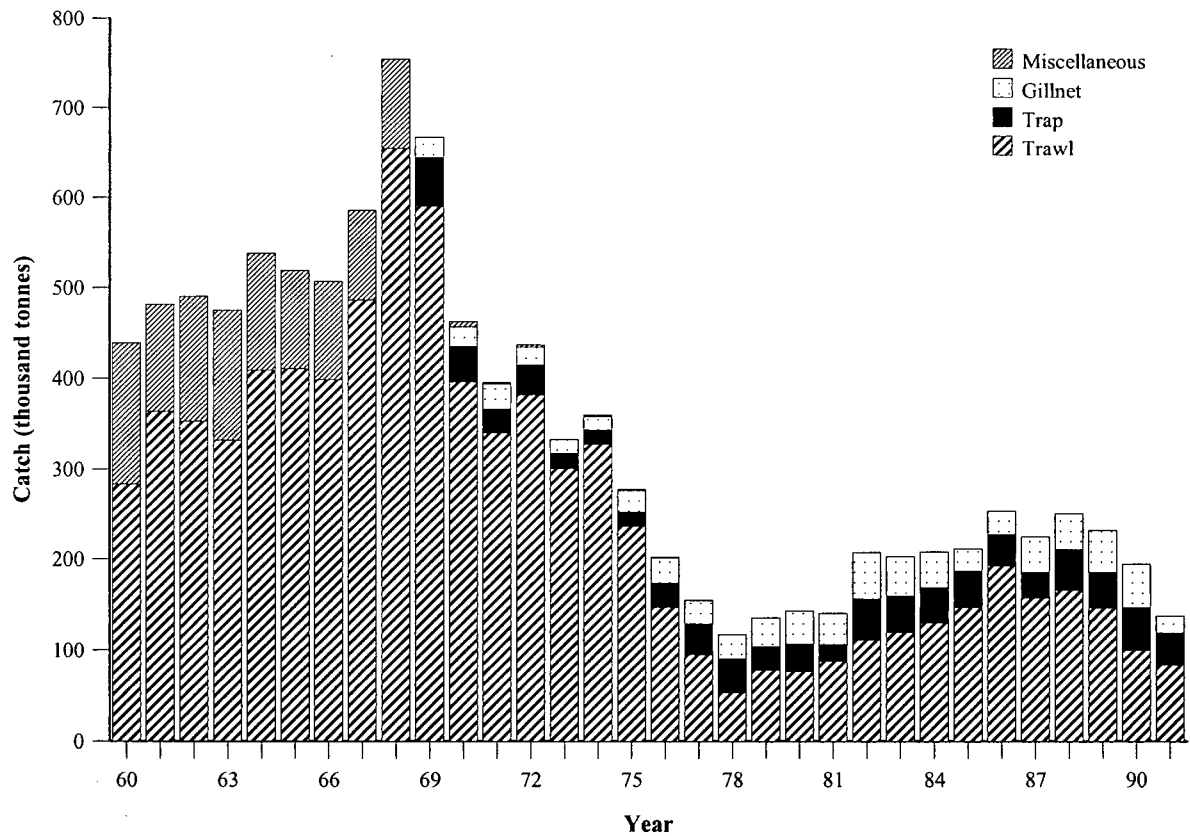


Figure 4.9 Total annual catch per gear in NAFO data set. Miscellaneous gear is probably a mixture of gillnet and trap catches (see text).

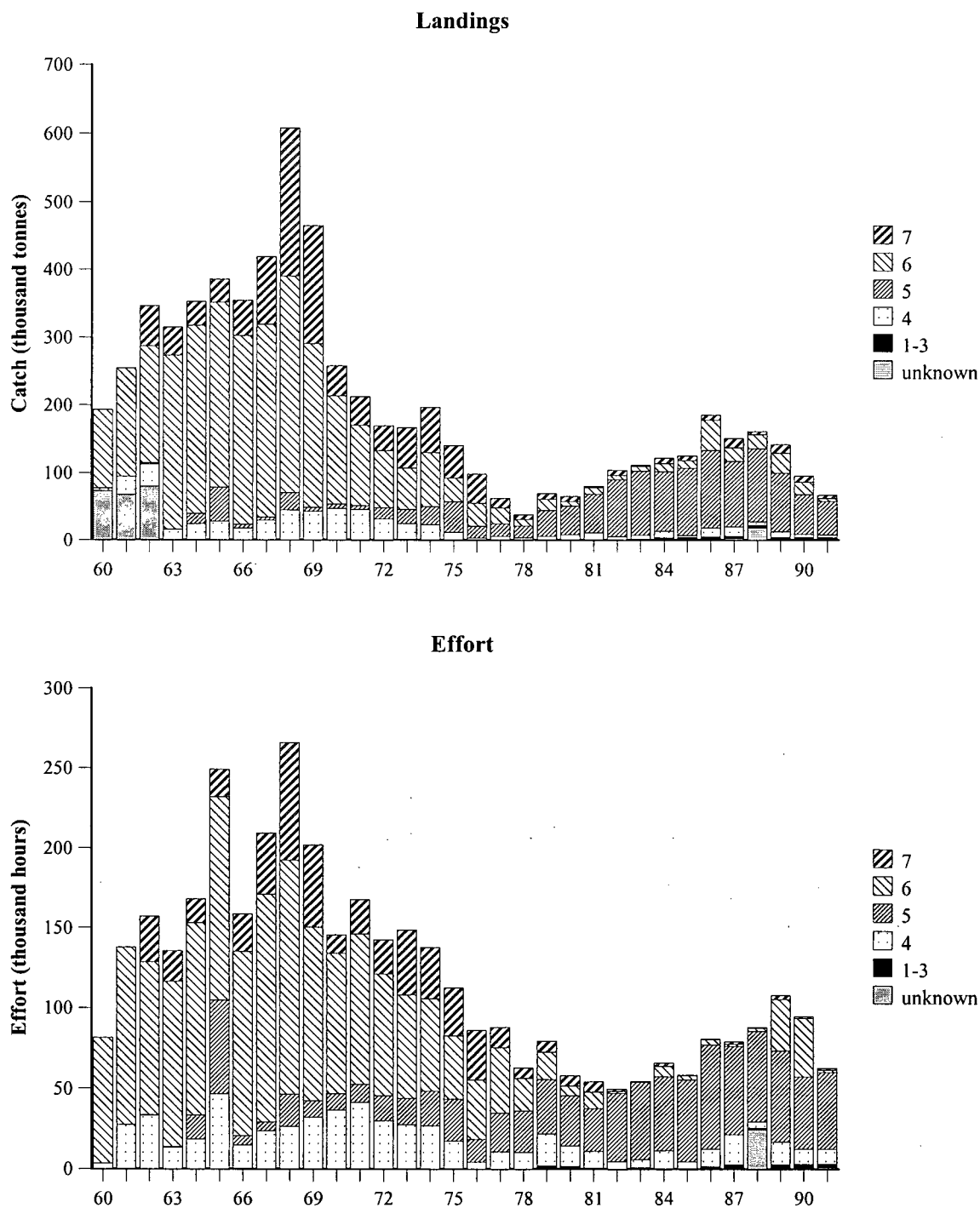


Figure 4.10 Proportion of the catch and effort directed towards cod for each trawler gross tonnage class from the NAFO data set. Gross tonnage class are defined in Table 4.2.

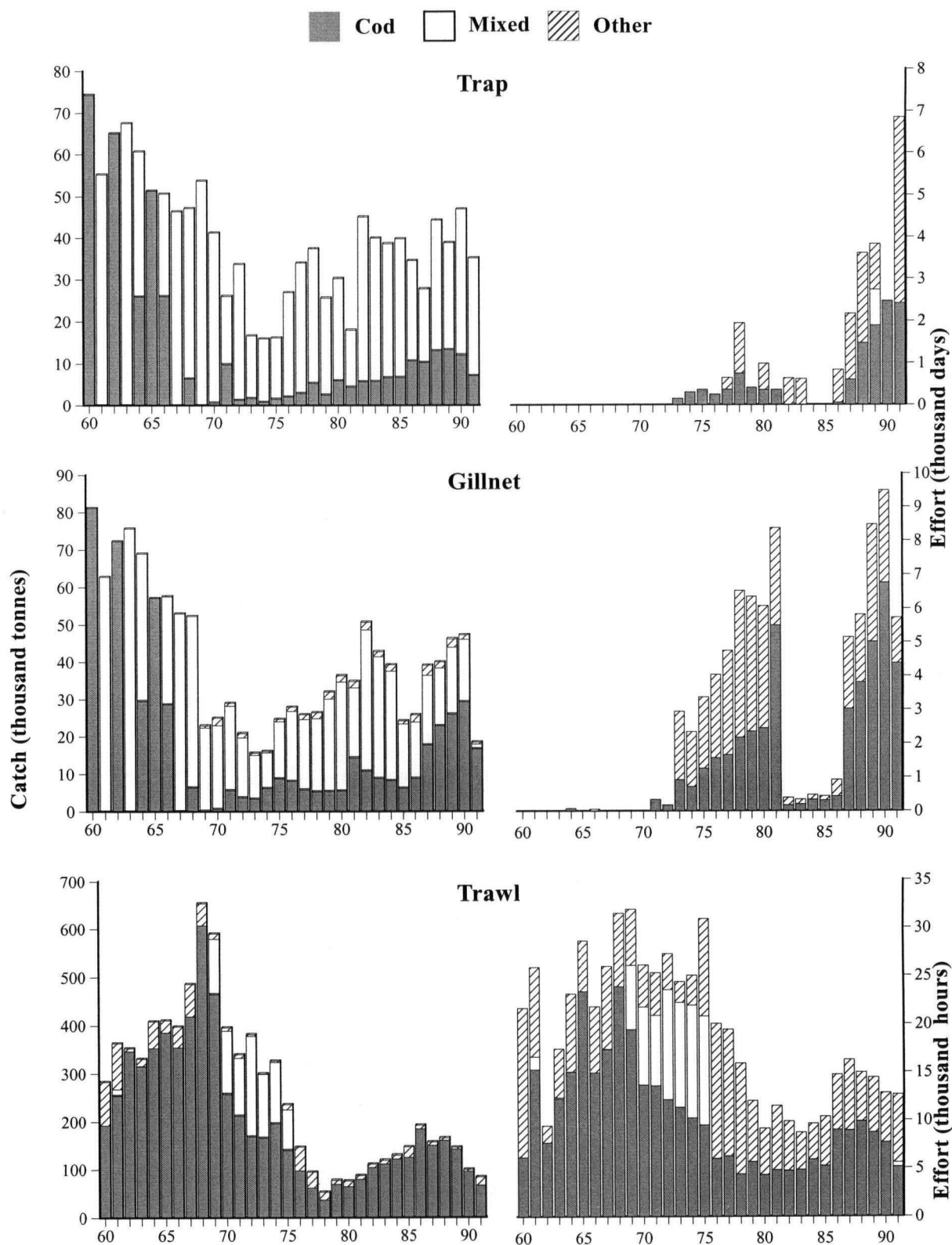


Figure 4.11. Catch and effort by gear and species targeted in the NAFO data set for years 1960-1991. Gillnet and trap of the 1960s were derived from the "miscellaneous" category in the data set (see text).

Resulting catch and effort

Once the data compilation was done, the second step was to reconstruct effort data for the period 1960-1991 using the NAFO data only. To reconstitute missing effort and focus on only one type of fishery, landings for year y and month m of the fishery targeting other species (t) were attributed effort in the same proportion as in the cod-targeting fishery (c) as follows.

$$Effort_{y,m,t} = Catch_{y,m,t} * CPUE_{y,m,c}^{-1}$$

Trawlers of unknown size, being mainly from foreign countries were attributed to class 6 vessels. Missing CPUE for particular months were replaced by the decadal average by season or the annual CPUE (Table 4.8). In absence of any effort data for gillnets and traps in the 1960s, CPUE from the 1970s has been used as a minimum measure of effort. This led to constant and low CPUE during these two decades (Figure 4.12). Effort was low in most of the 1980s and thus CPUE was higher.

Table 4.8 Number of months for which the average monthly CPUE was present in the data (Original) compared to CPUE substituted from other period and seasons.

Gear	Period	CPUE origin		Total number
		Original average	Substituted	
Trap	1960-1970	0	154	154
	1971-1980	59	94	153
	1981-1991	78	120	198
	Total	137	368	505
Gillnet	1960-1970	4	261	265
	1971-1980	173	86	259
	1981-1991	182	126	308
	Total	359	473	832
Trawl	1960-1970	381	14	395
	1971-1980	346	13	359
	1981-1991	234	19	253
	Total	961	46	1007

A second attempt to reconstruct the trawlers' effort was made using standardised CPUE for the period 1980-1991, obtained from the analysis of variance described in the observer data section. Compared to the previous reconstruction, the estimated effort was two times higher for 1982-1985 and decreased rapidly after 1988. However, trawling technology has improved greatly between 1960 and 1991 and therefore one trawling day in 1989 is likely worth more than it was in 1960. Thus, CPUE for the 1980s are probably too high in comparison with those of the 1960s.

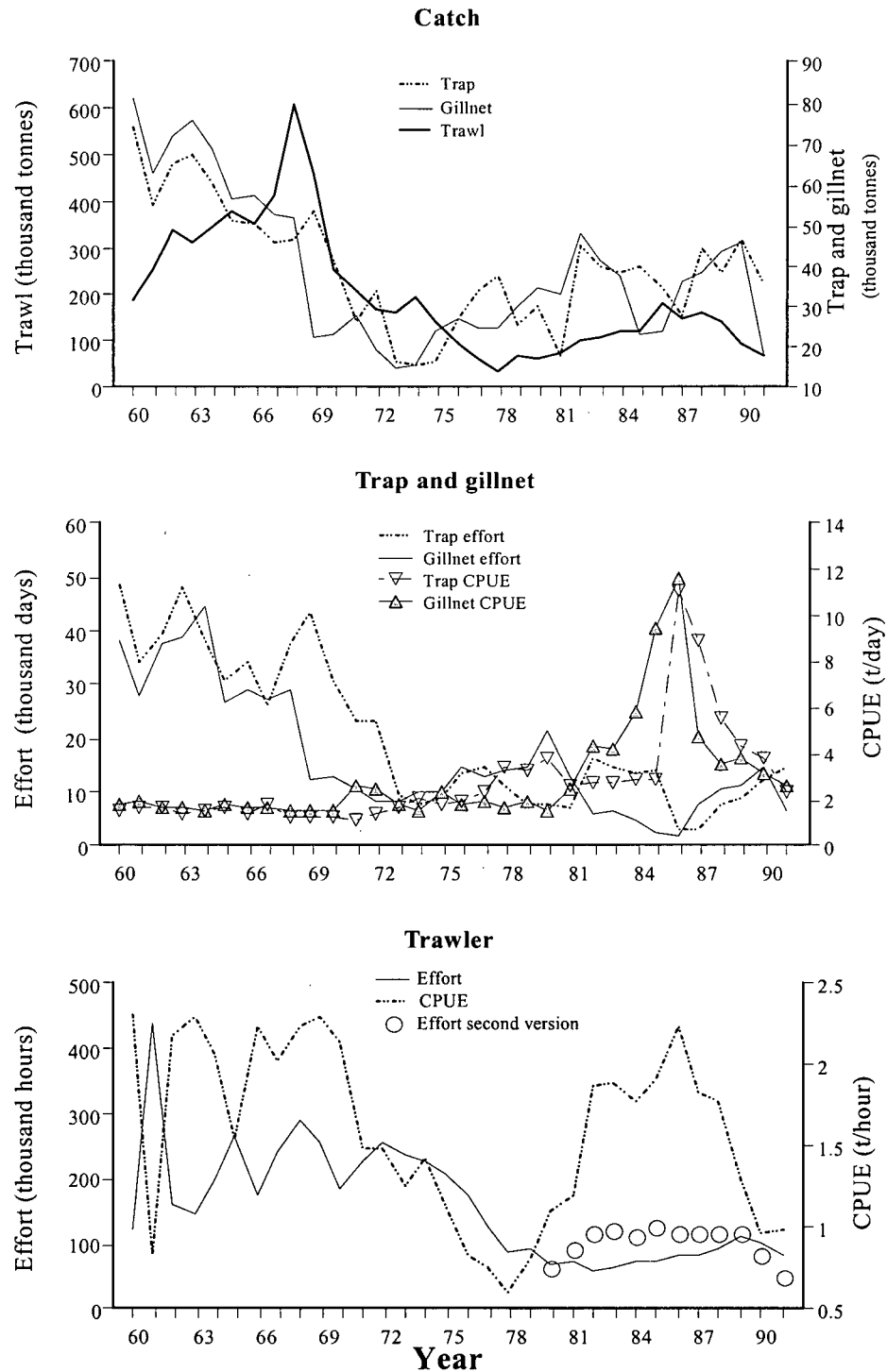


Figure 4.12 Catch, effort and CPUE for trawlers, gillnets and traps as extracted from NAFO data. Catch data includes fisheries targeting cod and mixed species while effort has been increased as a proportion of the cod fishery. The second version of effort for trawl has been obtained using standardised CPUE from the observer data (see text).

Table 4.9 Percentage of boats smaller than 20 m built at each period in Newfoundland, as determined in 1991 (Program Coordination and Economics Branch, 1993). Age of vessels are in parenthesis.

Length		1975-1980	1980-1985	After 1985
Feet	Metres	(11-15 years)	(5-10 years)	(≤ 5 years)
< 25	< 8	26	32	26
25-34	8-10	36	22	16
35-44	10-14	60	12	9
45-54	14-17	66	-	10
55-64	17-20	24	6	36

It is unlikely that trap and gillnet (inshore fishery) CPUE did in fact increase in the 1980s as the previous reconstruction showed. Instead, data from interviews of inshore fishers hinted at increasing effort and fishing power while CPUE was decreasing (Neis, 1992; Hutchings and Ferguson, 2000). First, inshore fishers often complained about declining catch which prompted the formation of the Task Group on Newfoundland Inshore Fisheries in 1987 and the Northern Cod Review Panel in 1989. Second, fishing power increased in all fleets during the 1970s and the 1980s. Compare to the vessels in use in the early 1970s, the new ones were larger, deeper, more powerful, and had twice the cargo capacity in each size class (Program Coordination and Economics Branch, 1993). Government subsidies and loans combined with excessive optimism in the industry promoted the expansion of the fleet throughout the 1970s and 1980s (Table 4.9). The introduction of mechanical hauling allowed to handle more gear per day, and electronic navigation systems and sonars increased efficiency and allowed fishers to venture further offshore (Hutchings and Myers, 1995). As fish became scarcer fishers adopted traps with more efficient designs (Hutchings and Myers, 1995). Finally, mesh size decreased in both gillnets and traps as a response to the disappearance of large fish (Neis, 1992; Hutchings and Ferguson, 2000).

CONCLUSION

The present catch data analysis shows the difficulties of keeping track of catch and effort generated by several users in large territories. The small vessel fleet was poorly monitored and a lot of essential data about the actual fishing capacity and the active number of fishers was missing. I made no attempt to reconstruct the part of the catch that may have never been reported or that may have been dumped at sea, although such allegations have been made (Hutchings and Ferguson, 2000). For modelling purposes, it was sufficient to link the results of the stock assessment and the reported catch it is based on.

Fishing effort has been systematically misreported from 1960 to 1991 for all three gears. The fact that small boats had no obligation to carry logbooks deprived biologists and managers of potentially useful information. The observer data set provided a basis for comparison for the trawlers catch per unit effort with the commercial catch data sets for the last decade only. It showed that even trawlers, which are more closely monitored, are under-reporting effort. Unfortunately, the observer program partially monitored small

trawlers and gillnetters, while other gears were ignored. Precise standardisation was rendered pointless because it was only possible for the last decade.

The effort profile reconstructed from the commercial catch data introduced a bias in the calculation of CPUE and catchability. In addition, the misreported effort made it difficult to reconstruct the fishing events of the last 30 years. The first spatially-structured model (Chapter 5) used Newfoundland landings completed with the observer data to generate a fine spatial scale (NAFO unit areas) image of the fishery for the period 1984-1991. The implications of employing such a biased effort profiles (Figure 4.5) is discussed in Chapter 5. The second model (Chapter 6) is based on total landings (NAFO records) for the period 1960-1991. In an attempt to circumvent the lack of data, the effort profile has been reconstructed by using additional historical and anecdotal data.

Chapter 5.

Could marine reserves have prevented the collapse of the northern cod in 1984? ³

INTRODUCTION

No-take marine reserves are regarded as a tool for reducing the risk of overfishing and for rebuilding stocks and ecosystems. They would serve as a buffer to management errors, overestimation of stocks, inaccurate catch statistics and inadequate control of fishing effort (Ballantine, 1991a; Guénette *et al.*, 1998). Most empirical and modelling work shows that sedentary species would benefit from a reserve, especially when reproductive capacity is taken into account (Bohnsack, 1996; Guénette *et al.*, 1998; Guénette and Pitcher, 1999), but because migrating fish are likely to move outside the reserve boundaries at times, modelling of marine reserves should account for directed movements (Beverton and Holt, 1957; Guénette *et al.*, 1998; Guénette and Pitcher, 1999). Of all papers addressing the impact of large movements outside a reserve, only Attwood and Bennett (1995) and Die and Watson (1992b) explicitly include directed movements, i.e., migration.

The present paper is intended to explore the potential use of marine reserves for the northern cod (*Gadus morhua*) of the East Coast of Newfoundland (Canada). This cod fishery was closed in 1992 when the stock was found to be at historical low levels (Lear and Parsons, 1993). The estimated spawner biomass decreased from 1.6 million metric tonnes in 1962 to 22 thousand tonnes in 1992, a decline largely attributed to overfishing (Hutchings and Myers, 1994; Taggart *et al.*, 1994; Myers *et al.*, 1996; Walters and Maguire, 1996). We examine two questions: Would the implementation of marine reserves in the mid-1980s have prevented the stock collapse, and how would marine reserves compare with other management measure such as seasonal closures and decrease of effort? We used an age- and spatially structured model that included a stock recruitment function. Cod seasonal migrations were explicit in the model and the fishery was simulated using catches from trawl, gillnet and trap.

MATERIAL AND METHODS

Study area

The area modelled was the Newfoundland shelf from the coast to the 2000 m bathymetric line, comprising NAFO divisions 2J, 3K and 3L (Figure 5.1). The area was divided in square cells about half a degree wide (30 nm); these constitute spatial units of our model.

Data

Catch statistics and observer data for the reference period (1980-1991) were obtained from the Department of Fisheries and Oceans of Canada (DFO; St. John's, Newfoundland, Canada). Although five gears are used to catch cod, we modelled the three main ones, trap, gillnet and trawl which together accounted for 88%

³ Adapted from: Guénette, S., T.J. Pitcher, and C.J. Walters. in press. The potential of marine reserves for the management of northern cod in Newfoundland. Bulletin of Marine Science.

(range, 1980-1991: 79-92%) of the total catch; trawlers alone accounted for 48% (range: 41-50%) of the landings. Catch statistics for Canadian vessels are reported by unit (subdivisions of NAFO divisions, Figure 5.1) and by month. The effort (in hours) is the amount of time during which the trawl is in the water; or, for each period of 24 hours, the number of gillnets (in 100-m units) multiplied by the number of times the nets were cleared; or the number of times traps were emptied multiplied by the number of traps. However, fishing effort is largely misreported, especially for vessels smaller than 10 m long (Anne Marie Russell, Department of Fisheries and Ocean, St. John's, Newfoundland, pers.comm.). Catch and location of catch are considered more trustworthy. For simulation purposes, boats with and without crab licenses were assumed to have similar catch per unit effort, thus the number of hours declared was upgraded in proportion of the catch, by period, season and by unit. Because the proportion of the effort declared varies also among years and it is especially low from 1982-1986, the average catch per unit effort used to complete the data were not computed for each year but for two periods: 1980-1985 and 1986-1991.

Data from the Observer Program were recorded with detailed information (latitude and longitude) on spatial distribution of effort for trawlers and to a lesser extent for gillnetters (see Kulka *et al.*, 1996, for detailed information). The catch statistics for each unit were apportioned to cells using the information from the Observer data. Because of incomplete coverage of vessels before 1987 (Kulka *et al.*, 1996) and because of low catches in certain periods, the percentage of catch and effort in each cell has been computed by period

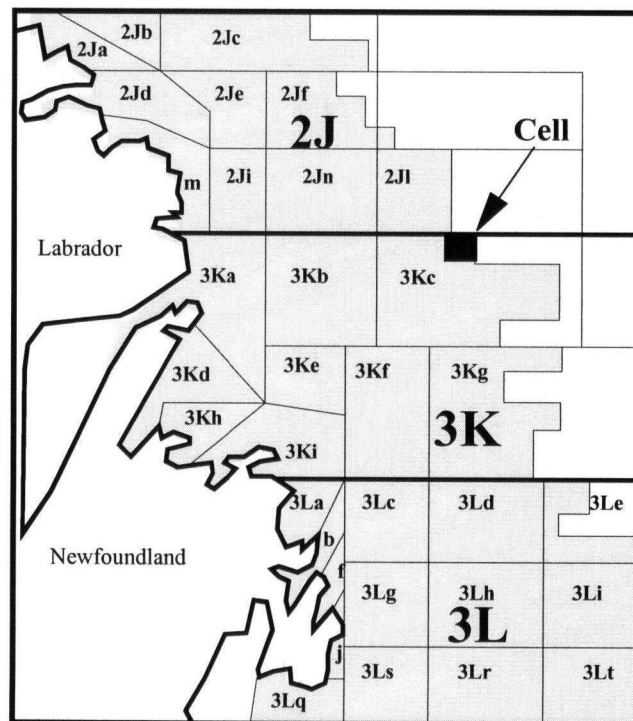


Figure 5.1 Study area (shaded) showing NAFO divisions (2J, 3K, 3L), their subdivisions (unit areas) used for statistics purposes, and the size of a cell which is the spatial unit of the model.

