

little fish
BIG IMPACT

Managing a crucial link in ocean food webs

A report from the Lenfest Forage Fish Task Force



The Lenfest Ocean Program invests in scientific research on the environmental, economic, and social impacts of fishing, fisheries management, and aquaculture. Supported research projects result in peer-reviewed publications in leading scientific journals. The Program works with the scientists to ensure that research results are delivered effectively to decision makers and the public, who can take action based on the findings. The program was established in 2004 by the Lenfest Foundation and is managed by the Pew Charitable Trusts (www.lenfestocean.org, Twitter handle: @LenfestOcean).



The Institute for Ocean Conservation Science (IOCS) is part of the Stony Brook University School of Marine and Atmospheric Sciences. It is dedicated to advancing ocean conservation through science. IOCS conducts world-class scientific research that increases knowledge about critical threats to oceans and their inhabitants, provides the foundation for smarter ocean policy, and establishes new frameworks for improved ocean conservation.

Suggested citation:

Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., Heppell, S.S., Houde, E.D., Mangel, M., Pauly, D., Plagányi, É., Sainsbury, K., and Steneck, R.S. 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean Program. Washington, DC. 108 pp.

Cover photo illustration: shoal of forage fish (center), surrounded by (clockwise from top), humpback whale, Cape gannet, Steller sea lions, Atlantic puffins, sardines and black-legged kittiwake.

Credits

Cover (center) and title page: © Jason Pickering/SeaPics.com

Banner, pages ii–1: © Brandon Cole

Design: Janin/Cliff Design Inc.

Diagrams, pages 19, 63, 70, 78, 86: Sue-Lyn Erbeck



little fish
BIG IMPACT

Managing a crucial link in ocean food webs

A report from the Lenfest Forage Fish Task Force

April 2012

CONTENTS

Task Force Members	iv	CHAPTER 3	
Acknowledgements	v	Approaches and Strategies for Forage Fish	
Preface	vi	Management: Lessons Learned	16
Our Mission	vi	Management Based on Precaution: Moratoriums	17
Our Approach	vii	Management Based on Empirical Reference Points	17
Workshops	vii	Prey length and age	17
Review of existing theory and practice	vii	Reproductive output	18
Case studies	vii	Predator condition and reproductive success	18
Quantitative methods	viii	Management Based on Reference Points	
Developing Conclusions and Recommendations	viii	from Stock Assessments	20
CHAPTER 1		Reference points based on	
Introduction: Little Fish, Big Impact	2	age-structured approaches	20
Fishing a Moving Target	3	Constant targeted yield or fishing mortality:	
Current Demand for Forage Fish	4	MSY approaches	21
The Need for Precautionary Management	5	Spawning potential approaches	21
Statement of Problem	9	Variable F determined from a biomass-fishing	
CHAPTER 2		mortality control rule	22
Biological and Ecological Characteristics		Management Based on the Use of	
of Forage Fish and their Implications for		Biomass Thresholds	23
Fisheries Management	10	Krill in the Antarctic: The use of precautionary	
Catchability	11	biomass thresholds	23
Age-Structure Truncation and Conservation		Herring in Alaska: The use of a harvest threshold	
of Fecundity	11	biomass based on egg surveys	23
Assessment of the Resilience and Recovery		Sardines in California, Oregon, and Washington:	
Potential of a Population	12	The use of a harvest biomass threshold with an	
Steepness of the Stock-Recruitment Relationship	12	explicitly coupled environmental variable	24
Sources of Mortality and Management Implications	13	Management Based on Potential Biological	
Sustainability of Other Ecosystem Components	13	Removal Principles	24
Localized Depletion	14	Management Based on Temporal and	
Accounting for Interacting Species	14	Spatial Approaches	26
Summary	15	Steller sea lions in the	
		Aleutian Islands and eastern Bering Sea	27
		African penguins in the Benguela	27
		North Sea sand eel	28
		Antarctic krill	29
		Summary	29



CHAPTER 4
Case Studies of Forage Fisheries 30

Antarctic Ecosystems: The Central Role of Krill 32

The Baltic Sea: An Impoverished Ecosystem 34

Barents Sea: The “Capelin Limit Rule” 36

The Benguela Upwelling System:
 A Tale of Two Fisheries 38

The California Current: Supporting Multiple
 Forage Fish and Invertebrates 40

Chesapeake Bay: Undervalued Forage Species
 and Concerns of Localized Depletion 42