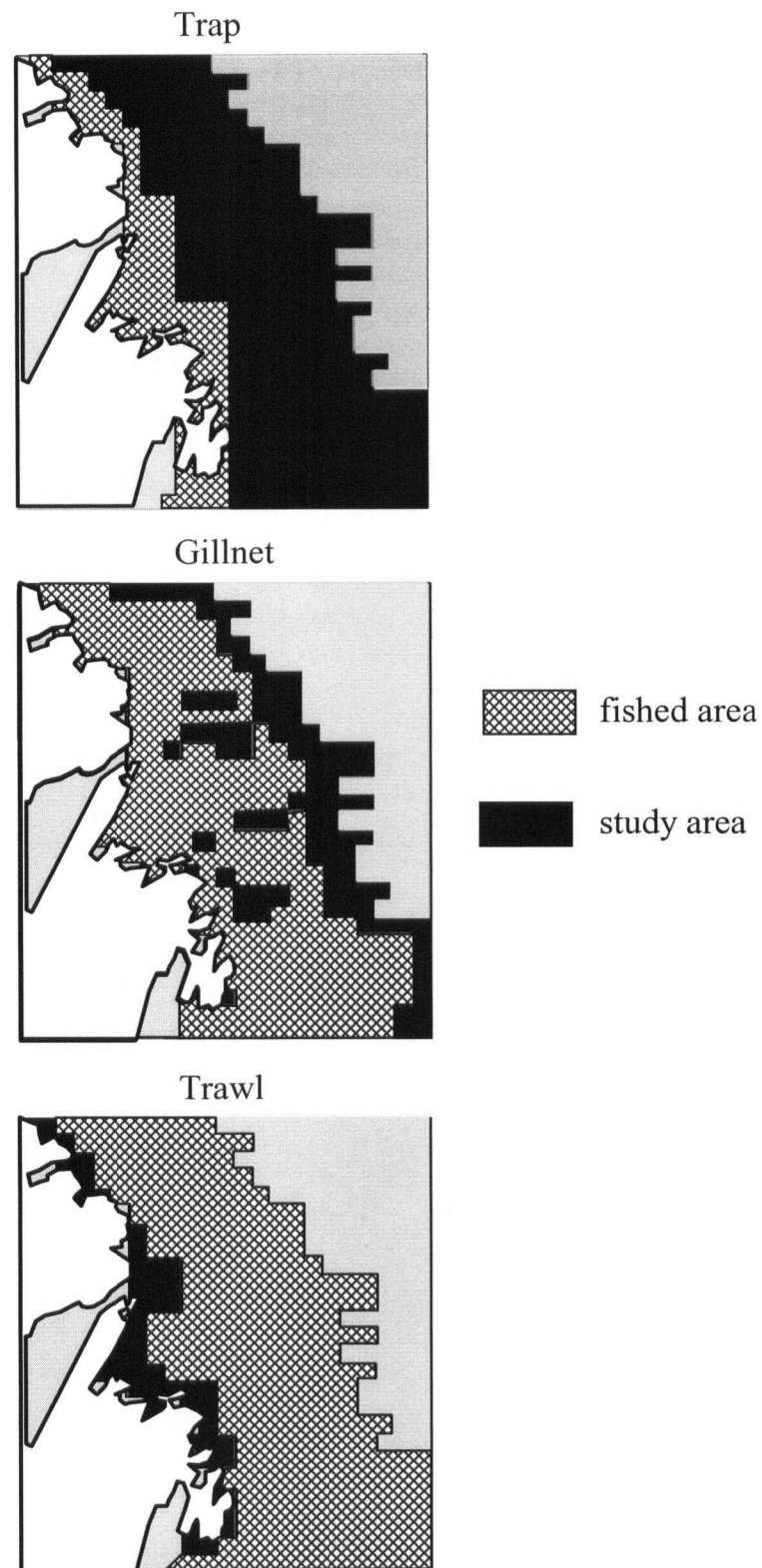


Figure 5.2 Fishing grounds for each gear used in the model, as derived from the catch statistics and the observer data.

(1980-1985 and 1986-1991) and by season rather than by year and month. Thus, the catch apportioned to a cell i at year y and month m , for model parameters estimates is:

$$catch_{y,m,i} = catch_{y,m,u} * Prop_{p,s,i}$$

where $catch_{y,m,u}$ is the catch reported for unit u by fishers and $Prop_{p,s,i}$ the ratio of the catch in cell i on the total catch in unit u as reported by observers for period p and season s . Catches from traps were confined to the coastal units (Figure 5.2) and, in absence of observer data, were equally apportioned to all the cells in the unit.

Traps are used from May to September although 54% of the landings occur during the month of July (Figure 5.3). Gillnets are used almost year-round but 57% of their landings occur in July and August. A large proportion of the trawl catch is taken in the winter (January to March) at the shelf break, although the effort is relatively low during this period. The summer catch comes mainly from the northern Grand Banks. The catchability of cod by trawl is about 10 times higher for January and February than during the rest of the year.

For the study period, catch per unit effort (CPUE) per year,

$$\ln CPUE = \left(\sum_{i=1}^I \ln(catch_{i,gear} * effort_{i,gear}^{-1}) \right) * n^{-1}$$

where n is the number of cells, increased slightly for traps and gillnets as the biomass decreased (Figure 5.4). However, gillnet CPUE shows an odd increase in 1991. Trawl CPUE was more irregular exhibiting

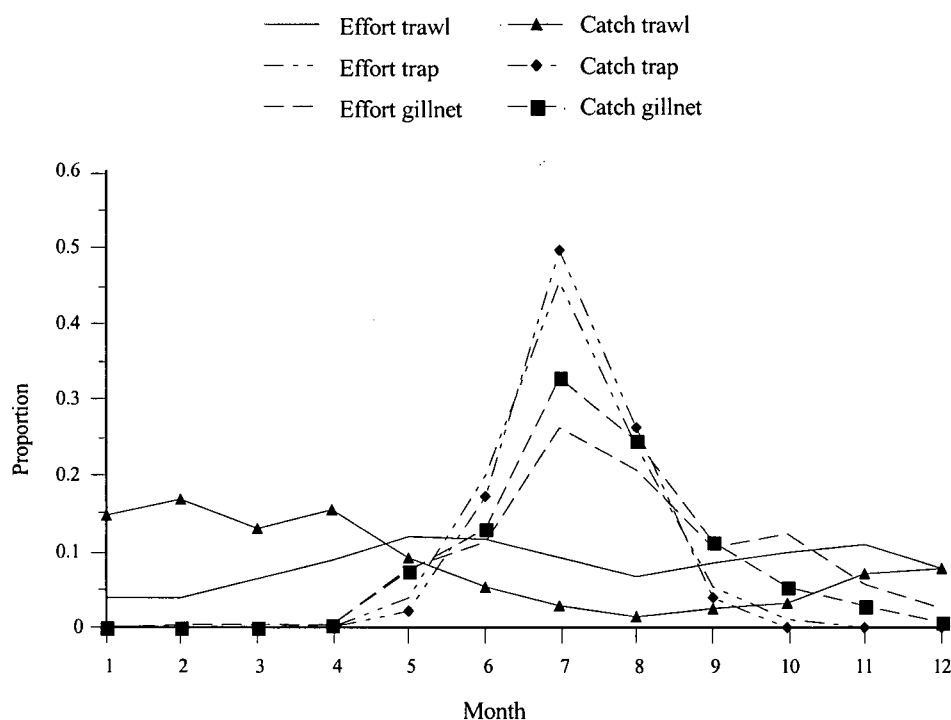


Figure 5.3 Monthly proportion of average catch and effort for the three gears between 1980-1991 used in the simulations.

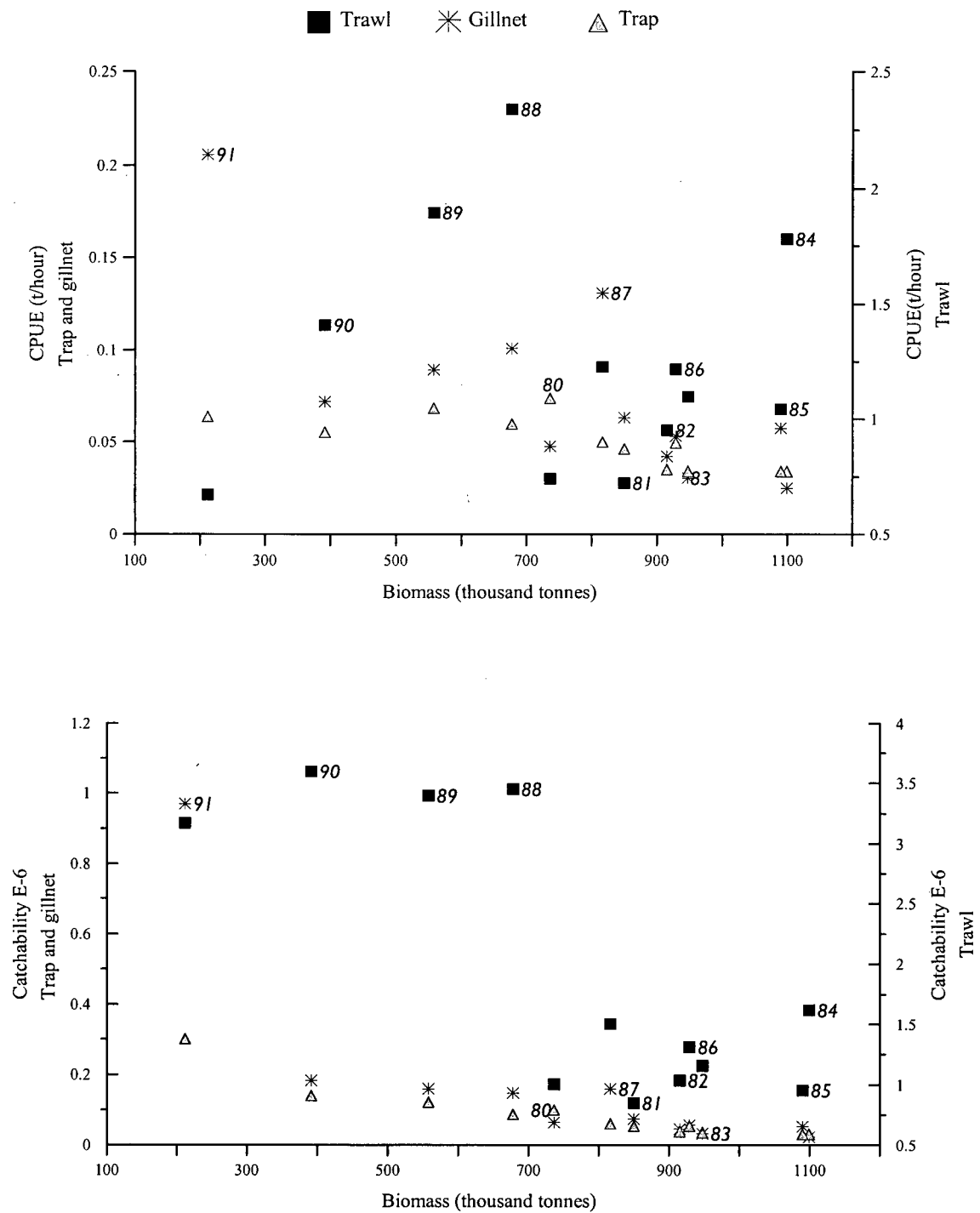


Figure 5.4 Catch per unit effort (CPUE) and catchability as a function of the population biomass observed during the period 1980-1991. For clarity, the year corresponding to a particular biomass is indicated once for all gears (number besides symbol).

a large increase in 1984 and 1988 and then declined from 2.5 to 0.7 in 1991. Catchability (q), computed as $CPUE * Biomass^{-1}$, increased by 61% for trawl, 82% for gillnets and 90% for traps.

Model

To simulate possible effects of marine reserves, we developed a multiple-stock age structured accounting model where the numbers of fish at age for each stock are distributed and move over the grid of half-degree cells shown in Figure 5.1. The age-structure accounting for each cohort for each stock involves prediction of recruitment at age 1 from an egg-recruitment relationship, then fishing and natural mortality losses over time. Natural mortality losses are accounted for on an annual basis, whereas spatially distributed fishing losses are removed on a monthly basis (to account better for movement and for seasonal changes in the spatial distribution of fishing effort). The following subsections describe the main assumptions used in the accounting calculations. The accounting system used in the "FISHMOD" shell was developed at UBC (C. Walters, pers. comm.) and has been utilised for a variety of spatial populations assessments, such as lingcod in British Columbia, and sharks and shrimps in Australia.

Movement patterns

The stock structure of northern cod is largely unknown, although evidence suggests the presence of numerous stocks (Lear and Parsons, 1993) and possibly distinct inshore and offshore stocks (stocks remaining in the offshore areas) (Lear and Parsons, 1993; Lilly, 1996; Ruzzante *et al.*, 1996; Neis *et al.*, 1999). We examine only the case of the offshore stocks which undergo seasonal migration as generally described by Lilly (1996), Lear and Parsons (1993) and Taggart (1997). Cod spend the winter moving along the break of the continental shelf in large and relatively tight aggregations (Kulka *et al.*, 1995; Wroblewski *et al.*, 1995). They start their migration toward the continent in the spring and spend the summer slowly travelling north and feeding. They migrate back offshore in the fall, the Labrador group earlier than the others (Taggart, 1997). For the purposes of our model, we did not attempt to define formal stocks but only groups that share similar movement patterns (Figure 5.5), as suggested by the tagging experiments (Lear, 1984; Taggart, 1997) and observer records on offshore trawlers (Kulka *et al.*, 1995; Wroblewski *et al.*, 1995). Thus four groups have been defined: Labrador coast, Belle Isle Bank, Southern Newfoundland and Northern Grand Bank (Figure 5.5).

We simulated the seasonal migration pattern for each group or substock by defining a target cell (attraction site) for each age group and month. Because no precise information was available, target cells were defined so that the simulated movement was visually similar to observed migration patterns, and resulting distributions approximately matched fishing concentrations observed during the years 1980-1992. The proportion of the population that moved from one cell to another was computed 10 times a month. At each step, fish are not allowed to move more than one cell. Fish followed the target cell more or less tightly depending on the value of a random movement component (RMC). RMC was made to increase in the summer when cod disperse along the shelf and to decrease in the winter to yield tighter schools at the edge of the shelf (Kulka *et al.*, 1995; Wroblewski *et al.*, 1995). This variable was specific for each age and month. Because the area occupied by cod decreased with their abundance (i.e. range collapse) during the period 1980-1991 (Hutchings, 1996; Atkinson *et al.*, 1997), RMC of age a , year y and month m of the simulation varied with the cod biomass present at the beginning of the year:

$$RMC_{y,a,m} = b * \ln(RMC_{0,a,m} * VulnB_y * B_{ref}^{-1}) - c$$

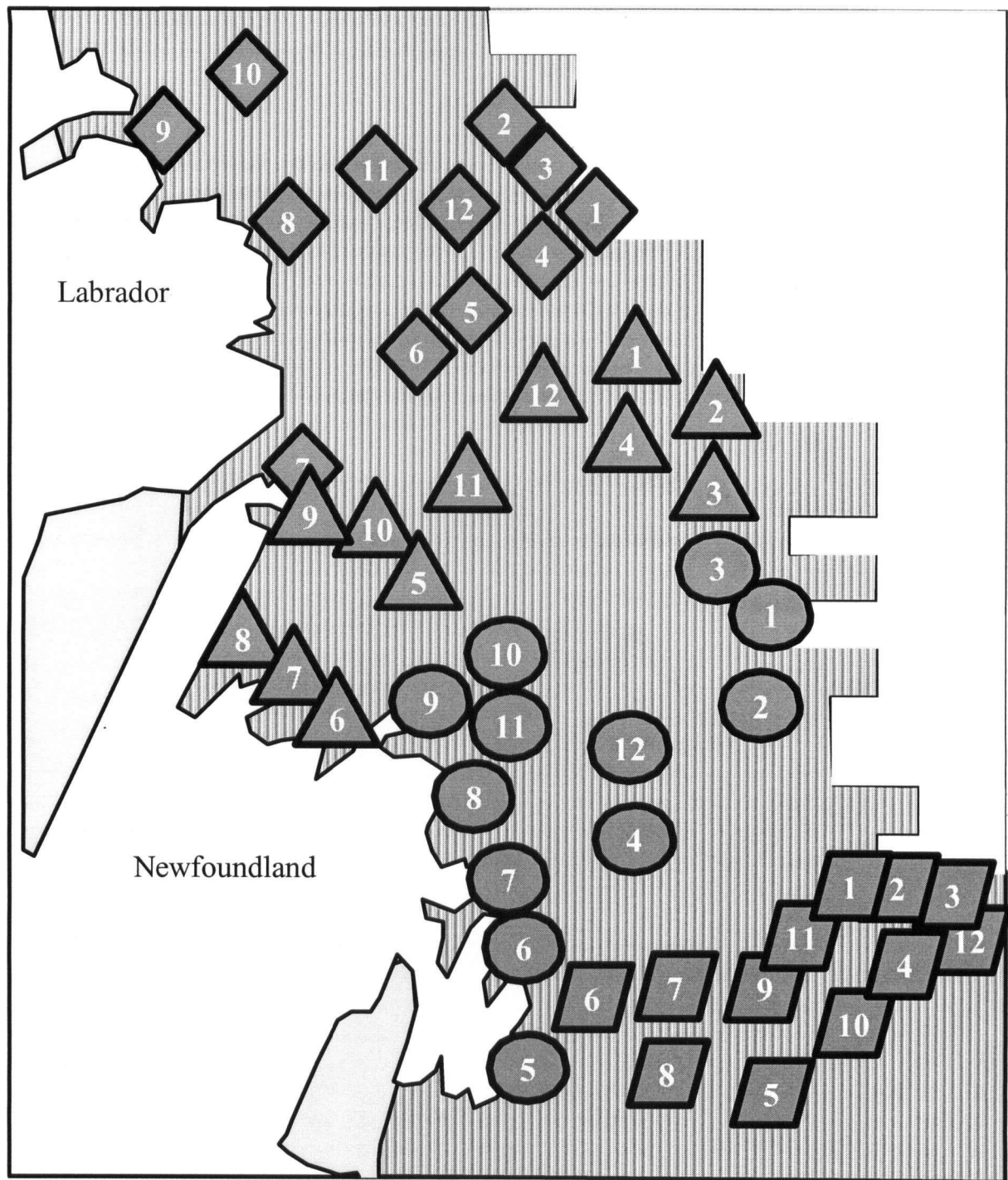


Figure 5.5 Location of the monthly target cells (numbers in geometric symbols) for 5 yr-old cod used to generate seasonal migration for the four cod groups: Labrador coast (diamond), Belle Isle Bank (triangle), southern Newfoundland (ellipse) and northern Grand Bank (parallelogram).

where $RMC_{0,a,m}$ is the initial random movement component for age a at month m , $VulnB_y$ is the biomass of cod vulnerable to the fishery at the beginning of the year, B_{ref} is the vulnerable biomass of cod in the first year of the simulation (1984), and b and c are constants. The equation was calibrated to decrease the area by twofold as population abundance decreased; Atkinson *et al.* (1997) showed that the area containing 90% of biomass decreased by about threefold between 1984 and 1992. The RMC, b and c parameters were varied in test simulations until the model produced seasonal distribution patterns similar to observed distributions from catch data. Values of RMC parameter that were used produced distribution area roughly similar in size (area covered) and seasonal movement to that deduced from the available data. Predicted effects of spatial closures were found to be quite insensitive to the RMC values used.

Population parameters

Population abundance estimates for the years 1980-1991 were obtained from the 1996 stock assessment (Shelton *et al.*, 1996). From 1980 to 1984, the population showed an increase in biomass due to uncharacteristically high levels of recruitment. The increase was very small compared to the general decline starting in the 1960s, but still created difficulties in fitting the model. Because we were interested only in the collapsing phase we began the simulations in 1984. We assumed that the instantaneous natural mortality rate (M) is 0.2 year⁻¹, for all years. Vulnerability at age was calculated as:

$$Vul_a = F_a * F_A^{-1}$$

where F_A is the instantaneous fishing mortality for adult fishing fully recruited to the fishery as estimated with virtual population analysis over years 1985-1991 (Shelton *et al.*, 1996). Data on weights at age and proportion of mature females at age for year 1989 were obtained from Shelton *et al.* (1996) and Morgan and Trippel (1996), respectively (Table 5.1). Fecundity at age was calculated using Pinhorn's (1984) equation:

$$Fecundity_a = age^{2.26} + 6918$$

Although fecundity is more closely related to size than age (May, 1967), we used fecundity at age for convenience and also because the model does not include any growth variation through time. A Beverton and Holt type spawner-recruit relationship was built following the procedure outlined in Appendix 5.1. K , the carrying capacity

Table 5.1 Mean weight, maturity and vulnerability schedules used in the model.

Age	Weight (kg)	Maturity	Vulnerability
1	0.064	0	0
2	0.18	0	0
3	0.44	0	0.1
4	0.77	0.002	0.3
5	1.2	0.016	0.5
6	1.58	0.123	0.7
7	1.91	0.551	0.8
8	2.25	0.915	1
9	2.77	0.989	1
10	3.63	0.999	1
11	3.78	1	0.9
12	5	1	0.8

Table 5.2 Number of nursery cells attributed to each cod group in the model.

Group	Number	%
Labrador coast	26	19.5
Belle Isle Bank	44	33.1
Northern Grand Bank	44	33.1
Southern Newfoundland	31	23.3
Total:	133	

in the equation, was apportioned into each group proportionally to the number of nursery cells (Table 5.2). The annual recruitment (at 1 year old) was calculated separately for each stock.

Fishing

The model generates catch by using the observed monthly spatial distribution of effort as derived from the statistics, or simulated effort obtained by distributing the monthly total effort to cells according to assumed fisher behaviour. The first method was only used to assess model behaviour and to adjust movement and fishing parameters. All simulations were obtained with the second method. Spatial effort simulations were based on the assumption that fishers concentrate on cod aggregations and are able to locate them rapidly, which we believe trawlers do. Hunting behaviour is minimal for traps because they are less mobile and are confined in coastal zones. Gillnetters have increased their hunting behaviour by using echo sounders and electronic navigation.

We used a gravity model to allocate effort where the effort applied by each gear in each cell i is a function of the monthly historical effort ($HistE$):

$$Effort_{i,m,gear} = HistE_{m,gear} * Attract_{i,m} * Attract_m^{-1}$$

and the attraction power of that cell ($Attract_{i,m}$) compared to the sum of attraction for all the cells ($Attract_m$):

$$Attract_{i,m} = \sum_{i=1}^I Attract_{i,m}$$

Local attraction to one cell i at month m is defined as

$$Attract_{i,m} = VulBiom_{i,m}^h$$

where h , the hunting power, is set at 1.7 for traps, 2.5 for gillnets and 3 for trawlers, and the vulnerable biomass defined as

$$VulBiom_i = \sum_{a=1}^A Biom_{a,i} * Vul_a$$

As explained earlier, the catchability increased with decreasing biomass. Preliminary runs of the model showed that the simulated range-collapse mechanism was not sufficient to generate the high catch rate and catchability observed in historical data. The observed increase in catch rate could be explained by two factors. As abundance decreased, cod still aggregated in large schools (Hutchings, 1996), which are easy to locate with modern searching devices. Also, as abundance decreased, schools would be more discretely localised within a cell, so the time spent searching for schools within a cell would increase, and schools would eventually be encountered regardless of the total biomass available. Therefore, the catchability would increase as abundance decreased. In our model, the catchability within each cell was made to increase with decreasing abundance, as:

$$q_{m,gear} = q_{0,gear} * Bref * d * (VulBiom^e)^{-1} \quad \text{modified from Pitcher (1995)}$$

where $q_{0,gear}$ is the nominal q for each gear, $Bref$ is a reference, or unexploited biomass (6 million tonnes, an arbitrary reference point) and d and e constants computed separately for each gear. The equations were calibrated so that catchability would increase by a factor of 11 for gillnet and of 7 for trawl and trap

between 1984 (the highest biomass) and 1991 (the lowest biomass). In addition, the exploitation rate (u) within a cell follows the catch equations:

$$u_{i,m,gear} = 1 - \exp(-q_{m,gear} * Effort_{i,m,gear} * (1 + q_{m,gear} * Htime * VulBiom_i)^{-1})$$

where $u_{i,m,gear}$ is the exploitation rate for month m , cell i and a particular gear and the time spent handling an aggregation ($Htime$) is kept constant at 0.1. Finally, the yield (in tonnes) is obtained by:

$$Y_{i,m,gear} = u_{i,m,gear} * VulBiom_i$$

Simulations

Because the probability of fish that will cross the reserve boundaries is a function of the perimeter to area ratio (Beverton and Holt, 1957), we tried to design simulated reserves (collections of model cells closed to fishery) in compact shapes. The smaller reserve size (5%) was placed in cells that were historically highly fished. Larger marine reserves were obtained by addition of cells contiguous to those already present, expanding offshore and to a lesser degree inshore (Figure 5.6).

Three types of scenarios were simulated for periods of up to 40 years starting in 1984. In the first, marine reserves of different sizes were implemented without any other management measures. In the second, seasonal closures for trawl and gillnet were implemented alone or in conjunction with marine reserves. Trawl seasonal closure would cover the months of January to May, when pre-spawning and spawning aggregations occur offshore (Hutchings, 1995). Gillnet fishing would be permitted only June through August. In 1984, such closures would have cut the trawl catch by 30% and the gillnet catch by 28%. In the third, we examined the case where reserves and seasonal closures were implemented but stimulated an increase of 10 or 20% in effort starting in 1984 and kept constant in subsequent years. This increase is conservative compared to the increase in effort and power observed in 1980s.

For the years 1984 to 1991, the historical monthly distribution of effort was used in all simulations. After 1991, fishing effort was defined as the average historical effort between 1984-1991. Scenarios are compared among themselves and with the observed (historical) level of catch and biomass. Monthly catch per unit effort computed as $catch_{m,gear} * effort_{m,gear}^{-1}$ was used to compare the quality of fishing on available grounds for periods of high catch levels. Thus, when necessary, trap and gillnet CPUE were compared for the month of July, and trawls for the months of February and July. An efficient management scenario should avoid a population collapse during the simulated period.

RESULTS

The model was able to reproduce the population crash and the high level of catches that were observed up to year 1991 (Figure 5.7). There are discrepancies of up to 20 % in some years, especially for trawl and gillnet, that may be due to inaccuracies in monthly simulated catches.

Used alone, marine reserves smaller than 40% of the total area did not change the total catch and hence did not prevent the population collapse. Reserves of 50% only slowed the decline (Figure 5.8). A marine reserve of 80% allowed the stocks to rebuild slowly and decreased the catch by half, from the observed 200,000 tonnes, to about 100,000 tonnes. Such a large marine reserve decreases the available fishing areas to the point where those left are submitted to very high fishing rates. Competition would be high on the fishing grounds, and simulated CPUE decreased by 30% for trawlers in July, by 50% for traps, and 50% for

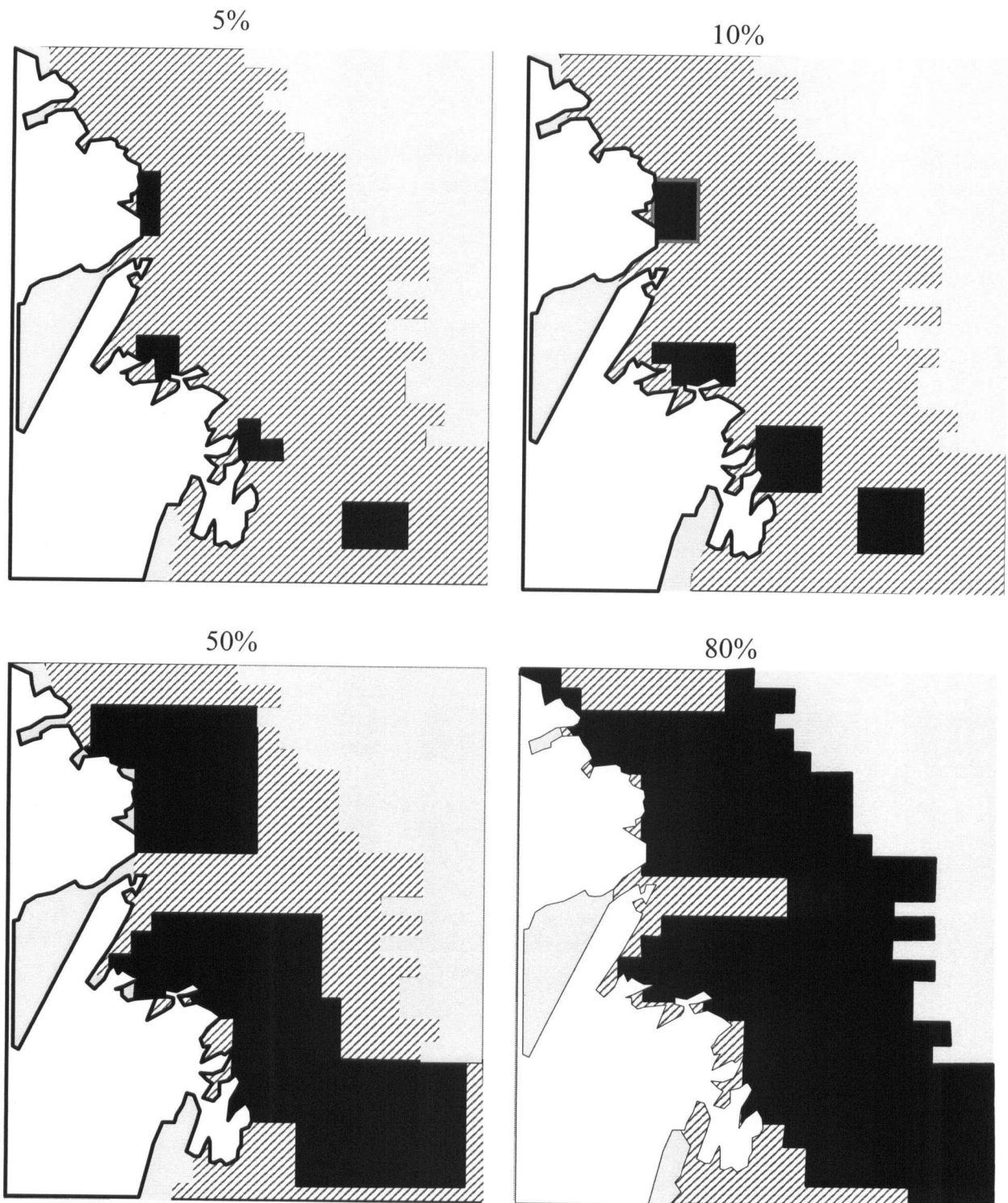


Figure 5.6 Location of marine reserves (black) covering 5, 10, 50 and 80% of the study area (hatched). 20% marine reserve is illustrated in Figure 11A.

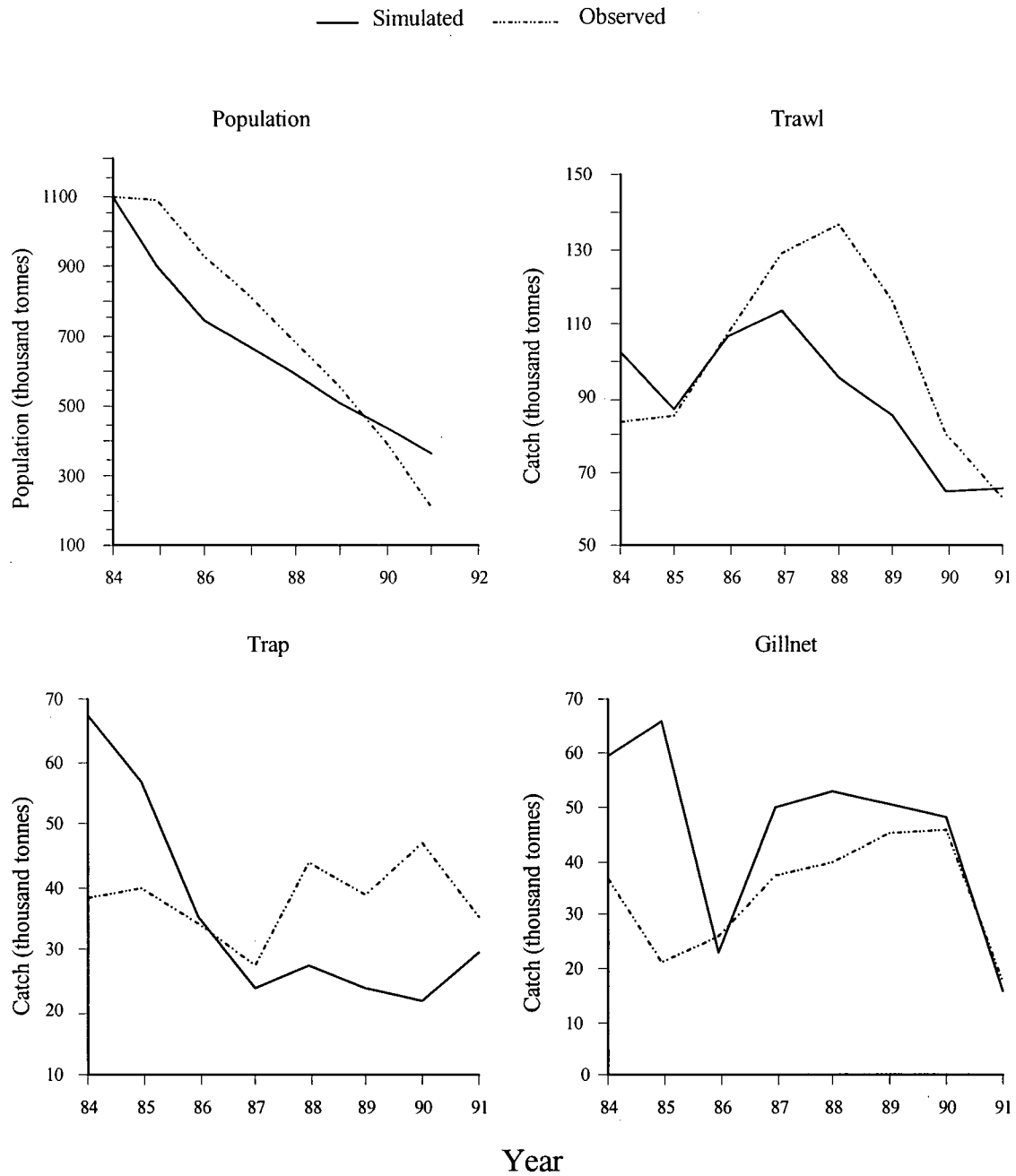


Figure 5.7 Comparison of observed and simulated population size and catch for trawl, trap and gillnet using historical monthly effort for years 1984-1991.

gillnets (Figure 5.8). February CPUE for trawls decreased to July level because the aggregation area (shelf break) was closed to fishing.

Winter trawl closure would decrease the catch for that gear by 50%, but most of the spared fish would be taken later in the season by the trap and gillnet sectors resulting in a minor impact on the population level. Used alone, the trawl and gillnet closures only delayed the occurrence of the population crash (Figure 5.9). The addition of a reserve comprising at least 20% of the area would allow for the rebuilding of the population. Winter trawl closure and a 50% marine reserve would allow the population to rebuild faster than would an 80% reserve alone. In both cases the catch would drop below 100 thousand tonnes. When accompanied by both trawl and gillnet closures, a direct reduction of effort by 50% (providing that it could be achieved) would have an effect on the population level similar to that of a marine reserve covering 50% of the fishing grounds. If fishers were to increase effort in expectation of additional gains at the opening of the season, the benefits of marine reserves would be reduced, and the rebuilding of the population would be proportionally slowed (Figure 5.10).

In the last scenario, where trawl and gillnet closure were accompanied by a 20% reserve, three reserves locations were compared (Figure 5.11). The original 20% reserve proposed encompassed a large proportion of the coastal area, limiting catches by traps and gillnets (Figure 5.11). Moving portions 1, 2 and 3 of the reserve slightly further offshore (Figure 5.11B) would decrease their efficiency and requiring a larger total reserve, to achieve the same result (Figure 5.12). Moving portion 3 inshore yielded results more like those of the configuration in Figure 5.11A.

We also simulated the use of reserves covering the outer limit of the shelf (offshore reserve) and others covering the migration paths of the four stocks (corridor reserves, Figure 5.13). These new designs, both covering 50% of the shelf, were compared to the original 50% reserve design (Figure 5.6). Although the corridor and offshore designs protected the stocks slightly better than the no-reserve scenario, they led to faster stock depletion than did the original design (Figure 5.14). The offshore reserve favoured gillnets and traps by effectively closing the shelf break to fishing and leaving the rest of the shelf open. Compare to a no-reserve scenario, the corridor reserves decreased CPUE for all fleets by closing both inshore and offshore areas.

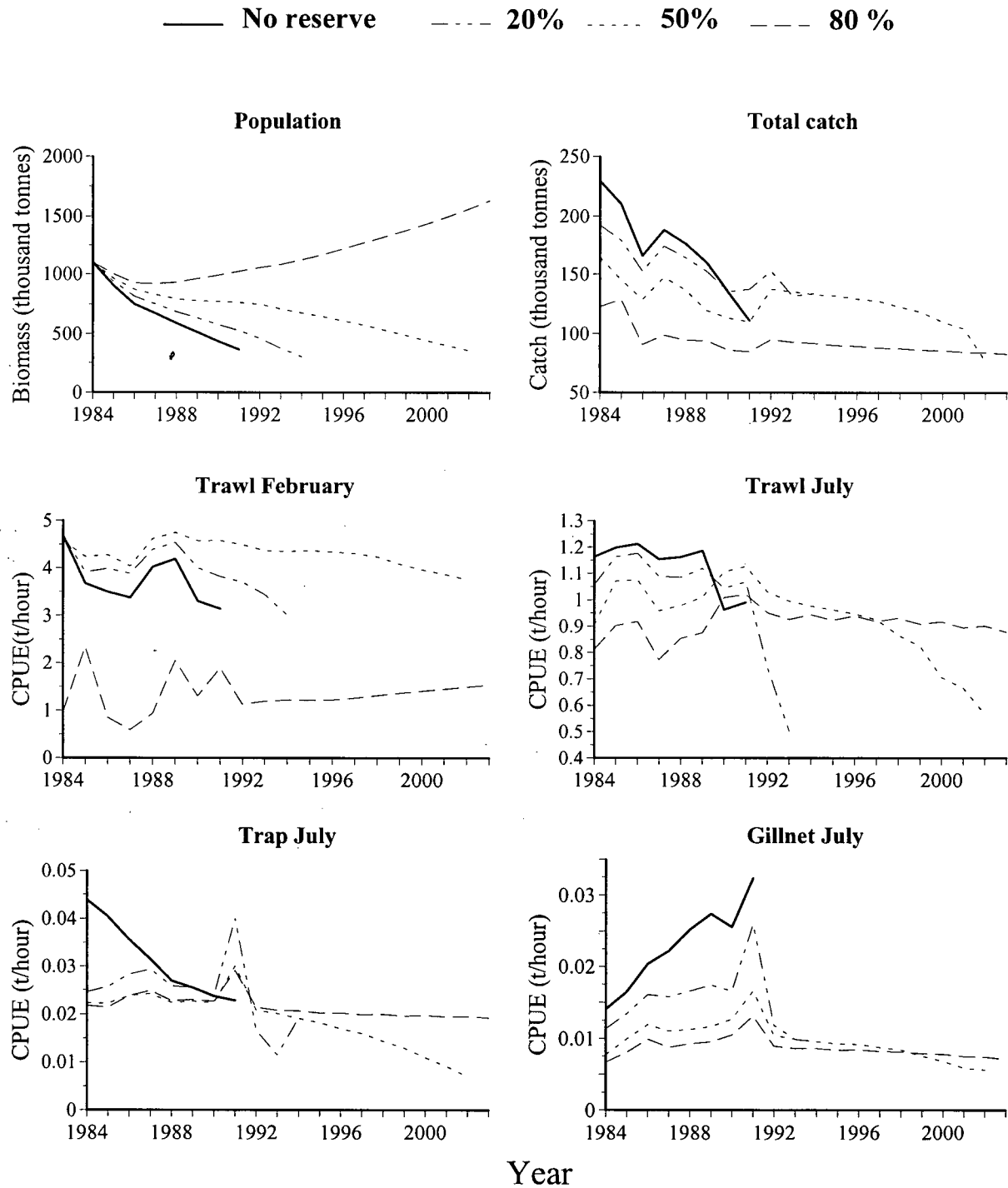


Figure 5.8 Population size, total catch and catch per unit effort for trawl (February and July), trap and gillnet (July) for three scenarios: without and with marine reserves covering 20, 50 and 80% of the fishing ground.

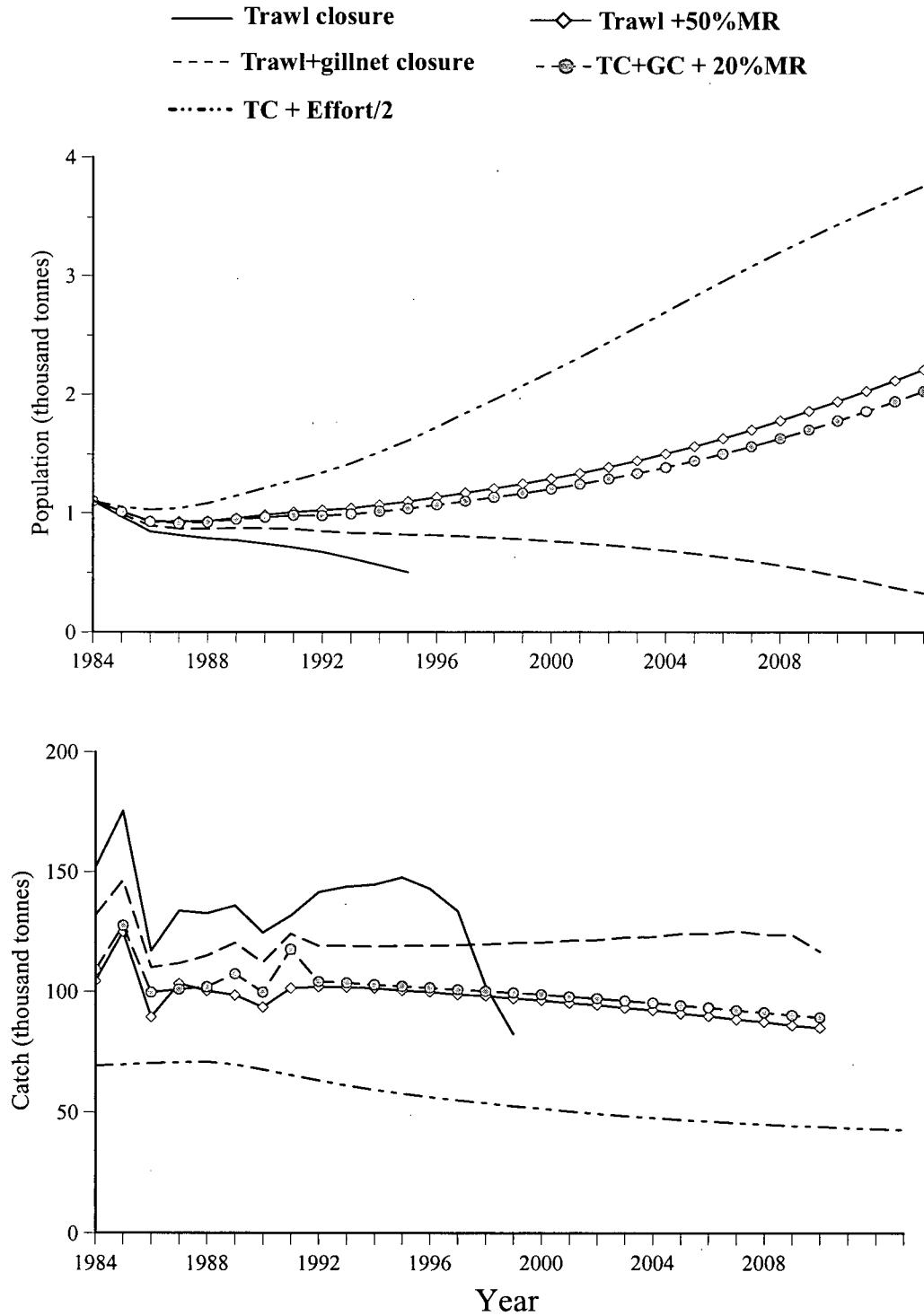


Figure 5.9 Population size and total catches for trawl closure (TC) and gillnet closure (GC) used alone, in conjunction with marine reserves, or direct halving of trap and gillnet effort (Effort/2).

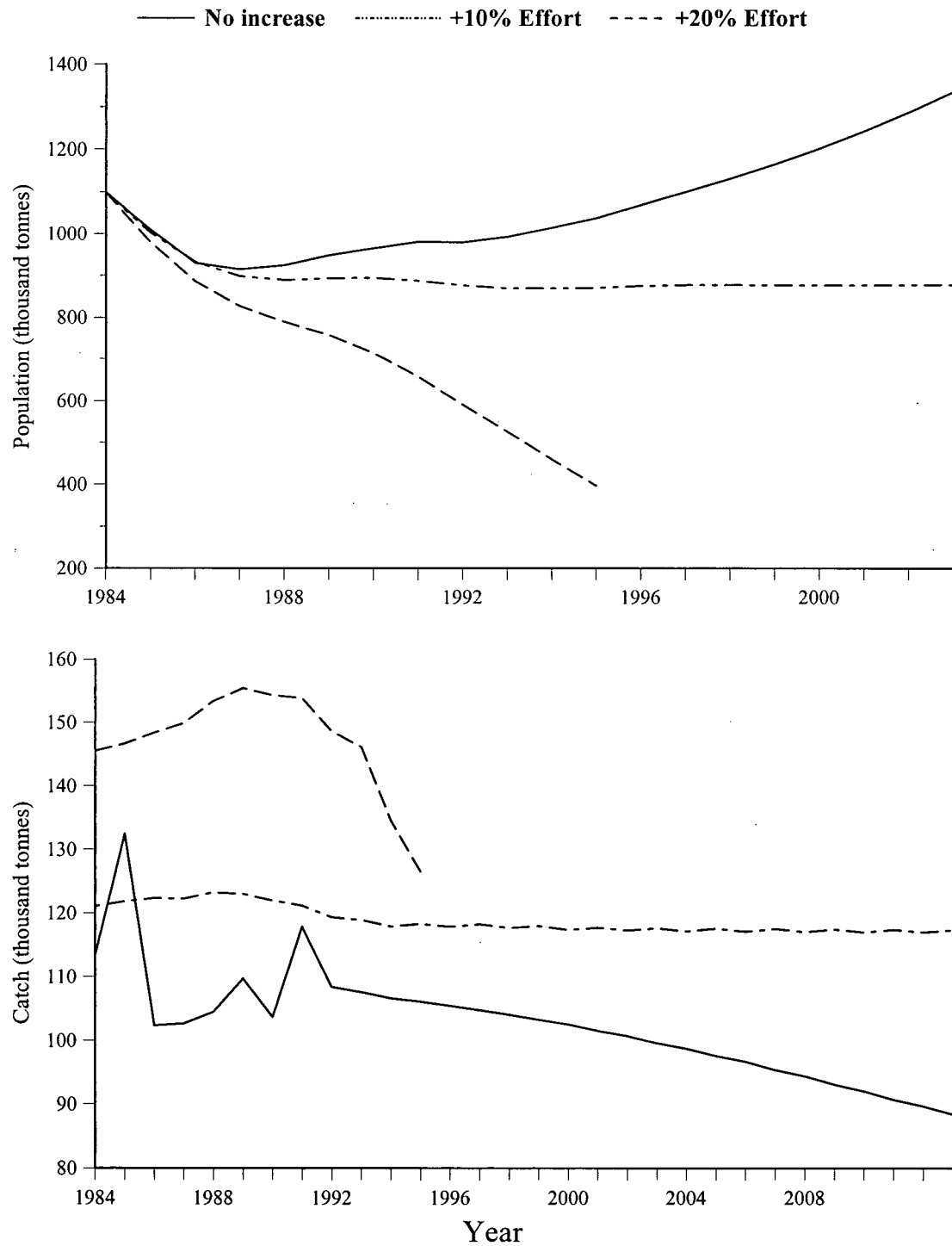


Figure 5.10 Impact of increasing effort by 10 or 20% when seasonal closures for trawl and gillnet are accompanied by a 20% marine reserve.