Gulf of Maine: A Trophic and
 Socioeconomic Cornerstone 44

The Humboldt Current and the World’s
 Largest Fishery 48

The North Sea: Lessons from Forage Fish
 Collapses in a Highly Impacted Ecosystem 50

CHAPTER 5
Direct and Supportive Roles of Forage Fish 54

Methods 55

 Importance of forage fish to predators 56

 Calculating the direct and supportive roles
 of forage fish to commercial fisheries 57

 Global estimate of forage fish economic value
 to fisheries 57

Results 57

 Extent of predator dependency on forage fish 57

 Importance of forage fish to commercial fisheries 58

 Latitudinal comparisons 61

 Comparisons across ecosystem-types 62

 Global estimate of forage fish value to fisheries 62

 The supportive contribution of forage fish
 to all ecosystem consumers 63

Major Findings and Conclusions 65

CHAPTER 6
**Comparison of Fisheries Management
 Strategies and Ecosystem Responses to
 the Depletion of Forage Fish** 66

Methods 67

 Harvest control rules 69

 Parameters for stochastic runs 71

 Presentation of the results 71

 Predator response prediction 72

Results 72

 Deterministic model results using the
 constant yield control rule 72

 Deterministic model results using the
 constant fishing control rule 72

 Stochastic constant fishing control rules 77

 Stochastic step function rules 78

 Stochastic hockey stick control rule 79

 Comparison of control rules using deterministic
 and stochastic models 79

 Comparison of control rules with stochastic models 79

Major Findings and Conclusions 83

CHAPTER 7
Key Findings and Recommendations 84

Key Findings 84

Recommendations 88

Concluding Remarks 92

Glossary 93

List of Acronyms 97

Literature Cited 98

Appendices

Can be found online at:

<http://www.lenfestocean.org/foragefish>

TASK FORCE MEMBERS



Lenfest Forage Fish Task Force Members, from left:

Marc Mangel, David Conover, Éva Plagányi, Bob Steneck, Tim Essington, Selina Heppell, Ed Houde, Philippe Cury, Keith Sainsbury, Ian Boyd, Dee Boersma, Daniel Pauly, Ellen Pikitch.

Photo: Christine Santora

Dr. Ellen K. Pikitch, Chair, Professor and Executive Director of the Institute for Ocean Conservation Science, School of Marine and Atmospheric Sciences, Stony Brook University, USA

Dr. P. Dee Boersma, Professor and Director of the Center for Penguins as Ocean Sentinels, University of Washington, USA

Dr. Ian L. Boyd, Professor and Director of the NERC Sea Mammal Research Unit and the Scottish Oceans Institute, University of St Andrews, UK

Dr. David O. Conover, Professor, School of Marine and Atmospheric Sciences, Stony Brook University, USA

Dr. Philippe Cury, Director of the Centre de Recherche Halieutique Méditerranéenne et Tropicale, France

Dr. Tim Essington, Associate Professor, School of Aquatic and Fishery Sciences, University of Washington, USA

Dr. Selina S. Heppell, Associate Professor, Department of Fisheries and Wildlife, Oregon State University, USA

Dr. Edward D. Houde, Professor, University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, USA

Dr. Marc Mangel, Distinguished Professor and Director of the Center for Stock Assessment Research, University of California, Santa Cruz, USA

Dr. Daniel Pauly, Professor, Fisheries Centre, University of British Columbia, Canada

Dr. Éva Plagányi, Senior Research Scientist, Marine and Atmospheric Research, CSIRO, Australia

Dr. Keith Sainsbury, Professor, Institute of Marine and Antarctic Science, University of Tasmania, Australia, and Director of SainSolutions Pty Ltd

Dr. Robert S. Steneck, Professor, School of Marine Sciences, University of Maine, USA

Project Director: **Christine Santora**, Institute for Ocean Conservation Science, School of Marine and Atmospheric Sciences, Stony Brook University, USA

ACKNOWLEDGEMENTS

The Task Force extends our gratitude to the many people who helped bring this report to fruition. A project of this scale and complexity requires a team of support, and we thank the students and administrative consultants who assisted: Konstantine Rountos, Tess Geers, Natasha Gownaris, Shaily Rahman, Jesse Bruschini, Lorraine Rubino, Michelle Pilliod, and Faye Rogaski. Our EwE analyses were informed and conducted by Steve Munch, Charles Perretti, Joel Rice, and Kristin Broms. Many talented individuals provided their Ecopath and EwE models, and we are grateful for their contributions. The EwE module was developed for us by Villy Christensen and Sherman Lai, and the ex-vessel price database used for our Ecopath value analysis was provided by Reg Watson and Rashid Sumaila. We also thank A.O. Shelton and Matt Wright for their contributions.