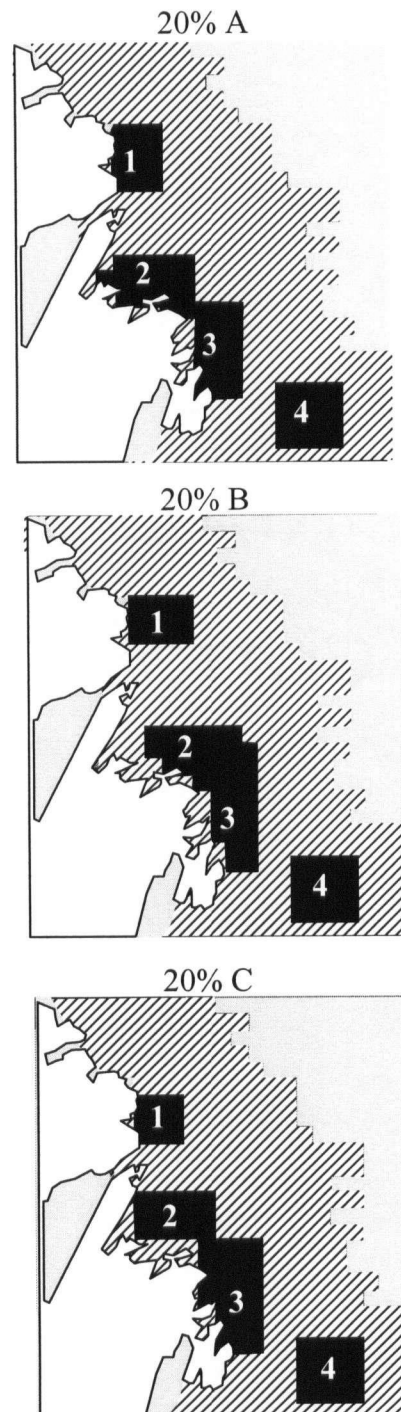


Figure 5.11 Three different locations for a 20% marine reserve. A. Original one used in precedent simulations, B. Displacement of portions 1, 2 and 3 slightly offshore, C. Portion 3 is moved inshore.

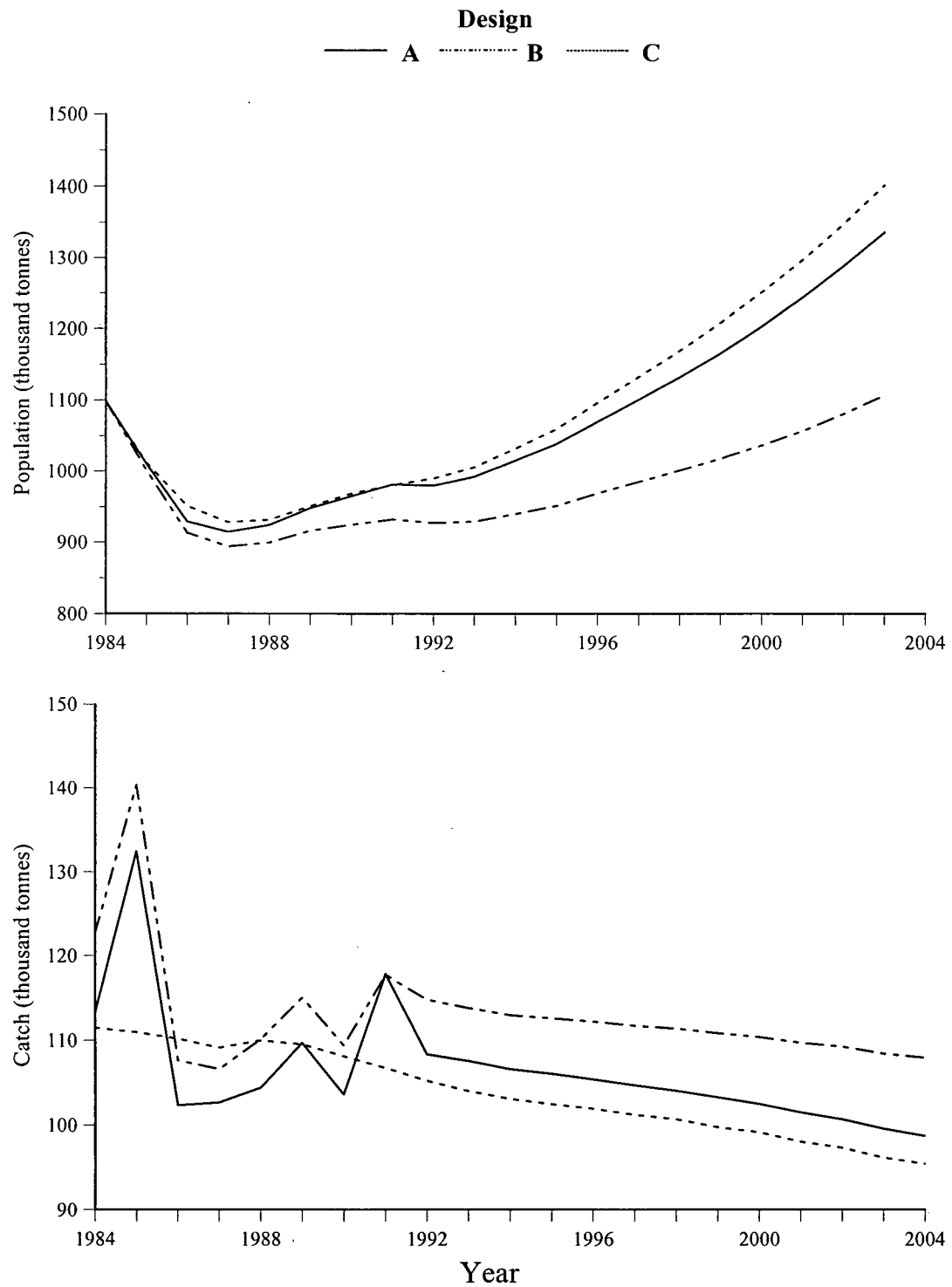


Figure 5.12 Population sizes and total catches for three different locations for 20% marine reserves as illustrated in Figure 5.11

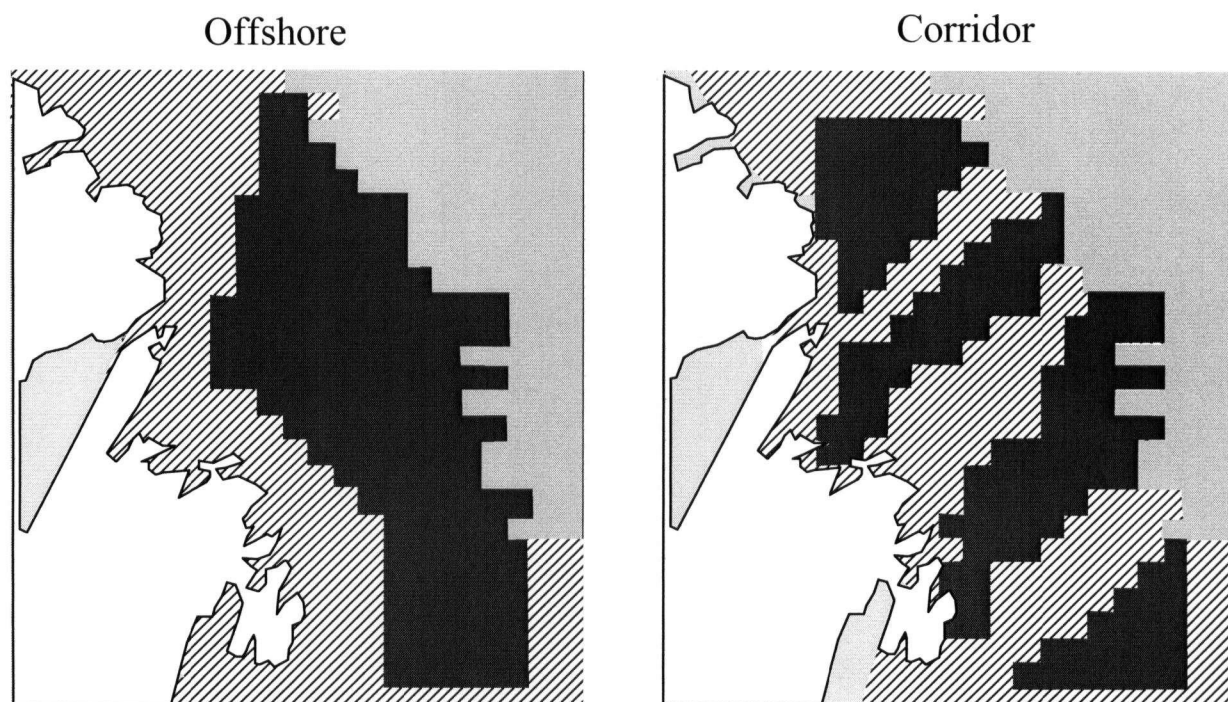


Figure 5.13 Offshore and corridor locations of marine reserves (black) covering 50% of the shelf (hatched).

DISCUSSION

Our results show that migrations and the high fishing capacity were crucial factors limiting the potential efficacy of marine reserves. The present modelling of trawl and gillnet fishing behaviour was adequate to compare scenarios for the period of the collapse, but discrepancies between the observed and simulated catches indicate that it would be risky to extrapolate the results to scenarios with larger cod biomass such as were found in the 1950s.

Data

Catch and effort data on which this model is based are rather incomplete and make it difficult to discern the real trends. The increases in observed CPUE and catchability shown in Figure 5.4 are highly variable and are biased by effort misreporting. In addition, they include the parallel increase in fishing power and in nominal effort that took place in the 1980s. In the present model, catchability was linked to total biomass, implicitly assuming that an increase in biomass would always result in a decrease in catchability and hence in catch. In consequence, the conclusions drawn from this study are only valid for the period 1984-1991.

There are indications that fishing power increased in all fleets. Compared to the vessels in use in the early 1970s, the new ones are larger, deeper, more powerful, and have twice the capacity in each size class (Program Coordination and Economics Branch, 1993). In 1991, 26% of vessels smaller than 8 m long and 16% of 8-10 m long vessels were built after 1985. (Table 4.7). Vessels of 19-20 m long, fully equipped with hydraulics and electronic navigation system, have been built in response to very good market conditions for cod in 1986-87 (Program Coordination and Economics Branch, 1993). These vessels are responsible

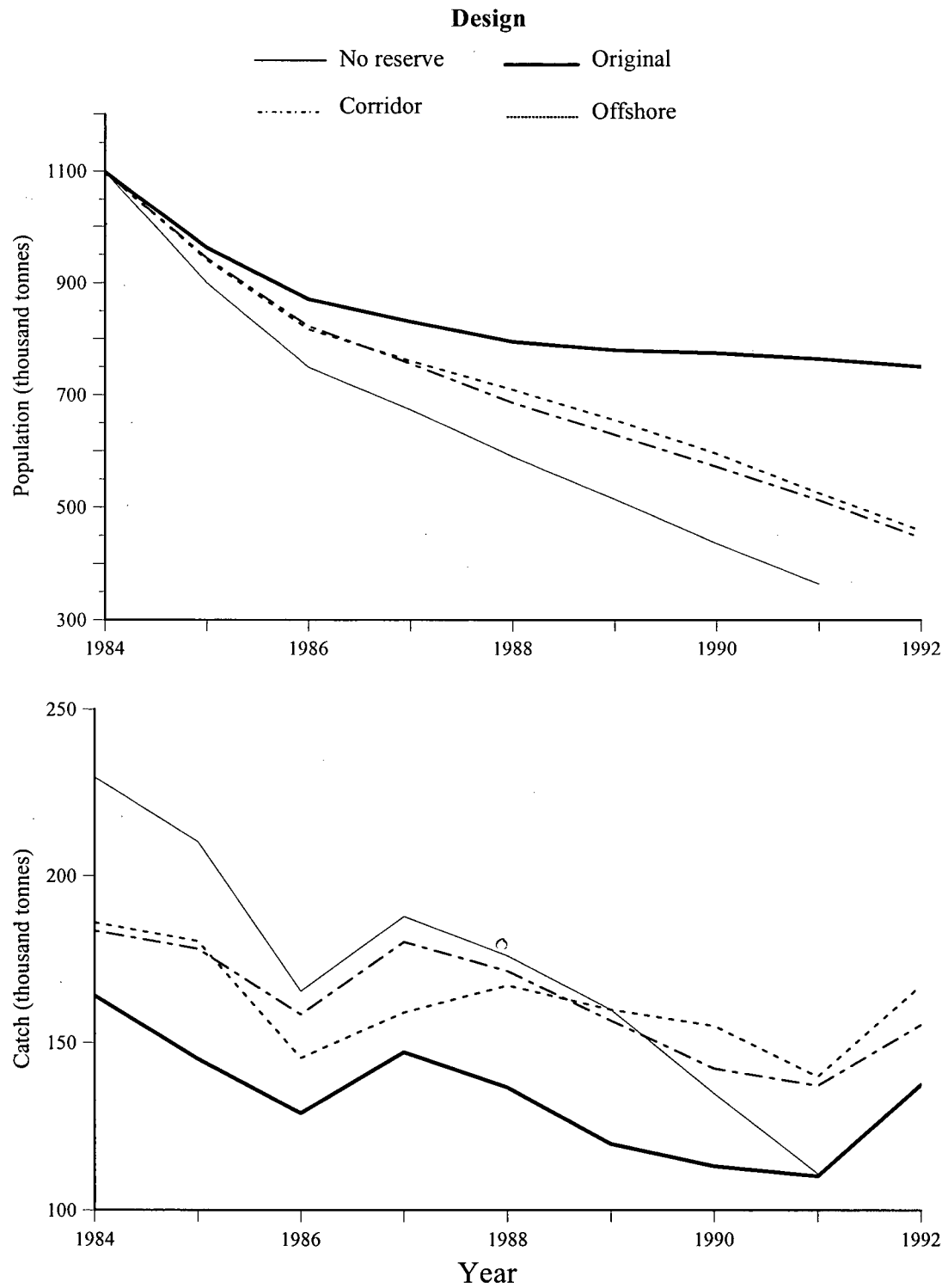


Figure 5.14 Population sizes and total catches for three reserve designs (see Figure 5.13).

for 60% of the catch on Virgin Rock (zone 3Lr, Figure 5.1) that started after 1982 (Hutchings and Myers, 1994), using gillnets. Neis *et al.* (1999) reported an annual increase in fishing power (gear, engine power, vessel capacity) of 20% before 1980 for gillnetters and even larger during the 1980s. The annual percentage of change for traps was estimated at less than 15%, but we did not have enough information on vessel type in relation to their catch to include this factor in the calculation of the CPUE, so only nominal effort was used.

The degree of hunting power that is assumed for each gear is crucial to the evaluation of different scenarios. For example, closing the offshore area will confer less benefit if the other gears start catching more fish. Also, the model does not allow for changes in temporal fishing strategies. For example, a closure of the winter fishery may trigger a redistribution of fishing effort at the reopening. This shift has been seen in other fisheries, and modelling suggests that it decreases the expected benefits of a seasonal closure (Watson *et al.*, 1993). Finally, like all other age-structured models, these results depend on the vulnerability at age. If fishers changed fishing grounds and caught a bigger proportion of small fish, fishing mortality would increase and the benefits of most management scenarios would decrease.

Avenues for improvement would be to examine more thoroughly the ratio of searching time to fishing (handling) time which proved to be an essential component in the cod collapse phenomenon. Also, the use of indirect indices such as fuel consumption might help to approximate the level of increase in effort in the inshore fishery. It would also be interesting to examine how marine reserves could be used as a buffer for management errors in a context where the usual stock assessment and quotas are used. Finally, more direct assumptions about the relationship between effort and biomass would help.

Migrations

Numerous authors have hinted that large movements of fish would lessen the efficiency of no-take marine reserves (Beverton and Holt, 1957; Polacheck, 1990; Bohnsack, 1993; DeMartini, 1993; Holland and Brazee, 1996; Guénette and Pitcher, 1999). Our results confirmed these conclusions and emphasized the need for additional management measures as suggested in Chapter 2. The inclusion of directed migrations and spatial effort responses yielded less optimistic results than those of a simple age-structured model (Chapter 3), mainly because the latter implied that a part of the population resides in the reserves. In addition, we modelled a depleted population that could hardly sustain any industrial fishing for a long time. In this case, the use of marine reserves alone would not achieve much protection unless the effort was reduced substantially. Including more movement patterns to represent the complex stock assemblage present in the area would not have changed the general conclusions of this paper.

Fishing capacity and restrictions

Our simulations also suggested that, following implementation, fishing effort would be concentrated around the reserves. This agrees with observations in the Philippines (Russ and Alcala, 1996b) and in the North Sea (ICES, 1994; Lindeboom, 1995). At high levels of effort, such as those observed for the cod fishery, a large reserve would result in a concentration of effort on the few remaining grounds, thus causing extreme local depletion and finally a substantial decrease in catch per unit effort for fishers. However there may be a limit to the concentration of effort of fixed gear in a given area, which was not included in this model. An important decrease in CPUE could trigger a race for fish and a new series of investment in fishing gear, thus increasing the catchability in the remaining open areas (Walters and Parma, 1996). In the 1980s, the need to maintain their income (Neis, 1992), and availability of money from unemployment programs and

loan programs to upgrade or replace boats led to a large increase in fishing power (Program Coordination and Economics Branch, 1993). Reactions like this are not negligible.

In the model, we chose to reduce the effort by means of seasonal closures, because these are easier to implement than other methods like boat and gear regulations or direct fleet reduction. Hutchings (1995) suggested using winter closures (Jan-May) for trawlers to restore the 'natural' refuges that existed before the trawler's era (1950s). Closing the fishery during winter when cod aggregate tightly regardless of the stock size, would greatly decrease cod vulnerability. Although not included in our model, fishing on spawning aggregations (March to May) could disturb cod mating behaviour (Brawn, 1961) and unbalance the sex ratio (Morgan and Trippel, 1996). Behavioural disturbance was thought (mainly by fishers) to be very important for haddock (*Melanogrammus aeglefinus*) when the spawning ground closure was discussed in the 1970s (Halliday, 1988). Unfortunately, the fishing capacity has increased tremendously since the 1950s and the "inshore" fleet is now more mobile and has access to the whole shelf, destroying the potential "de facto reserve" of the 1950's. Our results show that seasonal closures may not offer sufficient protection unless accompanied by marine reserves. Only a complete ban on trawls or, even better, on both gillnets and trawls would have reduced the effort sufficiently to lead to population rebuilding during the 1980's.

The goal of these simulations was not to predict the exact optimal location and shape of marine reserves for northern cod, but the results show that marine reserves must be located where fishing effort is substantial and act as complement of other management measures. For example, in presence of gillnet and trawl closure, reserves were more efficient in places where gillnets and traps were used intensively. Besides probable improvement in benthic structure and communities, marine reserves could help fisheries management by limiting the fishing effort.

As stock increases, the pressure to reinvest profits in the fishery and increase effort will become important (Beverton and Holt, 1957; Ludwig *et al.*, 1993) and will reduce the effect of any management measure. Marine reserves would have to be very large (80%) to compensate for a possible increase in effort and catchability. If we were to resume fishing with the same effort and the same attitude after six years of closure, the population would soon collapse again. In the last decade, the cod fishery was landing the same amount of cod (200-250 thousand tonnes) as in the 1950s, from an adult cod population that was a fifth of that of the 1950s, generating extreme fishing mortalities (Hutchings and Myers, 1994; Hutchings and Myers, 1995; Myers *et al.*, 1996; Walters and Maguire, 1996; Myers *et al.*, 1997a). Although an increase in fleet capacity seems hard to conceive, some fishers in the inshore fleet are said to be upgrading their boats for an eventual reopening of the cod fishery (Jon Lien, Memorial University, St. John's, Newfoundland, personal communication). Surely fishers active involvement in fisheries management and a profound change of attitude would play a large role in avoiding another collapse. Taking fisher's knowledge into account (Neis, 1995; Fischer *et al.*, 1997), making them part of the management process (Pitcher *et al.*, 1998), sharing information and responsibilities in the decision and monitoring process, would be crucial in that regard.

Conclusion

Results show that used alone, only a large marine reserve would have protected the cod from a population collapse. By themselves, seasonal closures would not control fishing mortality enough to avoid the collapse. Because of the intense competition between the inshore fishery (trap and gillnet) and the trawlers, any fish that survived during the seasonal closure would be caught later by any of the three gears. In comparison, a direct decrease in fishing effort would be slightly more efficient than a large reserve. However, a decreasing effort is eminently difficult to achieve in reality. Combined with seasonal closures, moderate

size marine reserves could have prevented a collapse. A satisfactory reserve design would include areas where stocks concentrate, and account for the associated management measures. For example, when accompanied by a winter trawl closure for example, reserves should be located closer to the shore to protect cod from gillnets and traps. However, any increase in fishing effort would decrease the benefits of this type of management scenarios. Finally, the rebuilding of cod stocks implies a decrease in catches even in the presence of marine reserves.

Chapter 6.

Could marine reserves have prevented the collapse of the northern cod in 1960?

INTRODUCTION

It has often been repeated that marine reserves could act as a hedge against management mistakes to prevent overexploitation (see Chapter 2). The present chapter was intended to evaluate if reserves, used with quotas, could have prevented overexploitation for northern cod. The model used in this analysis is based on the spatial model described in Chapter 5 but begins much earlier in 1960 when the cod population was larger. Briefly, the model was age- and spatially- structured and included four stocks distinguished by their movement patterns. Cod migrations were simulated using a target cell that was age and month-specific. Cod followed the target cell more or less, depending on the level of random movement. Fishing was based on historical data of catch and effort for the principal gears, trawl, trap and gillnet. The model allows the use of quotas alone or in conjunction with marine reserves defined as no-take areas.

Given the assumed pattern of increased fishing effort for the period 1960 to 1991, three questions are examined: 1. Would marine reserves have prevented overexploitation? 2. How would marine reserves complement a quota system? 3. Would overexploitation have been avoided if trawlers had not been used?

MATERIAL AND METHODS

Construction of effort scenarios

In Chapter 4, effort and catch data was shown to be incomplete. Missing effort was reconstructed using decadal average CPUE, which still did not yield credible CPUE and effort profiles. Moreover, nominal effort may not be comparable among decades. In the absence of better data, effort profiles were constructed by using information from interviews and anecdotes to provide likely scenarios of fishing effort from 1960-1991. For each gear type, effort was modified as little as possible to generate a catch similar to that of the NAFO catch data described in Chapter 4. These scenarios were utilised in the model as the monthly historical effort used to generate the catch.

Gillnet effort scenario

The NAFO effort data for 1960 (44593 net•days) led to CPUE of almost 2 tonnes per net per day, which is probably an overestimation. Templeman (1966) stated that the number of gillnets in 2J3KL increased from 1400 in 1960 to 14500 in 1964 as a result of an increase in the number of fishers and the amount of gear they were each using (Table 6.1). Assuming the 1400 nets were each used 200 days a year, effort would amount to 280000 net•days, that is 290 kg by net•day. However, increasing the effort by two between 1960 and 1964 was sufficient to obtain the observed catch. From this starting point, an effort profile was derived using the estimates of the number of gillnets per fisher based on interviews as presented in Hutchings and Ferguson (2000) (Table 6.2), and additional information about the number of fishers (Table 6.3). In the resulting effort scenario, gillnet effort was about four times higher in 1991 than in 1960 (Figure 6.1). In the 1980s, the scenario's CPUE are in the same order of magnitude as those found by Hutchings and Ferguson (2000), assuming one haul per day. The relatively stable CPUE between 1987 and 1990 is a direct consequence of the slow growing effort assumed in the scenario for these years.

Table 6.1 Number of gillnets and traps reported in Templeman (1966).

Gillnets			Traps	
	number	rate of increase	number	rate of increase
1960	1400		2870	
1964	14500	10.36	3420	1.19

Table 6.2 Evolution of the number of gear per fisher obtained from Hutchings and Ferguson (2000).

Gillnet			Traps		
	number	rate of increase		number	rate of increase
1960	15		1960	2.1	
1970	22	1.47	1970	2.6	1.24
1978	58	2.64	1982	2.9	1.12
1980	76	1.31	1991	3.3	1.14

Table 6.3 Rationale for the effort scenario constructed for gillnets.

Year	Scenario	Justification
1960	280000 net•days adjusted to 290 kg•net ⁻¹ •day ⁻¹	
1964	Effort ₁₉₆₀ * 2	Minimum effort required to generate the observed catch and decrease in CPUE by half as described by Templeman (1966). The number of fishers increased by 33% between 1957 and 1964 (Harris, 1998).
1970	Effort ₁₉₆₀ * 1.47 = Table 6.2	} The number of fishers decreased by half due to a sharp decrease in CPUE (Lear and Parsons, 1993), while the number of nets per fisher increased (Table 6.2)
1974	Effort ₁₉₆₄ * 0.8	
1980	Effort ₁₉₇₄ * 2.1	By 1980, the 200 mile Exclusive Fisheries Jurisdiction led to a dramatic increase of the number of fishers (Lear and Parsons, 1993). Diverse subsidies allowed to increase fishing capacity with boats and technology. Number of nets per fisher increased by 30% between 1978 and 1980.
1987	Effort ₁₉₈₀ * 1.01 rate from Table 6.2	} Smaller increase in effort than suggested by Table 6.2.
1991	Effort ₁₉₈₇ * 1.05 rate from Table 6.2	

Table 6.4 Rationale for the effort scenario constructed for traps.

Year	Scenario	Justification
1960	82596 trap•days adjusted to 290 kg	adjusted to 900kg•trap ⁻¹ •day ⁻¹ derived from Templeman (1966)
1964	Effort ₁₉₆₀ * 1.16	A bit smaller than in Table 6.2 but sufficient to generate the observed catch
1965-1969	Effort _{original} * 2.5	Scale up the original effort to match the 1960 effort level
1975	Effort ₁₉₆₉ * 0.8	The number of fishers decreased by half due to a sharp decrease in CPUE (Lear and Parsons, 1993), while the number of traps by fishers increased by about 10% (Table 6.2)
1980	Effort ₁₉₇₂ * 2.1	By 1980, the 1977 200 mile Exclusive Fisheries Jurisdiction led to a dramatic increase of the number of fishers (Lear and Parsons, 1993). Diverse subsidies allowed to increase fishing capacity with boats and technology. The number of traps per fisher increased by 12%.
1991	Effort ₁₉₈₀ * 1.15	As in Table 6.2

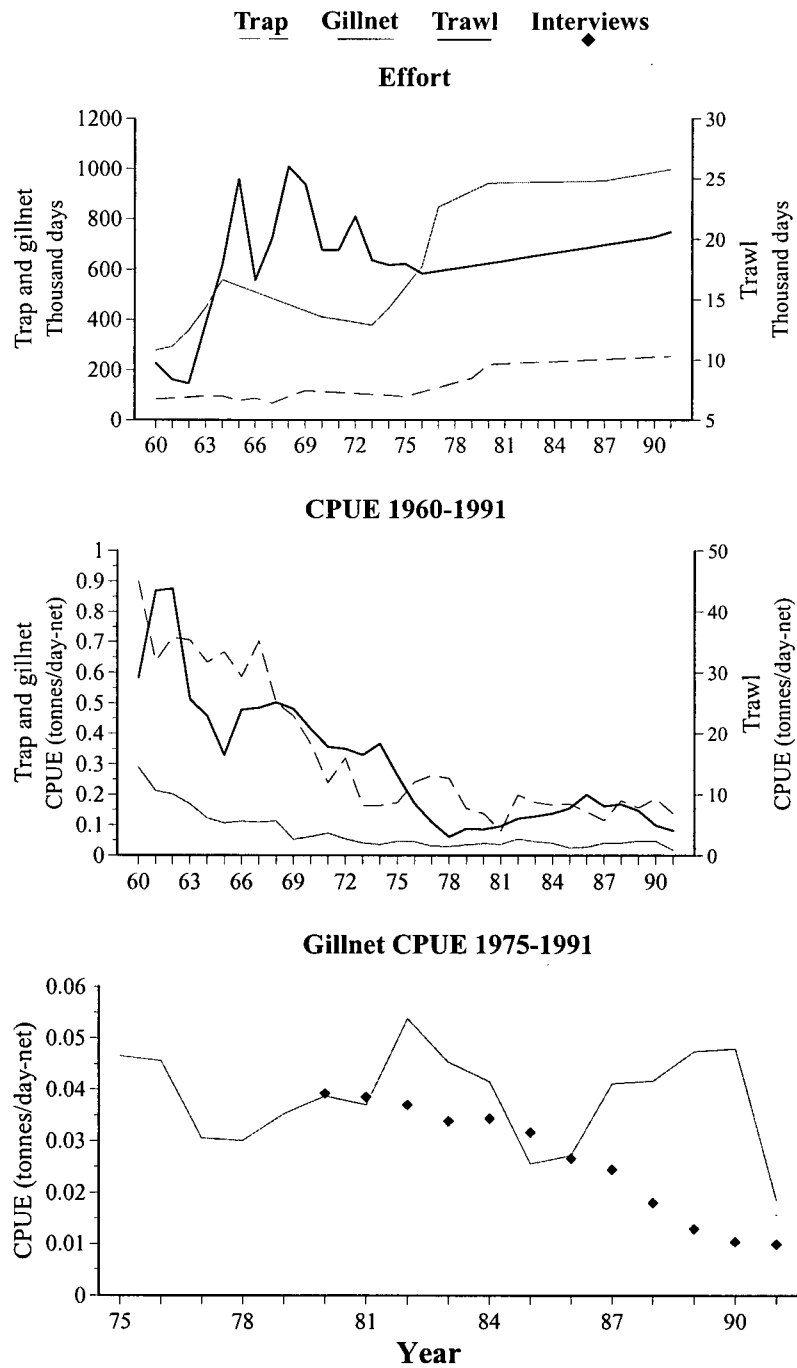


Figure 6.1 Effort and CPUE for each gear type following the scenarios of effort for years 1960-1991. Gillnet CPUE for the 1980s, obtained from interviews (Hutchings and Ferguson, 2000), are given for comparison.

Trap effort scenario

According to Templeman (1966), there were 2870 traps in 1960 and 3420 in 1964, an increase of 19% (Table 6.1). Fleming (undated) reported catches of 1588 tonnes for the summer of 1962 using 50 traps in Bonavista Bay, equalling 32 tonnes per trap. Hutchings and Myers (1995) reported seasonal catch of 210 and 57 tonnes per trap in 1938 and 1945 respectively. In the light of the continually declining inshore catch, Fleming's statistics are plausible. Assuming 8 weeks for a season and 5 days a week (Chen, 1993), catch per day was estimated at 0.9 ton per day. Returning to Templeman's data, 2870 traps fishing for 40 days equals 648 kg trap•day⁻¹. Given the lack of data on the number of traps, the calculation of effort for 1960 was based on the CPUE of 0.9 tonne per day. Thus, the 1960 effort was estimated at 82596 trap•days. In subsequent years, effort was increased based on the number of gear used per fisher (Table 6.2) and the number of fishers present in the fishery. According to the effort scenario, trap effort increased by about three between 1960 and 1991.

Trawl effort scenario

Little additional information has been published on the effort fluctuations of trawlers during the 1970-1980s. It is assumed that under no regulation, catch and effort would be freely reported before 1977. Subsidies and joint ventures encouraged fishing capacity to stay high and further increase over the 1970s and 1980s (see Appendix 6.1). An increase of 20% over the period 1977-1991 was sufficient to generate catch similar to the one observed (Figure 6.1). Even if the number of trawlers decreased, their fishing capacity probably matched the fleet from 1960s.

Table 6.5 Weight, vulnerability and maturity at age used in the model (adapted from Shelton *et al.* 1996)

Age	Weight (kg)	Vulnerability	Maturity
1	0.05	0	0
2	0.20	0	0
3	0.43	0.1	0.002
4	0.75	0.3	0.16
5	1.14	0.5	0.123
6	1.61	0.7	0.551
7	2.15	0.82	0.915
8	2.77	1	1
9	3.46	1	1
10	4.23	1	1
11	5.06	1	1
12	5.96	1	1
13	6.93	1	1
14	7.98	1	1
15	9.09	1	1
16	10.27	1	1
17	11.51	1	1
18	12.82	1	1
19	14.20	1	1
20	15.65	1	1

Model

The spatial structure, stock structure and number, and their movement patterns were kept as described in Chapter 5. The age structure has been expanded to 20 years because older cod were important in the catch of the 1960s (Shelton *et al.*, 1996) (Table 6.5). Average weights at age were taken from the commercial fishery in year 1985 (Shelton *et al.*, 1996) and smoothed using a non-linear regression. The vulnerability and maturity schedules of Chapter 5 were used and extended, assuming full vulnerability and maturity after age 12. It has been argued that overfishing resulted from a combination of cod aggregation behaviour, the collapse of their geographical range combined to the increased capacity to locate and catch fish. The model is expected to reproduce the collapse of the cod population based on these features alone. Thus particular

attention has been put into reproducing extreme fishing mortalities without artificially increasing q as an inverse function of the biomass as in Chapter 5.

Modifications made to the model

Several improvements have been made to improve the behaviour of the model. Historical recruitment anomalies were used to account for the different rate of recruitment success that have been observed over the 30 year period. Recruitment anomalies for years 1964 to 1991 have been defined as:

$$R_{a,y} = \ln (N_{a+2,y+2} / Eggs_y)$$

where $N_{a+2,y+2}$ is the number of 2 years old as calculated in the VPA (R. Ahrens, University of British Columbia, pers. comm.) (Figure 6.2). Eggs is the potential number of eggs defined as the biomass of adults multiplied by the specific fecundity. Recruitment anomalies for years 1960-1963 have been assigned as 1, 0.8, 0.8, 0.8 respectively based on relations found on a graph relating recruitment to water temperature anomalies found in Hutchings and Myers (1994). In the model, the number of one year old (N_1) is obtained as:

$$N_1 = (Eggs * \exp(Ra)) * \exp(-M)$$

assuming natural mortality of 0.2 between age 1 and 2 as for all other ages.

Range collapse was achieved using an equation that accounted for the larger biomass of the 1960s, although the difference made to the model's results was minimal:

$$RMC_{y,a,m} = (RMC_{0,a,m} * 300^{-1}) * a * VulnB_y * (1 + VulnB_y * b^{-1})^{-1}$$

where $RMC_{0,a,m}$ is the initial random movement for age a at month m , $VulnB_y$ is the vulnerable biomass at the beginning of the year.

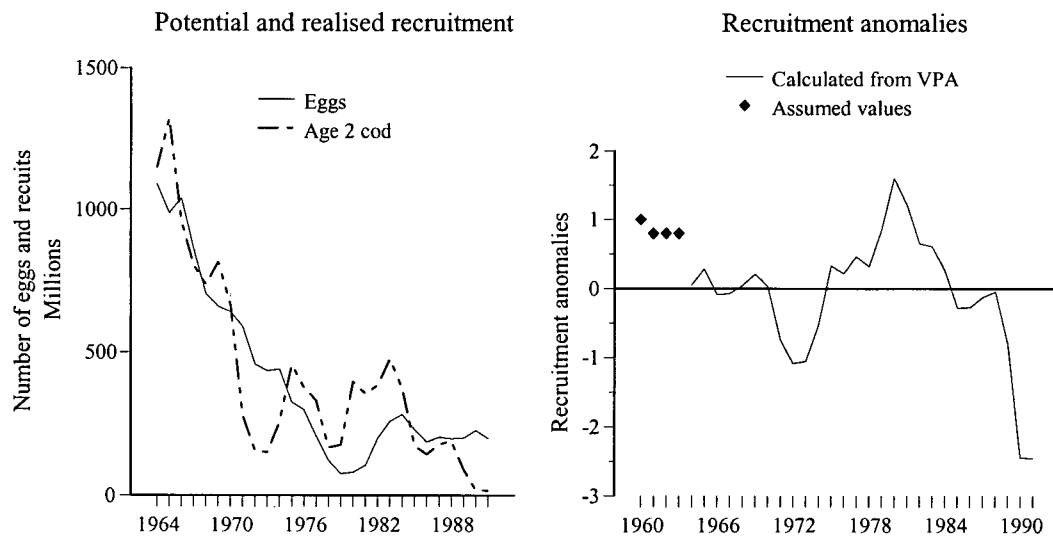


Figure 6.2 Potential (number of eggs) and realised (number of 2 years old two years later) recruitment and recruitment anomalies over the period 1964-1991.

The catch equation within each cell did not vary with biomass as it did in the previous chapter because I believed that effort profiles along with cod range collapse as defined earlier would be sufficient to generate the high exploitation rates observed in the late 1980s. The exploitation rate (u) for each cell (i), month (m) and gear is defined as:

$$u_{i,m,gear} = 1 - \exp(-q_{gear} * Effort_{i,m,gear})$$

where q_{gear} is the catchability defined as a constant for each gear.

As cod biomass decreased, fishers exploited a larger share of the juveniles in the population (Hutchings and Myers, 1994), meaning that vulnerability changed over time (Figure 6.3). Vulnerability at age a is defined as the ratio of the instantaneous fishing mortality of age a to the fishing mortality of fully recruited adults, as estimated with virtual population analysis (see Chapter 5). Vulnerability of age 4 to 7 cod was increased when vulnerable biomass decreased below 1500 thousand tonnes, which corresponds to year 1971, when there is a discrepancy between the simulated and observed population biomass. The vulnerable biomass $VulB$ for year y was calculated as:

$$VulB_y = \sum_{a=1}^A vul_{age,level} * B_{age,y}$$

where $vul_{age,level}$ is the vulnerability at age for high (level=1) or low (level=2) level of biomass. The vulnerability schedule 2 (Table 6.6) was based on vulnerability calculated from VPA for years 1971 and 1991, and modified to generate a sufficient level of catch and biomass. Changing the vulnerability has helped to increase exploitation rate in the late 1970s and 1980s.

Quota calculation

Because catch had to be compared to the attainment of an annual quota, and effort was often concentrated in a few months (winter for trawl, July for trap), catch was computed four times a month. A fleet using a particular gear was stopped upon reaching the gear's limit. Quotas were calculated as a proportion of the vulnerable biomass ($VulB_y$)

$$QuotaTotal_y = u * VulB_y$$

where u is the annual exploitation rate. The quota for each gear was obtained by

$$quota_{gear} = propq_{gear} * QuotaTotal_y$$

where $propq_{gear}$ is the proportion of the quota allocated to each gear. This proportion was set using the actual repartition of the catch between the three fleets, 50% for trawl and 25% each for trap and gillnet.

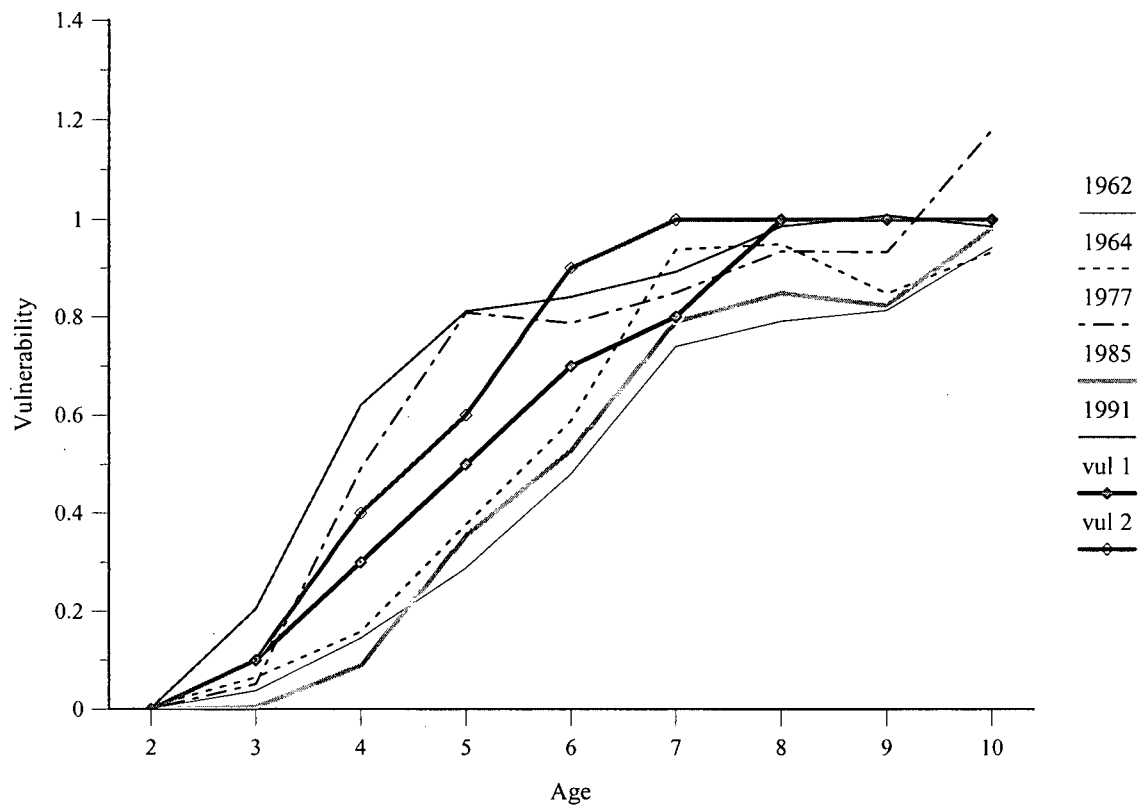


Figure 6.3 Vulnerability of selected years as obtained from a Virtual Population Analysis (R. Ahrens, UBC, pers. comm), and the two vulnerability schedules used in the model.

Table 6.6 Vulnerability schedules for the two levels of biomass used in the model. Vulnerability for age 8 to 20 are equal to 1 in both cases.

Age	1	2	3	4	5	6	7
Vulnerability level =1	0	0	0.1	0.3	0.5	0.7	0.8
Vulnerability level =2	0	0	0.1	0.4	0.6	0.9	1

Three types of scenarios were simulated for the period 1960-1991. In the first, a quota was used in isolation at two levels of exploitation rate, 0.2 and 0.4. The former case assumed perfect knowledge of the stock and thus the calculation of an adequate quota. The higher exploitation rate simulated a case of systematic stock overestimation that would lead to overly generous quotas. In the second scenario, quotas were used in conjunction with 50 and 80% marine reserves as described in Chapter 5 (Figure 5.6). The third scenario excluded trawlers from the fishery to test the statement that, by itself, the coastal fishery would have been sustainable.

RESULTS

The model generated population and total catch that were similar to the observed ones, except for discrepancies in the late 1970s and 1980s, where the model population is twice as high as the observed one. Traps and especially trawl catches generally followed the observed ones. Gillnet catches of the 1980s did not closely resemble the declared catches. The high level of exploitation (u) observed in the late 1970s and 1980s were not reproduced by the model, and catchability (q) remained constant (Figure 6.4 and 6.5). Several simulations and trial runs have been done in an attempt to reproduce the extreme fishing mortality that occurred in the late 1970s and 1980s, none of which were successful (see Appendix 6.2). This specific version was chosen based on visual comparisons with the observed population catch size. To be acceptable, the results had to comply to three criterion: 1. the general trends of population size and catch for each gear and for each decade; 2. increased catches from traps and gillnets would be acceptable only if they did not have precedence over that of the trawlers because the latter were fishing large aggregations and never had trouble finding and catching fish at any time; 3. fishing mortality should increase (as much as possible) during the late 1970s and 1980s.

As in Chapter 5, only large reserves used alone, would have prevented the collapse (graph not shown). Used alone, a quota based on an exploitation rate (u) of 0.2 (0.2 quota) would keep the stock roughly constant, and at a high level. Catch would have reached around 400 thousand tonnes (Figure 6.6), which is the maximum catch obtained between 1870 and 1950 (Hutchings and Myers, 1994). Beginning in 1965, the trawl quota would be reached in March. Gillnet and trap fisheries would not have been limited by a 0.2 quota until 1975, when fishing effort increased. An exploitation rate of 0.4 would give only a marginal protection to the population and would not have prevented the population crash (Figure 6.6). The coastal fishery would not have been constrained while the trawlers would have been limited in the early 1960s. The total catch would decrease from 545 thousand tonnes in 1969 to a maximum of 400 thousand tonnes in the 1980s.

When the quota was too high ($u = 0.4$), a large marine reserve (80%) would have helped avoid exploitation, keeping the exploitation rate under 0.16, and still allowed a total catch of 615 thousand tonnes in 1987 (Figure 6.7). In this case, the combination of a large population, a limit on catch by trawlers, and the increased fishing effort in the "inshore" fleet led to very large gillnet and trap catches in the 1980s (349 thousand tonnes). A 50% marine reserve would have held the biomass at a high level (2.5 times higher than with quota alone) but allowed the exploitation rate to increase over 0.2.

Without any trawl fleet, the cod population would not have collapsed in the 1970s, and exploitation rate would have reached 0.15 only by 1991. Assuming the same increase of inshore fishing effort in the late 1980s, total catches would have reached 700,000 tonnes in 1986 and declined in subsequent years. For the period 1976-1991, the no-trawlers and the quota-plus-80%-reserve scenarios have similar exploitation rates (Figure 6.7).

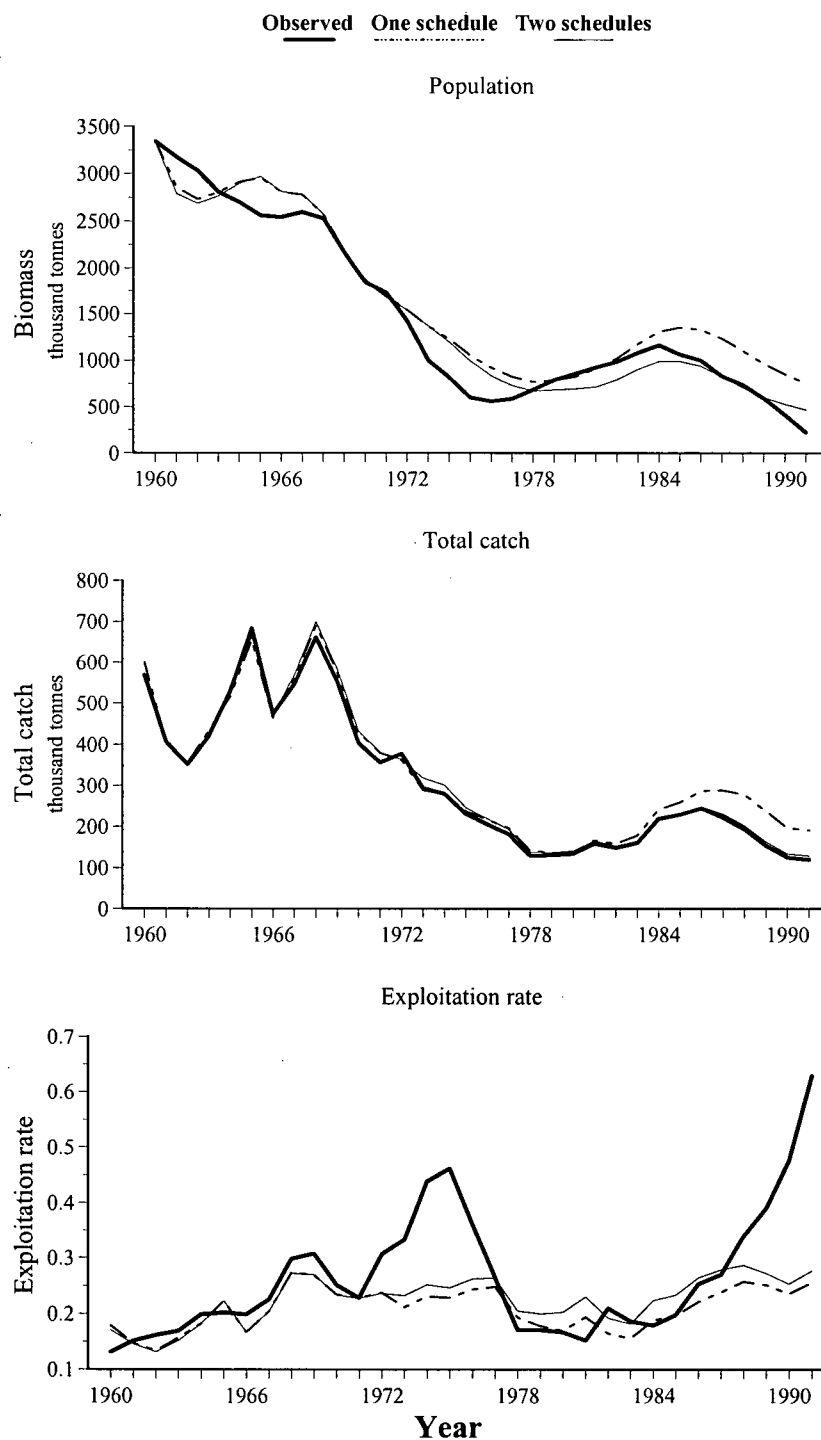


Figure 6.4 Population biomass, total catch and exploitation rate as observed and simulated using one vulnerability schedule (one schedule), and two schedules changing with biomass (two schedules, see text). The two schedule simulation is used as the baseline for the evaluation of fishery management scenarios.

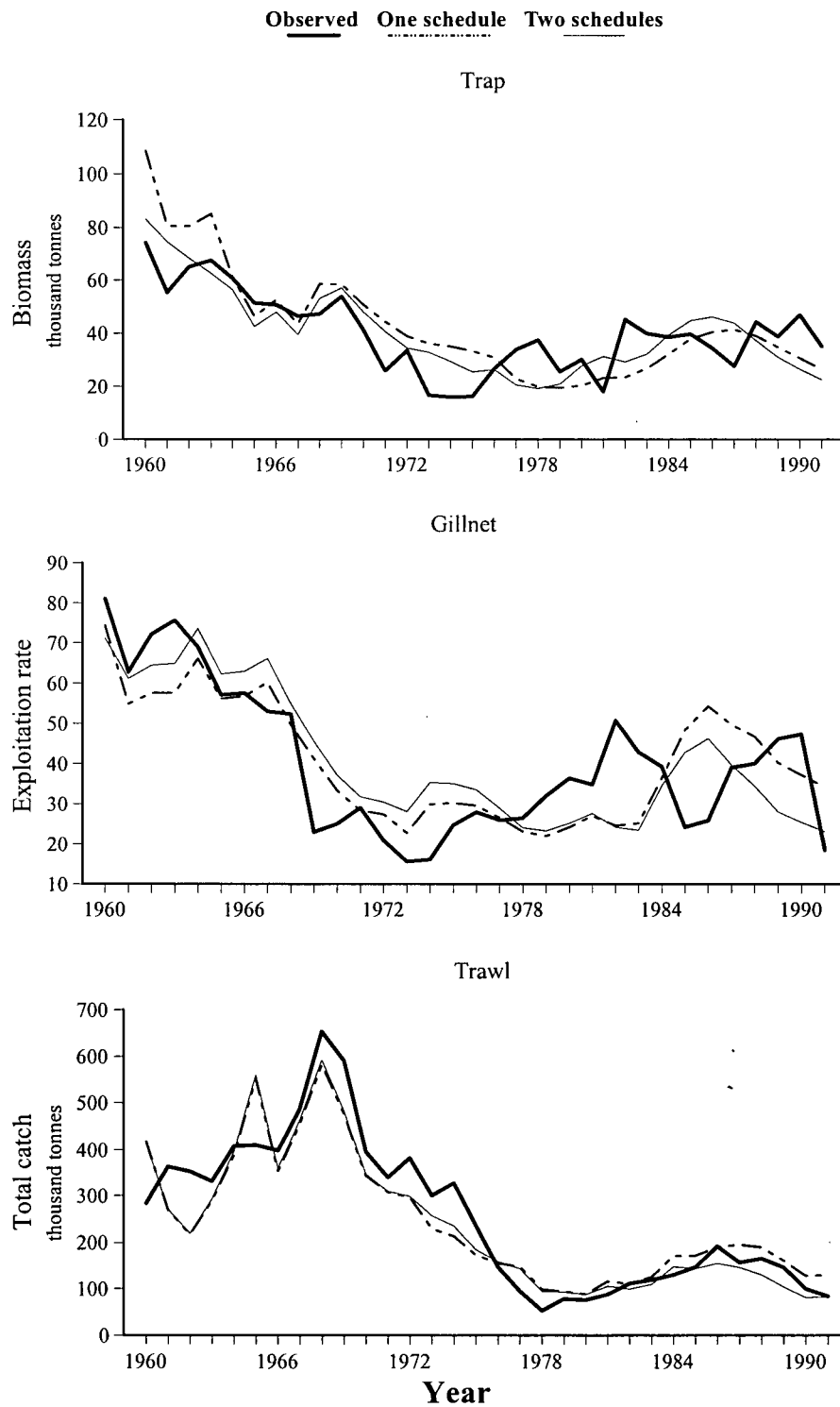


Figure 6.5 Catch per gear as observed and simulated using one vulnerability schedule (one schedule), and two schedules changing with biomass (two schedules, see text). The two schedule simulation is used as the baseline for the evaluation of fishery management scenarios.

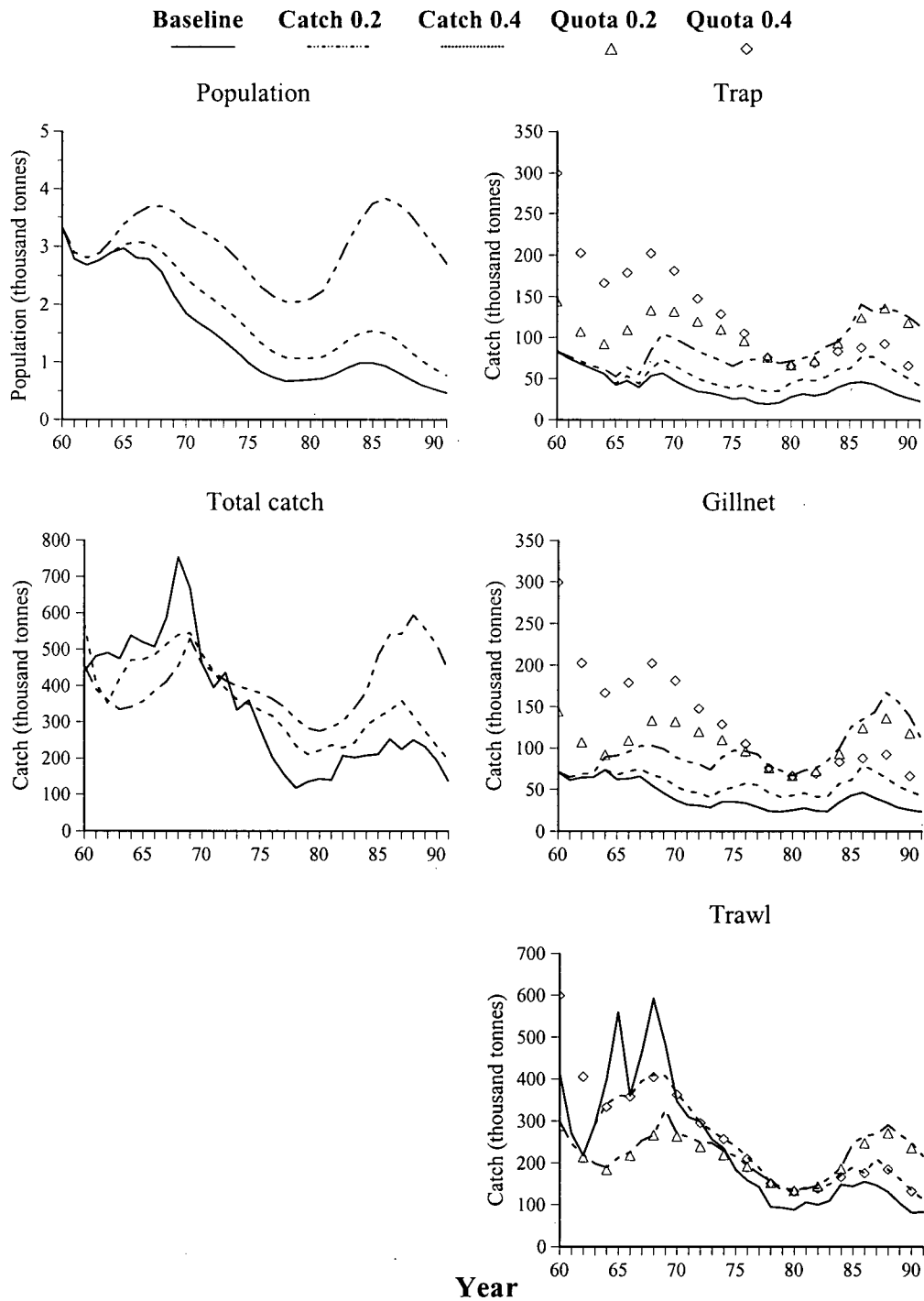


Figure 6.6 Population size, total catch, catch for each gear, and annual quota calculated for a conservative (0.2) and a large (0.4) exploitation rates. The baseline has no quota.

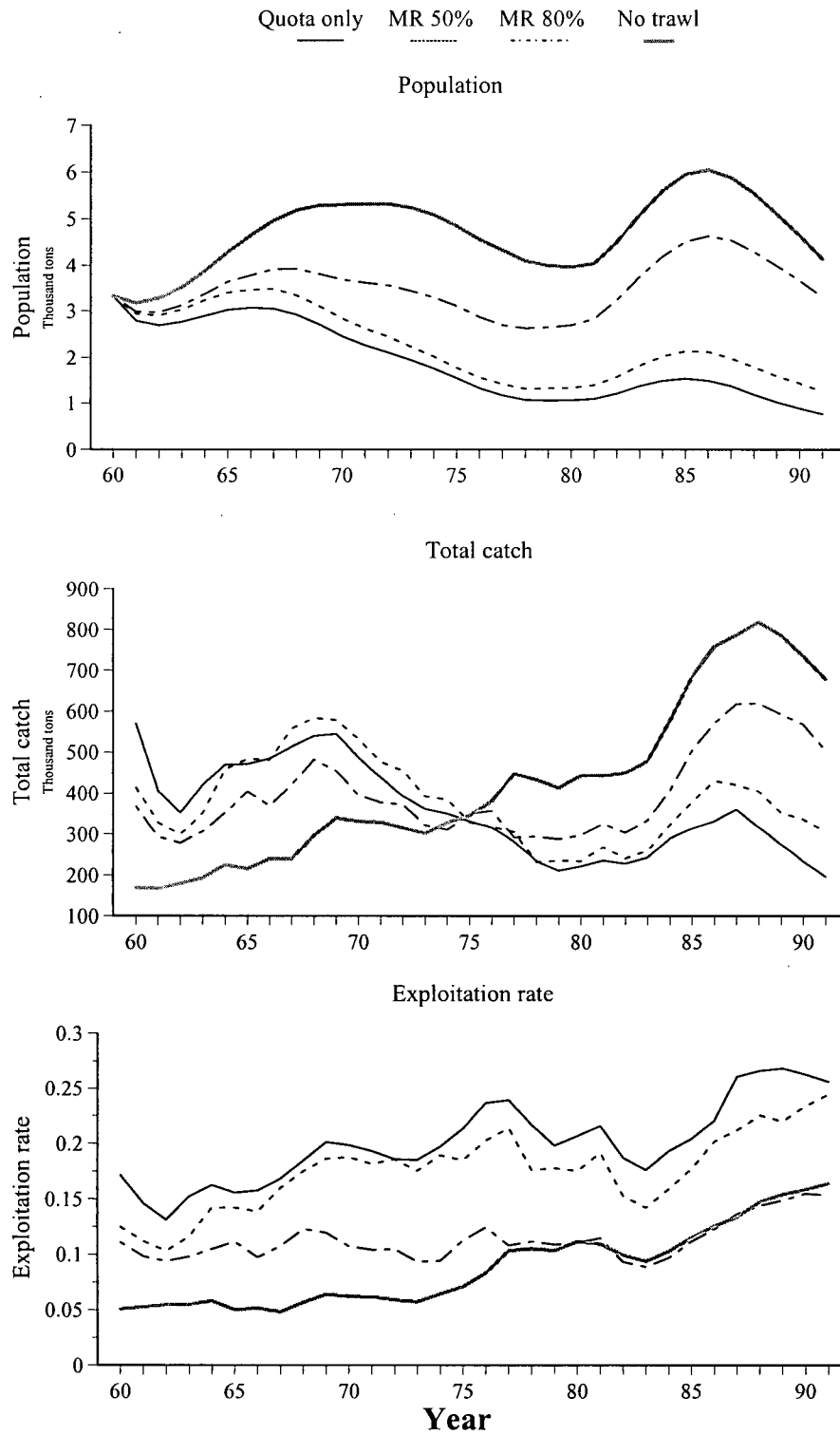


Figure 6.7 Population, catch size and exploitation rate in the case of overestimated quota (exploitation rate of 0.4) used in conjunction with 50 and 80% marine reserves.

DISCUSSION

The present model is a simplified deterministic version of the events that occurred during the period 1960-1991. The effort schedule used in the present model may be a plausible image of the actual fishing capacity but we do not have to believe it is accurate. In this model, as in reality, fishing capacity on the Newfoundland coast is characterised by competition between gears. In the early 1960s, Templeman (1966) mentioned the competition between offshore trawling and the coastal fishery during the period 1950-1964.

The vulnerability schedules used in the present version of the model, although crudely estimated, mean to account for indications that fishers were targeting increasingly smaller fish as the stock decreased (Hutchings and Ferguson, 2000). However modifying the vulnerability schedules still did not solve the discrepancy in the late 1970s, and resulted in the 1980s biomass being slightly lower than the observed. Also, the present model configuration does not reproduce the change in fishing grounds for gillnets that occurred during the observed period.

Three factors may explain the failure of the model to generate the high exploitation rates observed in the late 1970s and 1980s. First, the model may not concentrate cod enough as their biomass decreased. At the moment, the decrease in the area of distribution is driven by the decrease in biomass. An alternative, but not exclusive, mechanism would be that cod aggregation in smaller areas was controlled by external factors such as the size of the cold intermediate layer that decreased the area of suitable habitat independently of the size of the stock. Second, and more importantly, the procedure used to generate migration in the model may be allowing for too much diffusion and do not reproduce completely the observed hyper aggregation and range collapse (Rose and Kulka, 1999). Third, the model cod are assumed to be uniformly distributed within a model cell. In reality, cod were concentrated in dense schools, easy to detect, and thus catchability increased. The increased density in smaller areas is corroborated by acoustic surveys for years 1990-1993 in the Bonavista corridor (Newfoundland shelf) (Rose and Kulka, 1999) and recounting that trawlers tended to fish the edge of schools to avoid clogging their net (D. Kulka, pers. comm.). Thus, catchability within a cell should increase as an inverse function of the biomass present in the cell. In other words, the strategy utilised in Chapter 5 should use the biomass within a cell instead of the total biomass of cod. During the development of the present model, there was too much focus on effort scenarios and not enough on the increased catchability within cells.

Used alone or in conjunction with a quota system, only a large marine reserve (80%) would have prevented the collapse, while a 50% reserve would offer only partial protection against systematic mistakes in quota evaluation. These results are similar to those obtained on Chapter 5. In the absence of trawlers, the stock would have thrived during 1960-1970s, allowing for sustained high level of catch for the inshore fishery. However, the rate at which the model population is rebuilt may be overly optimistic because of the failure to generate high catchability when the stock is low and also perhaps the steep stock-recruitment relationship.

Assuming the effort profiles used reflect reasonably well what happened, the model showed that the "coastal" fishery acquired the means to deplete the stock in the last decade of the fishery, for the first time in history. Is this realistic? The increase in realised fishing power resulted from declining catches experienced by increasingly desperate fishers. However, it is reasonable to assume that expectations about profit and the number of persons who could live from the fishery would have increased as it did in the late 1950s (Harris, 1998) and the late 1970s (see Appendix 6.1). In addition, the use of new technologies would probably have increased in the coastal fishery regardless of the presence of the offshore fishery though perhaps at a slower pace. Perhaps the effort build-up would have been slower, but would that be a

guarantee of success in avoiding overexploitation? The importance for cod to sustain coastal communities, the need to supply inshore plants all year-round to make them profitable, and finally to provide fish on a continuous basis to international market would eventually have increased pressure towards overcapacity.

Chapter 7

The usefulness of marine reserves, a discussion

Marine reserves are increasingly seen as a tool to help replenish exploited marine resources by protecting part of the population. Chapter 2 reviews the literature on marine reserves used as a fisheries management tool. Since Beverton and Holt, several modelling studies have shown that reserves would provide protection to stocks submitted to high fishing pressure. Modelling suggests that marine reserves would generally result in a decrease in yield although in some cases, yield could potentially increase at high fishing mortality. Closing an area to fishing seems to be a very intuitive way to protect a population. Individual fish would live longer hence, the biomass, density and average size would increase within the reserve. This has been shown to be the case in several reserves throughout the world. Sedentary species are considered perfect candidates for that type of protection since their migration rate outside the reserve is low and thus exposure to fishing reduced. The mechanisms behind the alleged replenishment of fishing grounds are adult migration and larvae dispersal. Evidence of spillover of adults outside the reserve is often difficult to prove because of natural variations, change in fish behaviour, and the increase of fishing effort that occurs around the reserves. The rebuilding process may be slow and the capacity to detect small changes is often slim. For these reasons, benefits outside the reserve have been shown in only a few cases, namely in South Africa and the Philippines. Although larvae dispersal is more difficult to show, there is a large amount of literature on the need to identify source and sink areas to locate reserves properly. Populations protected in a reserve may be very dependent on other populations for part of their recruitment and reserves could lead to a false sense of security. However, the most interesting feature of reserves is their ability to provide resilience to overexploitation, thereby reducing the risk of stock collapse. Properly designed and coupled with other management practices reserves may provide a better insurance against uncertainties in stock assessment, fishing control and management mistakes. In that context, this strategy could be used for both sedentary and migratory species.

My objective was to explore the possibility of using marine reserves as a tool to limit exploitation and give protection against management mistakes for a migrating species, the Atlantic cod. However, most models reviewed are non-dynamic and do not account for the effect of depleting the biomass of large spawners and its consequences on stock-recruitment and weight-fecundity relations. The age-structured dynamic pool model (Chapter 3), included reproduction features and showed how marine reserves could protect cod spawners, allow for consistently higher recruitment and decrease the risk of collapse. Also, comparison of these results with equilibrium models found in the literature emphasizes the importance of stock-recruitment relationship to account for deficit in recruitment caused by overfishing. Faster rate of movement of fish decreased these advantages, but the higher spawner biomass and level of recruitment still provided advantages for the reserve regime. Moreover, even for highly mobile fish, the model suggested that a fish stock protected with a marine reserve would be more resilient to exploitation than when managed without it. However, these results assumed random movement of fish, not directed migration, and thus were probably overly optimistic.

The next step was to build a realistic spatially and temporally structured model that includes fish migrations and fishing behaviour (spatial redistribution of fishing effort in response to various changes). The model data was based on Newfoundland data for fish biology and the fishery characteristics. Catch data for that region (NAFO divisions 2J3KL, Figure 1.1) were used to provide basic information about the cod fishery. Chapter 4 describes the catch data compiled by the Department of Fisheries and Oceans and the Northwest Atlantic Fisheries Organization. Observer data was also examined to provide an independent evaluation of trawlers' catch per unit effort. This analysis provided information about the spatial and temporal distribution

of the catch, the evolution of catch per unit effort, and the relative contribution of each gear for Newfoundland and foreign fleets. Effort was shown to be dramatically under-reported. The effort schedule for years 1984-1991 was used without modification in Chapter 5. In contrast, the model used in Chapter 6 was based on effort profiles, for years 1960-1991, based on anecdotal and historical data.

Chapters 5 and 6 used an age and spatially-structured model that included the definition of four stocks with different patterns of seasonal migrations, geographical range dynamics, and seasonal aggregations. Fishers were assumed to behave like hunters in varying degrees depending on the gear they used. Because cod aggregated in dense schools as their biomass decreased, they were easily targeted by fishers and their catchability increased. The first spatially-structured model (Chapter 5) accommodated this behaviour by increasing q as the global biomass decreased, which biased the catch estimate as the cod population became larger. In the absence of such a link, Chapter 6 was unsuccessful at generating the high exploitation rate observed in the late 1980s. To my knowledge, this is the first time that reserves are evaluated for a migrating fish and included range dynamics. Holland (1998) built a bio-economic model that emphasises the choice of fishing grounds as a fishers' response to marine reserves. His model includes simple migrations but not range dynamics.

Whether the population size is low (1980s, Chapter 5) or high (1960s, Chapter 6), marine reserves, used in isolation, would not prevent a collapse unless they encompass most of the fishing grounds. However, very large reserves would have reduced the catch per unit effort in the remaining fishing grounds, possibly triggering an increase in investment in gears, defeating the purpose of the reserve. When used with moderate size reserves (20%), temporal closures for trawls and gillnets were successful at preventing a collapse and rebuilding the stock. Combined with winter closures, they would protect the stocks as long as fishers do not increase their effort. Finally, regardless of the management measure, the price of protecting the cod population translated into decreasing the catch during the studied period. This would mean no catch or at least a more reasonable catch for the trawl fleet in the 1960s (Chapter 6 model) and only half of the observed total catch in the 1980s (Chapter 5).

The use of temporal closures would not control the level of exploitation, especially if the effort was displaced to subsequent months. However, they could be useful to protect fish during crucial periods such as spawning. There is enough knowledge about the complexity of cod spawning behaviour (spatial segregation of males and females, choice of mates, complex mating behaviour) to warrant such closures. Their benefit would likely be greater than the mere number of spawners that do not get killed. Similarly, the fact that marine reserves would not be suitable to control exploitation for migrating species does not mean that they are not worthwhile. They could be used for protecting certain life stages to control juvenile fishing mortality (e.g. Zuwai crab, plaice) or to avoid habitat destruction or homogenisation (e.g. young stage of cod and the complexity of their habitat).

Used as a hedge against management mistakes, that is in conjunction with an overly optimistic quota system, only a large reserve would protect from a collapse. The arrival of big factory-trawlers on the Newfoundland shelf has been linked with diminished catch for inshore fishers in Newfoundland. Modelling showed that in absence of trawlers, the inshore fishery would have continued to catch around 200-300 thousand tonnes a year without overexploiting the stocks, assuming that effort would have remained stable.

The model assumed that fishing was the main cause of the decline and that environmental conditions had only marginal effects. Thus, recruitment was deterministic, growth was constant and there was no provision for cannibalism or interspecies interaction. Also, migrations were fixed in time and space, and there was no exchange between stocks. The second version of the model (Chapter 6) accounted for recruitment

variations during the studied version. Although the contribution of a decrease in production to the cod collapse is small compared to that of overfishing, it may be the reason why cod populations have not yet rebounded in the absence of fishing.

For maximal impact in this study, reserves were located on the best fishing grounds, assuming that fishers target the high abundance areas. Although this may be necessary for modelling purposes in such a system, this may be unacceptable to fishers who would consider it unfair and counterproductive. In turn, the temptation to cheat or to increase fishing power would become irresistible. The optimal location of a reserve may also differ depending on whether or not companion management measures are used.

An improved version of the model developed in Chapter 6 should include a mechanism to increase catchability as the biomass within a cell decreases in order to increase the model exploitation rate of the late 1970s and 1980s. It could also include a better schedule of vulnerability. It would also be interesting to include a mechanism to include possible effects of closed season on reproduction success, perhaps using fuzzy logic and qualitative information taken from studies on cod reproduction processes. The same technique could be applied to included the impact of trawling on the cod habitat and its consequences for juvenile cod survival. A step further would lead to ecosystem modelling because closing an area to fishing is likely to have impacts on the entire ecosystem rather than only on the target species.

In the current debate about the pertinence of marine reserves, it is sometimes stated that marine reserves, whatever their size, would be better than none. I submit that we should be very careful about marketing reserves in such general terms. Marine reserves are not the ultimate solution to all our problems. Raising expectations to an unattainable level would be deceiving and could result in negative perceptions before we have time to experiment. It seems vital to define specific objectives for a reserve that are verifiable and that would allow us to learn from it. Designing a proper monitoring design is no trivial matter as a lot of confounding factors may prevent us from discerning the benefits of closing an area to fishing. Two recent examples show how concomitant changes in environmental conditions, spawner biomass, and prey availability prevented the assessment of the benefits of a partial closure on juvenile survival (Frank *et al.*, in press; Pastoors *et al.*, in press).

References

- Alcala, A. C., and Russ, G. R., 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. , *Journal du Conseil International pour l'Exploration de la Mer*, 46:40-47.
- Alder, J., Sloan, N. A., and Uktolseya, H., 1994. Advances in marine protected area management in Indonesia: 1988-1993. , *Ocean Coastal Management*, 25:63-75.
- Alverson, L., Beamish, W., Gulland, J., Larkin, P., and Pope, J., 1987. A study of trends of cod stocks off Newfoundland and factors influencing their abundance and availability. Department of Fisheries and Oceans, Ottawa,, A report to the Honourable Tom Siddon, Minister of Fisheries by the Task Group on Newfoundland Inshore Fisheries, .
- Anderson, J. T., Dalley, E. L., and Carscadden, J. E., 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. , *Canadian Journal of Fisheries and Aquatic Sciences*, 52:115-125.
- Arenas, P., 1992. Spatial behaviour of fish and fishermen: the use of habitat selection and optimal foraging theory in fisheries. Southwest Fisheries Science Centre, National Marine Fisheries Service, La Jolla, California, PhD Thesis, University of Washington, WA, USA, LJ-92-09, 230 pp.
- Armstrong, D. A., Wainwright, T. C., Jensen, G. C., Dinnel, P. A., and Andersen, H. B., 1993. Taking refuge from bycatch issues: red king crab (*Paralithodes camtschaticus*) and trawl fisheries in the Eastern Bering Sea. , *Canadian Journal of Fisheries and Aquatic Sciences*, 50:1993-2000.
- Atkinson, D. B., Rose, G. A., Murphy, E. F., and Bishop, C. A., 1997. Distribution changes and abundance of northern cod (*Gadus morhua*) 1981-1993. , *Canadian Journal of Fisheries and Aquatic Sciences*, 54(Suppl. 1):132-138.
- Attwood, C. G., and Bennett, B. A., 1995. Modelling the effect of marine reserves on the recreational shore-fishery of the south-western Cape, South Africa. , *South African Journal of Marine Sciences*, 16:227-240.
- Auster, P. J., and Malatesta, R. J., 1995. Assessing the role of non-extractive reserves for enhancing harvested populations in temperate and boreal marine systems. pp. 82-89. *In*: N. L. Shackell and J. H. M. Willison, eds., *Marine protected areas and sustainable fisheries*, Science and Management and Protected areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Ballantine, B., 1991a. Marine reserves for New Zealand. University of Auckland, Auckland, New Zealand, Leigh Laboratory Bulletin, 25, 196 pp.
- Ballantine, W. J., 1991b. Marine reserves-the need for networks. , *New Zealand Journal of Marine and Freshwater Research*, 25:115-116.
- Ballantine, W. J., 1995. Networks of "no-take" marine reserves are practical and necessary. pp. 13-20. *In*: N. L. Shackell and J. H. M. Willison, eds., *Marine protected areas and sustainable fisheries*, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Bard, F. X., 1999. Amélioration des techniques de pêche aux thons en eau profonde dans le Pacifique centre-sud. Résultats d'un programme de recherches. pp. 149-173. *In*: XVIII Semana das Pescas dos Açores 1999, Horta, Portugal, March 22-26, 1999.
- Bennett, B., and Attwood, C. G., 1993. Shore-angling catches in the De Hoop Nature Reserve, South Africa, and further evidence for the protective value of marine reserves. , *South African Journal of Marine Sciences*, 13:213-222.

- Bennett, B. A., and Attwood, C. G., 1991. Evidence for recovery of a surf zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. , Marine Ecology Progress Series, 75(2-3):173-181.
- Beverton, R. H. J., Cooke, J. G., Csirke, J. B., Doyle, R. W., Hempel, G., Holt, S. J., MacCall, A. D., Policansky, D. J., Roughgarden, J., Shepherd, J. G., Sissenwine, M. P., and Wiebe, P. H., 1984. Dynamics of single species: group report. pp. 13-58. In: R. M. May, ed. Exploitation of marine communities, Springer-Verlag, Berlin.
- Beverton, R. J. H., and Holt, S. J., 1957. On the dynamics of exploited fish populations. Chapman and Hall, London, 11, 533 pp.
- Bohnsack, J. A., 1993. Marine reserves; they enhance fisheries, reduce conflicts, and protect resources. , Oceanus, 36:63-71.
- Bohnsack, J. A., 1996. Maintenance and recovery of reef fishery productivity. pp. 283-313. In: N. V. C. Polunin and C. M. Roberts, eds., Reef fisheries, Chapman and Hall, London.
- Botsford, L. W., 1981. The effects of increased individual growth rates on depressed population size. , American Naturalist, 117:38-63.
- Botsford, L. W., Castilla, J. C., and Peterson, C. H., 1997. The management of fisheries and marine ecosystems. , Science, 277:509-515.
- Botsford, L. W., Quinn, J. F., Wing, S. R., and Brittnacher, J. G., 1993. Rotating spatial harvest of a benthic invertebrate, the red sea urchin, *Strongylocentrotus franciscanus*. pp. 409-428. In: G. Kruse, D. M. Eggers, R. J. Marasco, C. Pautzke, and T. J. Quinn II, eds., Proceedings of the international symposium on management strategies for the exploited fish populations, Anchorage, Alaska, October 21-24, 1992, Alaska Sea Grant College Program, Fairbanks, Alaska. 93-02.
- Branch, G. M., and Moreno, C. A., 1994. Intertidal and subtidal grazers. pp. 75-100. In: W. R. Siegfried, ed. Rocky shores exploitation in Chile and South Africa., Springer-Verlag, Berlin, 103.
- Brander, L., 1996. A model of the costs to industry of closed areas. pp. 176-181. In: D. L. Burke, R. N. O'Boyle, P. Partington, and M. Sinclair, eds., Report of the Second Workshop on Scotia-Fundy groundfish management, Canadian Technical Report of Fisheries and Aquatic Sciences, 2100.
- Brawn, V. M., 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). , Behaviour, 18:177-198.
- Brown, M. W., Allen, J. M., and Kraus, S. D., 1995. Designation of seasonal right whale conservation areas in the waters of Atlantic Canada. pp. 90-98. In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Buxton, C. D., 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. , Environmental Biology of Fishes, 36:47-63.
- Buzeta, M. I., and Waiwood, K. G., 1982. Fecundity of Atlantic cod (*Gadus morhua*) in the southwestern gulf of St. Lawrence. , Canadian Technical Report of Fisheries and Aquatic Sciences, 1110:6p.
- Caddy, J. F., 1990. Options for the regulation of Mediterranean demersal fisheries. , Natural Resource Modeling, 4:427-475.
- Carr, M. H., and Reed, D. C., 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. , Canadian Journal of Fisheries and Aquatic Sciences, 50:2019-2028.
- Chen, X. H., 1993. Spatial and temporal variability of inshore cod landings in Labrador and eastern Newfoundland. M. Sc., Memorial University of Newfoundland, St. John's, Nfld. 107 pp.
- Clark, C. W., 1996. Marine reserves and the precautionary management of fisheries. , Ecological Applications, 6:369-370.
- Clark, M. R., in press. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. , Oceanologica Acta

- Crecco, V., and Overholtz, W. J., 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. , Canadian Journal of Fisheries and Aquatic Sciences, 47:385-394.
- Daan, N., 1993. Simulation study effects of closed areas to all fishing, with particular reference to the North Sea ecosystem. pp. 252-258. In: K. Sherman, L. M. Alexander, and B. D. Gold, eds., Large marine ecosystems; Stress mitigation and sustainability, AAAS Press, Washington DC.
- Davis, A. R., 1995. Over-exploitation of *Pyura chilensis* (Ascidiacea) in southern Chile: the urgent need to establish marine reserves. , Revista Chilena de Historia Natural, 68:107-116.
- Davis, G. E., and Dodrill, J. W., 1989. Recreational fishery and population dynamics of spiny lobster *Panulirus argus*, in Florida Bay, Everglades National Park, 1977-1980. , Bulletin of Marine Science, 44:78-88.
- DeMartini, E. E., 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. , Fishery Bulletin, 91:414-427.
- Deriso, R. B., 1987. Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. , Canadian Journal of Fisheries and Aquatic Sciences, 44 (Suppl. 2):339-348.
- deYoung, B., and Rose, G. A., 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. , Canadian Journal of Fisheries and Aquatic Sciences, 50:2729-2741.
- Die, D. J., and Watson, R. A., 1992a. Dissipation of spatial closure benefits as a result of non-compliance. , Mathematics and computers in simulation, 33:451-456.
- Die, D. J., and Watson, R. A., 1992b. A per-recruit simulation model for evaluating spatial closures in an Australian penaeid fishery. , Aquatic Living Resources, 5:145-153.
- Dragesund, O., Hamre, J., and Ulltang, Ø., 1980. Biology and population dynamics of the Norwegian spring-spawning herring. , Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177:43-71.
- Dugan, J. E., and Davis, G. E., 1993a. Applications of marine refugia to coastal fisheries management. In: J. E. Dugan and G. E. Davis, eds., International symposium on marine harvest refugia, San Antonio, TX, USA, Canadian Journal of Fisheries and Aquatic Sciences, 50:2029-2042.
- Dugan, J. E., and Davis, G. E., 1993b. Introduction to the International Symposium on Marine Harvest Refugia. In: J. E. Dugan and G. E. Davis, eds., International symposium on marine harvest refugia, San Antonio, TX, USA, Canadian Journal of Fisheries and Aquatic Sciences, 50:1991-1992.
- Dye, A. H., Branch, G. M., Castilla, J. C., and Bennett, B. A., 1994. Biological options for the management of the exploitation of intertidal and subtidal resources. pp. 131-154. In: W. R. Siegfried, ed. Rocky shores exploitation in Chile and South Africa., Springer-Verlag.
- Fairweather, P. G., 1991. Implications of "supply-side" ecology for environmental assessment and management. , Trends in Ecology and Evolution, 6:60-63.
- Faucher, A., and Whitehead, H., 1995. Importance of habitat protection for the northern bottlenose whale in the Gully, Nova Scotia. pp. 99-102. In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Ferreira, B. P., and Russ, G. R., 1995. Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. , Fishery Bulletin, 93:629-642.
- Fischer, J., Brace, A., Clarke, R., Donovan, W., Humby, E., Humby, P., McNamara, W., Peters, B., Rowe, L., Smith, E., and Smith, J., 1997. What you always wanted to know about fish in Trinity Bay but never dared to ask. Eco-Research Program, Memorial University, St. John's, NF, Canada A1C 5S7,, Occasional Paper, 13 pp.
- Fiske, S. J., 1992. Sociocultural aspects of establishing marine protected areas. , Ocean Coastal Management, 17(1):25-46.

- Fleming, A. M., undated. The Newfoundland Cod trap. Memorial University of Newfoundland, St. John's, Newfoundland, Biology 582 (Population Dynamics), Fishing gear and vessels, 25 pp.
- Francour, P., 1994. Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve Corsica, northwestern Mediterranean. , *Oceanologica Acta*, 17(3):309-317.
- Frank, K. T., Shackell, N. L., and Simon, J. E., in press. An evaluation of the Emerald/Western Bank juvenile haddock closed area. , *ICES Journal of Marine Science*
- FRCC, 1996. Quota controls and effort controls: conservation considerations. Fisheries Resource Conservation Council, Ottawa, ON, Canada, Discussion paper, FRCC.96.TD.3, 10 pp.
- Frederick, S. W., and Peterman, R. M., 1995. Choosing fisheries harvest policies: when does uncertainty matter? , *Canadian Journal of Fisheries and Aquatic Sciences*, 52:291-306.
- Garcia, S., and Demetropoulos, A., 1986. Management of Cyprus fisheries. , *FAO Fisheries Technical Paper*, 250:40 p.
- Goodridge, R., Oxenford, H. A., Hatcher, B. G., and Narcisse, F., 1997. Changes in the shallow reef fishery associated with implementation of a system of fishing priority and marine reserve areas in Soufriere, St. Lucia. pp. 316-339. *In: Proceedings of the 49th Gulf and Caribbean Fisheries Institute*, Christ Church, Barbados, Nov. 1996, Gulf and Caribbean Fisheries Institute, Fort Pierce, Florida.
- Gregory, R. S., and Anderson, J. T., 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. , *Marine Ecology Progress Series*, 146:9-20.
- Guénette, S., Lauck, T., and Clark, C., 1998. Marine reserves: from Beverton and Holt to the present. , *Reviews in Fish Biology and Fisheries*, 8:251-272.
- Guénette, S., and Pitcher, T. J., 1999. An age-structured model showing the benefits of marine reserves against overexploitation. , *Fisheries Research*, 39:295-303.
- Halliday, R. G., 1988. Use of seasonal spawning area closures in the management of haddock fisheries in the northwest Atlantic. , *NAFO Scientific Council Studies*, 12:27-36.
- Harris, M., 1998. Lament for an ocean. The collapse of the Atlantic cod fishery: a true crime story. McClelland & Stewart Inc., Toronto, Ontario, 342 pp.
- Hart, P. J. B., 1997. Controlling illegal fishing in closed areas: the case of mackerel off Norway. pp. 411-414. *In: D. A. Hancock, D. C. Smith, A. Grant, and J. B. Beumer, eds., Developing and sustaining world fisheries resources: the state of science and management: 2nd World Fisheries Congress proceedings*, Brisbane, Australia, August 1996, CSIRO, PO Box 1139 Collingwood, VIC 3006 Australia.
- Hilborn, R., and Walters, C. J., 1992. Quantitative fisheries stock assessment; Choice, dynamics and uncertainty. Chapman and Hall, New York, 570 pp.
- Holland, D. S., 1998. The use of year around closed areas for the management of New England trawl fisheries. PhD Thesis, University of Rhode Island, Kingston, RI, USA. 329 pp.
- Holland, D. S., and Brazee, R. J., 1996. Marine reserves for fisheries management. , *Marine Resources Economics*, 11:157-171.
- Hutchings, J. A., 1995. Seasonal marine protected areas within the context of spatio-temporal variation in the Northern cod fishery. pp. 39-47. *In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries*, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Hutchings, J. A., 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. , *Canadian Journal of Fisheries and Aquatic Sciences*, 53:943-962.
- Hutchings, J. A., and Ferguson, M., 2000. Temporal changes in harvesting dynamics of Canadian inshore fisheries for northern Atlantic cod, *Gadus morhua*. , *Canadian Journal of Fisheries and Aquatic Sciences*, 57:805-814.

- Hutchings, J. A., and Myers, R. A., 1993. Effect of age on the seasonality of maturation and spawning of Atlantic Cod, *Gadus morhua*, in the northwest Atlantic. , Canadian Journal of Fisheries and Aquatic Sciences, 50:2468-2474.
- Hutchings, J. A., and Myers, R. A., 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. , Canadian Journal of Fisheries and Aquatic Sciences, 51:2126-2146.
- Hutchings, J. A., and Myers, R. A., 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploration, harvesting technology, and management. pp. 39-93. In: R. Arnason and L. Felt, eds., The North Atlantic Fisheries: successes, failures, and challenges., The Institute of Island studies, Charlottetown, Prince Edward Island, 3.
- Hutchings, J. A., Myers, R. A., and Lilly, G. R., 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. , Canadian Journal of Fisheries and Aquatic Sciences, 50:2457-2467.
- ICES, 1994. Report of the Study Group on the North Sea "Plaice Box". Copenhagen,, ICES CM 1994/Assess:14, 52 pp.
- Jennings, S., and Lock, J., 1996. Population and ecosystem effects of reef fishing. pp. 193-218. In: N. V. C. Polunin and C. M. Roberts, eds., Reef fisheries, Chapman and Hall, London, 20.
- Johannes, R. E., 1978. Traditional marine conservation methods in Oceania and their demise. , Annual Review of Ecology and Systematics, 9:349-364.
- Kjesbu, O. S., 1989. The spawning activity of cod, *Gadus morhua* L., Journal of Fish Biology, 34:195-206.
- Kjesbu, O. S., Solemdal, P., Bratland, P., and Fonn, M., 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). , Canadian Journal of Fisheries and Aquatic Sciences, 53:610-620.
- Kondo, K., 1980. The recovery of the Japanese sardine: the biological basis of stock-size fluctuations. , Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177:332-354.
- Kulka, D. W., Pinhorn, A. T., Halliday, R. G., Pitcher, D., and Stansbury, D., 1996. Accounting for changes in spatial distribution of groundfish when estimating abundance from commercial fishing data. , Fisheries Research, 28:321-342.
- Kulka, D. W., Wroblewski, J. S., and Narayanan, S., 1995. Recent changes in the winter distribution and movements of northern Atlantic cod (*Gadus morhua* Linnaeus, 1758) on the Newfoundland-Labrador shelf. , ICES Journal of Marine Science, 52:889-902.
- Larkin, P. A., 1977. An epitaph for the concept of maximum sustainable yield. , Transactions of the American Fisheries Society, 106:1-11.
- Lauck, T., Clark, C. W., Mangel, M., and Munro, G. R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. , Ecological Applications, 8(Suppl. 1):S72-S78.
- Lear, W. H., 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and Eastern Newfoundland, as inferred from tagging studies. , Journal of Northwest Atlantic Fishery Science, 5:143-159.
- Lear, W. H., and Parsons, L. S., 1993. History and management of the fishery for Northern cod in NAFO divisions 2J, 3K and 3L. pp. 55-90. In: L. S. Parsons and W. H. Lear, eds., Perspectives on Canadian marine fisheries management, 226.
- Lilly, G. R., 1996. Observations on cod in the inshore environment of Eastern Newfoundland. , NAFO SCR Doc, 95/59:10.
- Lindeboom, H. J., 1995. Protected areas in the North Sea: an absolute need for future marine research. , Helgoländer Meeresuntersuchungen, 49:591-602.
- Ludwig, D., Hilborn, R., and Walters, C., 1993. Uncertainty, resource exploitation and conservation: lessons from history. , Science, 260:17 and 36.

- MacCall, A. D., 1976. Density dependance of catchability coefficient in the California pacific sardine, *Sardinops caerulea*, purse seine fishery. , California cooperative oceanic fisheries investigation report, 18:136-148.
- MacCall, A. D., 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, University of Washington Press, Seattle, 153 pp.
- Mace, P. M., 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. , Canadian Journal of Fisheries and Aquatic Sciences, 51:110-122.
- Mace, P. M., and Sissenwine, M. P., 1993. How much spawning per recruit is enough? , Canadian Special Publication of Fisheries and Aquatic Sciences, 120:101-118.
- Man, A., Law, R., and Polunin, N. V. C., 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. , Biological Conservation, 71:197-204.
- May, A. W., 1967. Fecundity of Atlantic cod. , Journal of the Fisheries Research Board of Canada, 24:1531-1550.
- McGarvey, R., and Willison, J. H. M., 1995. Rationale for a marine protected area along the international boundary between U.S. and Canadian waters in the Gulf of Maine. pp. 74-81. In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Mohn, R. K., 1996. Assessing closed areas with a fisheries model having several spawning components. In: D. L. Burke, R. N. O'Boyle, P. Partington, and M. Sinclair, eds., Second Workshop on Scotia-Fundy groundfish management, Canadian Technical Report of Fisheries and Aquatic Sciences, 2100:157-169.
- Morgan, M. J., and Trippel, E. A., 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua*). , ICES Journal of Marine Science, 53:820-826.
- Munro, G., Bingham, N., and Pikitch, E., 1998. Individual Transferable Quotas, community-based fisheries management systems, and virtual communities. , Fisheries, 23(3):12-15.
- Myers, J. P., Morrison, R. I. G., Antas, P. Z., Harrington, B. A., Lovejoy, T. E., Sallaberry, M., Senner, S. E., and Tarak, A., 1987. Conservation strategy for migratory species. , American Scientist, 75:19-26.
- Myers, R. A., Barrowman, N. J., Hoening, J. M., and Qu, Z., 1996. The collapse of cod in Eastern Canada: the evidence from tagging data. , ICES Journal of Marine Science, 53:629-640.
- Myers, R. A., Barrowman, N. J., and Hutchings, J. A., 1997a. Inshore exploitation of Newfoundland cod since 1948 as estimated from mark-recapture data. , Canadian Journal of Fisheries and Aquatic Sciences, 54 (Suppl. 1):224-235.
- Myers, R. A., Mertz, G., and Fowlow, P. S., 1997b. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. , Fishery Bulletin, 95:762-772.
- Myers, R. A., Rosenberg, A. A., Mace, P. M., Barrowman, N., and Restrepo, V. R., 1994. In search of thresholds for recruitment overfishing. , ICES. Journal of Marine sciences, 51:191-205.
- Nakken, O., 1998. Past, present and future exploitation and management of marine resources in the Barents Sea and adjacent areas. , Fisheries Management and Uncertainties Symposium, Bergen, Norway, Fisheries Research, 37:23-35.
- Neis, B., 1992. Fishers' ecological knowledge and stock assessment in Newfoundland and Labrador. , Newfoundland studies, 8:155-178.
- Neis, B., 1995. Fisher's ecological knowledge and marine protected areas. pp. 265-272. In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada, 300 pp.

- Neis, B., Felt, L., Schneider, D. C., Haedrich, R., Hutchings, J., and Fischer, J., 1996. Northern cod stock assessment: what can be learned from interviewing resource users? , DFO Atlantic Fisheries Research Documents, 95/45:28.
- Neis, B., Schneider, D. C., Felt, L., Haedrich, R. L., Fischer, J., and Hutchings, J. A., 1999. Stock assessment: what can be learned from interviewing resource users? , Canadian Journal of Fisheries and Aquatic Sciences, 56:1949-1963.
- Orensanz, J. M. L., Armstrong, J., Armstrong, D., and Hilborn, R., 1998. Crustacean resources are vulnerable to serial depletion - the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. , Reviews in Fish Biology and Fisheries, 8:117-176.
- Parsons, T. R., 1992. The removal of marine predators by fisheries and the impact of trophic structure. *In*: P. G. Wells and J. M. Bowers, eds., Marine Pollution Bulletin, 25(1-4):51-53.
- Pastors, M. A., Rijnsdorp, A. D., and Beek, F. A. V., in press. Effects of a partially closed area in the North Sea ('plaice box') on stock development of plaice. , ICES Journal of Marine Science
- Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. , Reviews in Fish Biology and Fisheries, 2:321-338.
- Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. , Trends in Ecology and Evolution, 10:430.
- Pauly, D., 1997. Putting fisheries management back in places. , Reviews in Fish Biology and Fisheries, 7:125-127.
- Peterman, R. M., and Steer, G. J., 1981. Relation between sport-fishing catchability coefficients and salmon abundance. , Transactions of the American Fisheries Society, 110:585-593.
- Pinhorn, A. T., 1984. Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. , Journal of Northwest Atlantic Fishery Science, 5:161-170.
- Pitcher, T. J., 1995. The impact of pelagic fish behaviour on fisheries. , Scientia Marina, 59:295-306.
- Pitcher, T. J., in press. Rebuilding as a new goal for fisheries management: reconstructing the past to salvage the future. , Ecological Applications
- Pitcher, T. J., and Pauly, D., 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. pp. 311-329. *In*: T. J. Pitcher, D. Pauly, and P. Hart, eds., Reinventing Fisheries Management, Kluwer Academic Publishers, Dordrecht, Holland, 435 pp.
- Pitcher, T. J., Watson, R., Haggan, N., Guénette, S., Kennish, R., and Sumaila, R., 1998. Marine reserves and the restoration of fisheries and marine ecosystems in the South China Sea. *In*: , Sarasota, Florida, November 1998, Essential Fish Habitat and Marine Reserves, William R. and Lenore Mote International Symposium in Fisheries Ecology.
- Plan Development Team, 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum, NMFS-SEFC-261, 40 pp.
- Polacheck, T., 1990. Year around closed areas as a management tool. , Natural Resource Modeling, 4:327-354.
- Polunin, N. V. C., and Roberts, C. M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. , Marine Ecology Progress Series, 100:167-176.
- Program Coordination and Economics Branch, 1993. Profile of harvesting capacity in the Newfoundland region. pp. 94-124. *In*: K. Storey, ed. The Newfoundland groundfish fisheries: defining the reality, St. John's, Newfoundland, Institute of Social and Economic Research. Memorial University of Newfoundland, St. John's, Newfoundland.
- Quinn, J. F., Wing, S. R., and Botsford, L. W., 1993. Harvest refugia in marine invertebrate fisheries: models and applications of the red sea urchin, *Stongylocentrotus franciscanus*. , American Zoologist, 33:537-550.
- Rakitin, A., and Kramer, D. L., 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. , Marine Ecology Progress Series, 131:97-113.

- Ramos-Espla, A. A., and McNeill, S. E., 1994. The status of marine conservation in Spain. , *Ocean Coastal Management*, 24:125-138.
- Richards, L. J., 1994. Trip limits, catch, and effort in the British Columbia rockfish trawl fishery. , *Transactions of the American Fisheries Society*, 14:742-750.
- Roberts, C. M., 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. , *Biological Conservation*, 9:816-826.
- Roberts, C. M., 1997. Ecological advice for the global fisheries crisis. , *Trends in Ecology and Evolution*, 12:35-38.
- Roberts, C. M., and Polunin, N. V. C., 1991. Are marine reserves effective in management of reef fisheries? , *Reviews in Fish Biology and Fisheries*, 1:65-91.
- Roberts, C. M., and Polunin, N. V. C., 1993a. Marine reserves: simple solutions to managing complex fisheries? , *Ambio*, 22:363-368.
- Roberts, T. W., 1986. Abundance and distribution of pink shrimp in and around the Tortugas Sanctuary, 1981-1983. , *North American Journal Fisheries Management*, 6:311-327.
- Roberts, T. W., and Polunin, N. V. C., 1993b. Effects of marine reserve protection on northern Red Sea fish populations. pp. 969-977. *In: Proceedings of the Seventh International Coral Reefs Symposium*, Guam. 2.
- Rogers-Bennett, L., Bennett, W. A., Fastenau, H. C., and Dewees, C. M., 1995. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. , *Ecological Applications*, 5:1171-1180.
- Rose, G. A., 1992. Indices of total biomass in the "Northern" and Gulf of St. Lawrence atlantic cod (*Gadus morhua*) stocks derived from time series analysis of fixed gear (trap) catches. , *Canadian Journal of Fisheries and Aquatic Sciences*, 49:202-209.
- Rose, G. A., 1993. Cod spawning on a migration highway in the north-west Atlantic. , *Nature*, 366:458-461.
- Rose, G. A., 1997. The trouble with fisheries science! , *Reviews in Fish Biology and Fisheries*, 7:365-370.
- Rose, G. A., and Kulka, D. W., 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. , *Canadian Journal of Fisheries and Aquatic Sciences*, 56(Suppl. 1):118-127.
- Rose, G. A., and Leggett, W. C., 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). , *Canadian Journal of Fisheries and Aquatic Sciences*, 48:843-848.
- Rowley, R. J., 1994. Case studies and reviews, Marine reserves in fisheries management. , *Aquatic conservation: marine and freshwater ecosystems*, 4:233-254.
- Roy, N., 1996. What went wrong and what can we learn from it? pp. 15-25. *In: D. V. Gordon and G. R. Munro, eds., Fisheries and uncertainty: a precautionary approach to resource management*, University of Calgary Press, Calgary.
- Russ, G., 1985. Effects of protective management on coral reef fishes in the central Philippines. pp. 219-224. *In: Proceedings of the Fifth International Coral Reef Congress*, Tahiti, 1985. 4.
- Russ, G. R., and Alcala, A. C., 1994. Sumilon Island Reserve: 20 years of hopes and frustration. , *NAGA, the ICLARM Quarterly*, 7 (3):8-12.
- Russ, G. R., and Alcala, A. C., 1996a. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. , *Marine Ecology Progress Series*, 132:1-9.
- Russ, G. R., and Alcala, A. C., 1996b. Marine reserves: rates and patterns of recovery and decline of large predatory fish. , *Ecological Applications*, 6:947-961.
- Russ, G. R., Alcala, A. C., and Cabanban, A. S., 1992. Marine reserves and fisheries management on coral reefs with preliminary modelling of the effects on yield per recruit. pp. 978-985. *In: Proceedings of the Seventh International Coral Reef Symposium*, Guam. 2.

- Ruzzante, D. E., Taggart, C. T., Cook, D., and Goddard, S., 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. , Canadian Journal of Fisheries and Aquatic Sciences, 53:634-645.
- Safina, C., 1995. The world's imperiled fish. , Scientific American, 273:46-53.
- Saville, A., 1980. Discussion and conclusions of the symposium on the biological basis of pelagic fish stock management. In: A. Saville, ed., Biological Basis of Pelagic Fish Stock Management, Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177:513-517.
- Saville, A., and Bailey, R. S., 1980. The assessment and management of the herring stocks in the North Sea and the west of Scotland. , Biological Basis of Pelagic Fish Stock Management, Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177:112-142.
- Shackell, N., and Lien, J., 1995. An under-utilized conservation option for fishery managers: marine protected areas in the northwest Atlantic. pp. 21-30. In: N. L. Shackell and J. H. M. Willison, eds., Marine protected areas and sustainable fisheries, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Shackell, N. L., and Willison, J. H. M., eds., 1995. Marine protected areas and sustainable fisheries. Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada, Vol. 300 pp.
- Shelton, P. A., Stansbury, D. E., Murphy, E. F., Lilly, G. R., and Bratley, J., 1996. An assessment of the cod stock in NAFO Divisions 2J+3KL. , DFO Atlantic Fisheries Research Documents, 96/80:65 pp.
- Shepherd, S. A., and Brown, L. D., 1993. What is an abalone stock: implications for the role of refugia in conservation. , Canadian Journal of Fisheries and Aquatic Sciences, 50:2001-2009.
- Sissenwine, M. P., and Shepherd, J. G., 1987. An alternative perspective on recruitment overfishing and biological reference points. , Canadian Journal of Fisheries and Aquatic Sciences, 44:913-918.
- Sladek Nowlis, J., and Roberts, C. M., 1997. You can have your fish and eat it too: theoretical approaches to marine reserve design. pp. 1907-1910. In: Proceedings of the 8th International Coral Reef Symposium, Panama City, Panama. 2.
- Smith, S. J., Hunt, J. J., and Rivard, D., eds., 1993. Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences, 120, 442 pp.
- Stoner, A. W., and Ray, M., 1996. Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. , Fishery Bulletin, 94:551-565.
- Sumaila, U. R., 1998. Protected marine reserves as fisheries management tools: a bioeconomic analysis. , Fisheries Management and Uncertainties Symposium, Bergen, Norway, Fisheries Research, 37:287-296.
- Symes, D., 1990. North Sea fisheries: trends and management issues. pp. 271-287. In: D. Freestone and T. Ijlst, eds., The North Sea: perspectives on regional environmental co-operation., International Journal of Estuarine and Coastal Law. 5, no. 1 3.
- Taggart, C. T., 1997. Bank-scale migration patterns in Northern cod. , NAFO Scientific Council Studies, 29:51-60.
- Taggart, C. T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P., 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. , ICES Marine Science Symposia, 198:140-157.
- Tegner, M. J., 1992. Brood-stock transplants as an approach to abalone stock enhancement. pp. 461-473. In: S. A. Shepherd, M. J. Tegner, and S. A. G. d. Proo, eds., Abalone of the world: biology, fisheries and culture, Blackwell Scientific Publications, Oxford, UK.

- Tegner, M. J., 1993. Southern California abalones: can stocks be rebuilt using marine refugia? , *Canadian Journal of Fisheries and Aquatic Sciences*, 50:2010-2018.
- Templeman, W., 1966. Marine resources of Newfoundland. Fisheries Research Board of Canada, Ottawa, Ontario, Canada, 154, 155 pp.
- Trippel, E. A., 1995. Age at maturity as a stress indicator in fisheries. , *BioScience*, 45:759-771.
- Ulltang, Ø., 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. , *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 177:489-504.
- Vincent, A. C. J., and Pajaro, M. G., 1997. Community-based management for a sustainable seahorse fishery. pp. 761-766. *In*: D. A. Hancock, D. C. Smith, A. Grant, and J. B. Beumer, eds., *Developing and sustaining world fisheries resources: the state of science and management: 2nd World Fisheries Congress Proceedings*, Brisbane, Australia, CSIRO, PO Box 1139 Collingwood, VIC 3006 Australia, ISBN 0 643 059857.
- Walsh, S. J., Brodie, W. B., Bishop, C. A., and Murphy, E. F., 1995. Fishing on juvenile groundfish nurseries on the Grand Bank: a discussion of technical measures of conservation. pp. 54-73. *In*: N. L. Shackell and J. H. M. Willison, eds., *Marine protected areas and sustainable fisheries*, Science and Management and Protected Areas Association, Centre for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Walters, C. J., 1998. Designing fisheries management systems that do not depend upon accurate stock assessment. pp. 279-288. *In*: T. J. Pitcher, D. Pauly, and P. Hart, eds., *Reinventing Fisheries Management*, Kluwer Academic Publishers, Dordrecht, Holland.
- Walters, C. J., and Maguire, J.-J., 1996. Lessons for stock assessment from the northern cod collapse. , *Reviews in Fish Biology and Fisheries*, 6:125-137.
- Walters, C. J., and Parma, A. M., 1996. Fixed exploitation rate strategies for coping with effects of climate change. , *Canadian Journal of Fisheries and Aquatic Sciences*, 53:148-158.
- Walters, C. J., and Pearse, P. H., 1996. Stock information requirements for quota management systems in commercial fisheries. , *Reviews in Fish Biology and Fisheries*, 6:21-42.
- Walters, C. J., and Punt, A., 1994. Placing odds on sustainable catch using virtual population analysis and survey data. , *Canadian Journal of Fisheries and Aquatic Sciences*, 51:946-958.
- Watson, R. A., Die, D. J., and Restrepo, V. R., 1993. Closed seasons and tropical penaeid fisheries: a simulation including fleet dynamics and uncertainty. , *North American Journal Fisheries Management*, 13:326-336.
- Williams, B. K., and Nichols, J. D., 1990. Modeling and the management of migratory birds. , *Natural Resource Modeling*, 4(3):273-311.
- Williams, D., and Russ, G. R., 1995. Reserves, resilience and recruitment. pp. 673-676. *In*: P. Dalzell and T. J. H. Adams, eds., *South Pacific Commission and Forum Fisheries Agency Workshop on the Management of South Pacific Inshore Fisheries*, Noumea, New Caledonia, SPC. 2.
- Winters, G. H., and Wheeler, J. P., 1985. Interaction between stock area, stock abundance, and catchability coefficient. , *Canadian Journal of Fisheries and Aquatic Sciences*, 42:989-998.
- Wroblewski, J. S., Kulka, D. W., Narayanan, S., Oake, A., Collier, A., and McGrath, B., 1995. Winter distribution and movements of northern Atlantic cod (*Gadus morhua*) along the Newfoundland-Labrador continental shelf edge derived from observations on commercial trawlers. , *Fisheries Oceanography*, 4:128-146.
- Yamasaki, A., and Kuwahara, A., 1989. Preserved area to effect recovery of overfished Zuwai crab stocks off Kyoto Prefecture. pp. 575-585. *In*: *Proceedings of the International Symposium on King and Tanner crabs*, Anchorage, Alaska, 1990, Sea Grant College Program, University of Alaska, Fairbanks, Alaska.

Younger, A., Kealey, K., Sinclair, M., and Trippel, E., 1996. Fisheries knowledge of spawning locations on the Scotian Shelf. pp. vii + 247 p. *In*: D. L. Burke, R. N. O'Boyle, P. Partington, and M. Sinclair, eds., Report of the Second Workshop on Scotia-Fundy groundfish management, Canadian Technical Report of Fisheries and Aquatic Sciences, 2100.

Appendix 3.1

Parameter calculations for stock-recruitment relationships

1. Using the Botsford incidence functions (Botsford, 1981) we assume that the number of eggs produced by the population is:

$$Eggs = R \sum_{a=1}^A l_a f_a = R \Phi_f = \sum_{a=1}^A N_a f_a$$

where l_a , N_a and f_a are respectively survivorship, number and fecundity at age. The population biomass is:

$$B = R \sum_{a=1}^A l_a w_a = R \Phi_b$$

where w_a is the weight at age. The unfished exploitable biomass per recruit is:

$$\Phi_{0,vw} = \sum l_{0,a} v_a w_a$$

where v_a is the vulnerability to fishing at age

2. Calculation of S_{\max}

S_{\max} is the slope of the stock recruitment curve near the origin and equals

$$S_{\max} = \Phi_{f \max, f}^{-1}$$

3. Calculation of K

At equilibrium, the Beverton and Holt recruitment curve may be expressed as:

$$R = R_0 \Phi_{0,f} S_{\max} (1 + k R_0 \Phi_{0,f})^{-1}$$

The biomass of an unfished population is:

$$B_0 = R_0 \Phi_{0,vw} \text{ thus } R_0 = \Phi_{0,vw} B_0^{-1}$$

By substituting R_0 in the recruitment equation, setting $B_0 = 1000$, and solving for k , we obtain:

$$k = (S_{\max} \Phi_{0,f} - 1) (B_0 \Phi_{0,f} \Phi_{0,vw}^{-1})^{-1} \text{ for the Beverton and Holt model}$$

and

$$k = \ln(S_{\max} \Phi_{0,f}) (B_0 \Phi_{0,f} \Phi_{0,vw}^{-1})^{-1} \text{ for the Ricker model}$$

Appendix 4.1

Analysis of observer data

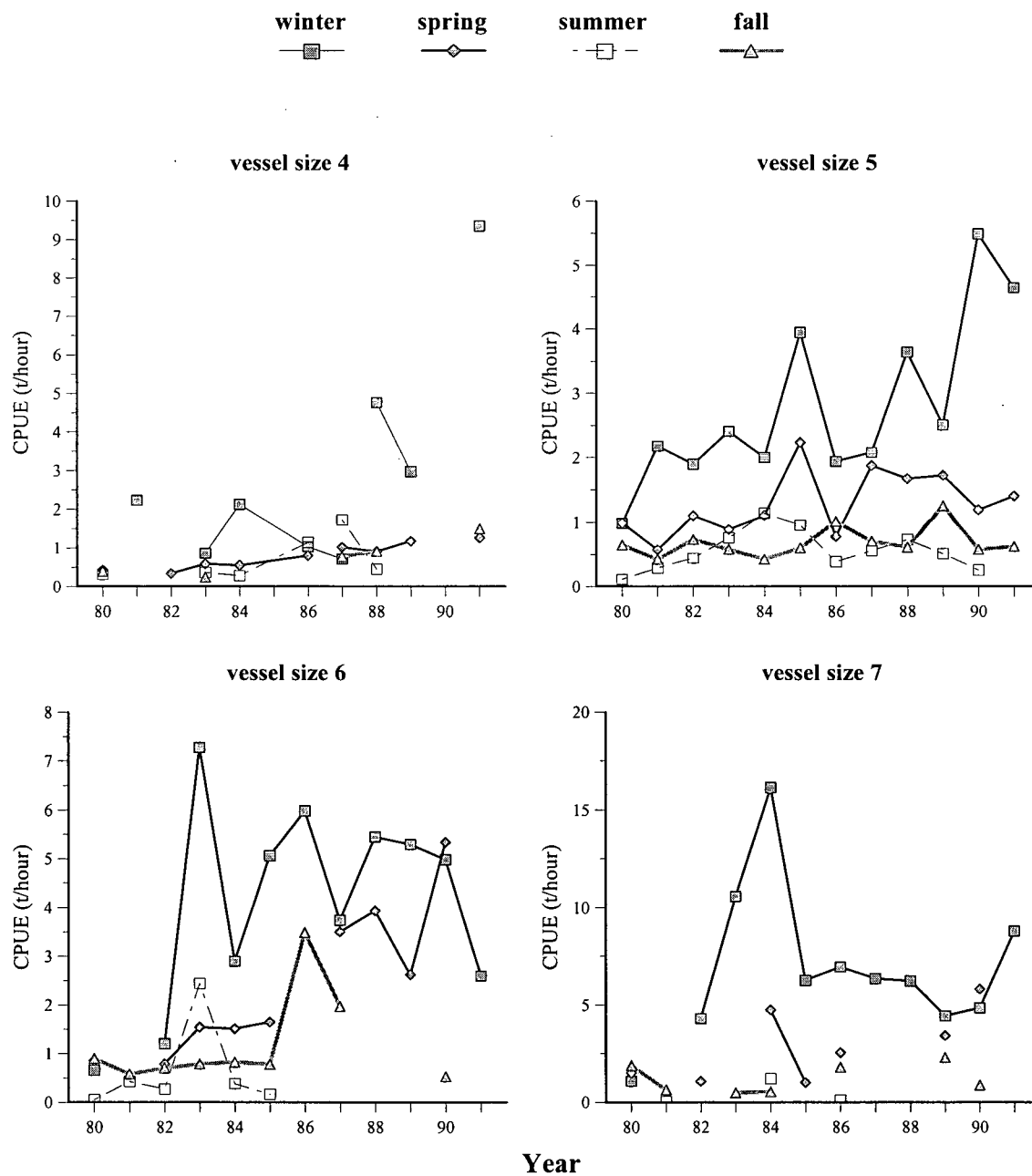


Figure A4.1 CPUE computed for 4 size class of trawler (defined in Table 4.2) by season and year as found in the observer data set.

Appendix 4.2

Analysis of NAFO data

Table A4.2 Catch and percentage of yearly catch by class of trawlers as found in the NAFO data set.

Vessel class	Year	Catch in tonnes				Percentage		
		Foreign	Nfld	Mari	Total	Foreign	Nfld	Mari
unknown	84	1205	-	-	1205	1.00		
unknown	85	880	-	-	880	1.00		
unknown	86	1539	28	-	1567	0.98	0.02	
unknown	87	1797	117	-	1914	0.94	0.06	
unknown	88	17192	363	-	17555	0.98	0.02	
unknown	89	-	406	-	406		1.00	
unknown	90	-	-	-	0			
unknown	91	-	682	-	682		1.00	
1	80	-	206	-	206		1.00	
1	83	-	30	-	30		1.00	
1	84	-	137	-	137		1.00	
1	85	-	88	-	88		1.00	
1	86	-	173	-	173		1.00	
1	87	-	50	-	50		1.00	
1	91	-	101	-	101		1.00	
2	80	-	279	-	279		1.00	
2	81	-	57	-	57		1.00	
2	82	-	232	-	232		1.00	
2	83	-	264	-	264		1.00	
2	84	1	684	-	685	0.00	1.00	
2	85	-	487	-	487		1.00	
2	86	-	509	-	509		1.00	
2	87	-	189	-	189		1.00	
2	88	-	-	8	8			1.00
2	89	-	-	-	0			
2	90	-	-	-	0			
2	91	-	1	-	1		1.00	
3	80	-	262	-	262		1.00	
3	81	-	157	-	157		1.00	
3	82	-	127	-	127		1.00	
3	83	-	1156	4	1160		1.00	0.00
3	84	-	1450	48	1498		0.97	0.03
3	85	-	2119	113	2232		0.95	0.05
3	86	-	2896	63	2959		0.98	0.02
3	87	-	3594	128	3722		0.97	0.03
3	88	-	3969	237	4206		0.94	0.06
3	89	-	3809	-	3809		1.00	
3	90	-	3652	-	3652		1.00	
3	91	-	2850	-	2850		1.00	
4	80	5079	2416	607	8102	0.63	0.30	0.07
4	81	7798	2306	1121	11225	0.69	0.21	0.10
4	82	1011	3937	299	5247	0.19	0.75	0.06
4	83	4264	977	688	5929	0.72	0.16	0.12
4	84	6624	1780	1258	9662	0.69	0.18	0.13
4	85	2154	1080	47	3281	0.66	0.33	0.01

Vessel class	Year	Catch in tonnes				Percentage		
		Foreign	Nfld	Mari	Total	Foreign	Nfld	Mari
4	86	10656	2183	484	13323	0.80	0.16	0.04
4	87	10041	3658	151	13850	0.72	0.26	0.01
4	88	237	5122	151	5510	0.04	0.93	0.03
4	89	5933	2577	343	8853	0.67	0.29	0.04
4	90	3626	1024	291	4941	0.73	0.21	0.06
4	91	3371	719	134	4224	0.80	0.17	0.03
5	80	1025	39542	7723	48290	0.02	0.82	0.16
5	81	839	52831	10519	64189	0.01	0.82	0.16
5	82	1038	69331	20520	90889	0.01	0.76	0.23
5	83	827	77519	24260	102606	0.01	0.76	0.24
5	84	1619	70122	24564	96305	0.02	0.73	0.26
5	85	8532	70835	26898	106265	0.08	0.67	0.25
5	86	12046	91591	17959	121596	0.10	0.75	0.15
5	87	2613	86932	14664	104209	0.03	0.83	0.14
5	88	29	95747	17036	112812	0.00	0.85	0.15
5	89	6105	69275	15814	91194	0.07	0.76	0.17
5	90	6977	53569	2107	62653	0.11	0.86	0.03
5	91	4159	46358	791	51308	0.08	0.90	0.02
6	80	7166	-	-	7166	1.00		
6	81	9723	-	-	9723	1.00		
6	82	6531	-	-	6531	1.00		
6	83	3726	-	3122	6848	0.54		0.46
6	84	7159	-	4970	12129	0.59		0.41
6	85	5396	-	5542	10938	0.49		0.51
6	86	35322	-	9706	45028	0.78		0.22
6	87	11748	3873	4260	19881	0.59	0.19	0.21
6	88	8242	7480	5159	20881	0.39	0.36	0.25
6	89	21811	2585	4809	29205	0.75	0.09	0.16
6	90	11178	4181	3484	18843	0.59	0.22	0.18
6	91	8396	578	3879	12853	0.65	0.04	0.30
7	80	12194	-	-	12194	1.00		
7	81	2234	-	-	2234	1.00		
7	82	8163	-	-	8163	1.00		
7	83	2744	-	-	2744	1.00		
7	84	8400	-	-	8400	1.00		
7	85	22849	-	-	22849	1.00		
7	86	7463	-	-	7463	1.00		
7	87	7604	-	6026	13630	0.56		0.44
7	88	600	-	4258	4858	0.12		0.88
7	89	669	7584	4732	12985	0.05	0.58	0.36
7	90	2226	3546	4136	9908	0.22	0.36	0.42
7	91	6912	1419	3485	11816	0.58	0.12	0.29

Appendix 5.1

Building the stock-recruitment relationship

1. Estimating the initial biomass B_0 :

We defined B_0 by comparing the biomass of the population computed with a virtual population analysis (VPA) (1962-1991) and the biomass estimated from a Schaefer biomass model (1954-1991):

$$B_{t+1} = B_t + r * B_t * (1 - B_t * B_0^{-1}) - C_t$$

Our goal was to estimate roughly the cod biomass in 1954 when the fishing rate was very low (Robert Arhens, Fisheries Centre, UBC, Vancouver, personal communication). We used the catch, and weight at age data (1962-1991) from the 1996 stock assessment (Shelton *et al.*, 1996), and the autumn survey abundance (1979-1991). Catch estimates for 1954 to 1961 were taken from Lear and Parsons (1993). The growth rate ($r = 0.26$) was taken from Myers *et al.* (1997b). We computed the biomass in 1954 by minimizing the difference between the two estimation techniques. The resulting biomass (B_0) of 3 years and older individuals is 5,600,000 tonnes.

2. Estimating the Beverton and Holt recruitment function

The Beverton and Holt recruitment function has the form:

$$R_y = Eggs_y * S_{max} * (1 + k * Eggs_y)^{-1}$$

We need to calculate S_{max} , and K . We define the biomass (Bpr) and eggs (Epr) per recruit as:

$$Bpr = \sum_{a=1}^A l_a * w_a \quad Epr = \sum_{a=1}^A l_a * f_a$$

where l_a , w_a and f_a are survivorship, number and fecundity at age respectively. The number of eggs ($Eggs_0$) and recruits (R_0) produced by the unfished population would then be:

$$Eggs_0 = B_0 * Epr * Bpr^{-1}$$

$$R_0 = B_0 * Bpr$$

S_{max} , the slope of the stock recruitment curve near the origin, equals:

$$S_{max} = Surv * R_0 * Eggs_0^{-1}$$

where $Surv (=4.2)$ is the ratio of the maximal survival of eggs for a very small population, to the survival for an unfished population. And finally K is obtained by:

$$k = S_{max} * R_0^{-1}$$

Appendix 6.1

Additional evidence of increase in effort

Coastal fishery

Between **1957 and 1964**, the number of fishers has increased by 33% after the implementation of an Unemployment Insurance program in 1957 (Harris, 1998).

Between **1964-1974**, due to a sharp decrease in CPUE, the number of fishers decreased by half (Lear and Parsons, 1993) while the number of gillnets by fisher doubled (Table 6.2). This is supported by fishers who recounted that between 1973-1977 in Trinity Bay, gillnetters maintained their catch by more than doubling the number of active nets (Fischer *et al.*, 1997).

Between **1975-1980**, the extension of the Exclusive Fisheries Jurisdiction to 200 miles led to a dramatic increase in the number of fishermen (Lear and Parsons, 1993), while the number of nets per fisher doubled (Table 6.3). Fishers were able to increase their effort as well as their range of action because new vessels were built. In fact, 30% of the small vessels (<35 feet), and 64% of the nearshore fleet (35-45 feet) present in 1991 were built during that period (Table 4.7). Neis *et al.* (1999) estimated at 20% per year the resulting increase in fishing capacity in the 1970s. Subsidisation of the new inshore vessels by the federal government were accompanied by provincial subsidies paying 30% of the latest technology (Harris, 1998). In addition, fuel and equipment became tax-free. All these benefits attracted new fishers in the industry (Harris, 1998) (see also Lear and Parsons, 1993).

Government subsidies and loans, as well as excessive optimism in the industry, promoted the renewal of the fleet throughout the **1970s and 1980s** (Table 4.7). The introduction of mechanical hauling enabled the handle of more gear in a day, and the widespread use of electronic navigation systems and sonar increased efficiency and allowed fishers to fish offshore with no visual bearings (Hutchings and Myers, 1995). As fish became scarcer fishers adopted traps with more efficient designs (Hutchings and Ferguson, 2000). Japanese traps have a roof which decreases the probability of losing fish in bad weather, and allow placement of trap in deeper water. Finally, mesh size decreased in both gillnets and traps as an answer to the disappearance of large fish (Neis *et al.*, 1999; Hutchings and Ferguson, 2000). The construction of new vessels, even after 1987, enabled fishers to explore offshore fishing grounds such as Virgin Rocks (unit area 3Lr) from 1982 (Hutchings and Myers, 1994). Clearly, the increase in number of fishers and the fishing capacity, although difficult to quantify, indicate more than the mere number of number of gillnets per fishers.

Offshore fishery (trawlers)

Harris (1998) reported the presence of 200 trawler-freezers on the Grand Banks between **1960-1975**, enjoying stable catch rates. By 1974, stocks were in poor shape and world-wide subsidies provided better equipment and increased efficiency. In **1977**, when Canada extended its jurisdiction to 200 miles, the Canadian fleet was not properly equipped to fish offshore so fishing continued through joint ventures. During the **1970-1980**, the trawl fleet also benefited from the above mentioned subsidies to buy boats and better equipment, and the fleet size increased. Inshore fishing grounds were said to be overcrowded and disputes between fishing gears increased (Harris, 1998). In the **mid-1970s**, Canadian fishers operating under licences for medium sized vessels (inshore and nearshore) increased their effort tremendously to maintain their catch in the offshore portion of Trinity Bay (Fischer *et al.*, 1997). By the early 1980s, the bay cod was considered exhausted. In the **1980s**, CPUE was said to decrease in spite of the increase in effort to the point where gillnetters applied for concurrent trawler licences (Harris, 1998). Enterprise allocations, quotas given to each of the two remaining fishing companies, Fishery Products International (Newfoundland) and

National Sea Product (Nova Scotia), led to the gradual diminution of the number of trawlers of size 6 and 7 (over 100 feet long) that they owned in the late 1980s (Program Coordination and Economics Branch, 1993). During that period, incentives for discarding increased for the captains working for large corporations (P. Fanning, DFO, Halifax, comm. pers.).

Appendix 6.2

List of modifications attempted

Here are the list of modifications made to the model in order to obtain a better fit with the observed data.

1. Variation of handling time in the catch equation: no impact on results.

Changed harvest equation from the Holling disc equation to conventional harvest equation:

1. Search of optimal combination of random movements and hunting power (the power to search and target aggregations for each fleet)
2. Modify migration trajectories so that cod travel more closely together: change catch for the whole period and creates a disadvantage for traps, especially in the 1960s.
3. Decrease random movements in winter and spring: not much improvement
4. Change in vulnerability schedule: help to increase exploitation rate although the biomass in the 1980s becomes too low.