We are grateful for the support and advice provided by our Policy Advisor, Chris Mann.

Special thanks to our project director, Christine Santora, and to Konstantine Rountos.

The Task Force held three meetings in the United States and one meeting in Peru, and we gratefully acknowledge the invaluable contributions of all the people involved in those meetings. From the U.S. meetings, we would like to thank the invited guests Andy Bakun, Beth Babcock, Ted Ames, John Annala, Jud Crawford, Jason Stockwell, David Townsend, and Mary Beth Tooley, as well as the Gulf of Maine Research Institute. From the Peru meeting, we want to express our gratitude to Juan Carlos Sueiro, Oscar de la Puente, Humberto Speziani, Sophie Bertrand, Tony Smith, Jorge Tam, Jaime Mendo, Cynthia Cespedes, Mariano Gutierrez, the Paracas National Reserve, and the TASA fishmeal plant. The meeting could not have been such a success without the hard work and guidance of Patricia Majluf, Santiago de la Puente, Alejandra Watanabe, and Lucia Sato, and we express our sincere thanks to these individuals.

Three anonymous reviewers lent their expertise and time to shaping the final form of this report, and we are grateful for their assistance.

This project was made possible through funding from the Lenfest Ocean Program.

PREFACE

Our Mission

With support from the Lenfest Ocean Program, the Institute for Ocean Conservation Science at Stony Brook University convened the Lenfest Forage Fish Task Force (Task Force), a panel of 13 preeminent marine and fisheries scientists from around the world. The primary purpose of the Task Force was to provide practical, science-based advice for the management of forage fish because of these species' crucial role in marine ecosystems and because of the need for an ecosystem-based approach to fisheries management (e.g., Pew Oceans Commission 2003, U.S. Commission on Ocean Policy 2004, Pikitch *et al.* 2004, McLeod *et al.* 2005, Levin *et al.* 2009). To date, scientific guidance for implementing an ecosystem-based approach to forage fisheries management has mostly focused on broad principles rather than specific goals, targets, or thresholds. In part, this is due to a lack of information about the impact of forage fish removal on marine ecosystems. The Task Force conducted original research and synthesis to advance scientific understanding and to inform our management recommendations.



Common seal foraging for herring, Baltic Sea, © Wolfgang Poelzer/SeaPics.com.

Our Approach

Workshops

The Institute for Ocean Conservation Science convened four workshops from May 2009 to December 2010. The purpose of these meetings was twofold: first, to develop and implement a work stream for investigation and analysis; and second, to gain firsthand knowledge of the circumstances under which forage fisheries operate. Our first and last meetings were deliberative in nature, and our second and third meetings presented opportunities for field trips and interaction with experts. During our second meeting, in Portland, Maine, we focused on Atlantic herring (*Clupea harengus*) and reserved one day for presentations and dialogue with those knowledgeable about this species and fishery. In May 2010, during our meeting along the coast of Peru, we considered the Peruvian anchoveta (*Engraulis ringens*) fishery, the largest forage fishery in the world. In addition to discussing the operation of the fishery with local biologists and politicians, we visited fish markets, a fish meal plant, and seabird reserves.

Review of Existing Theory and Practice

In developing our recommendations, we reviewed existing principles that have been used in managing forage fisheries and examined current applications around the world. In Chapter 1, we present an overview of the issues and provide context for why an ecosystem-based approach to management is necessary. In Chapter 2, we review biological and ecological characteristics of forage fish and their implications for management. These characteristics are important because they contribute to the dynamics of forage fish populations and their vulnerability to exploitation. In Chapter 3, we address a variety of assessment approaches and management strategies, describing their development and application. The methods discussed range from theoretically

derived to empirically based approaches. In particular, we elaborate on the use of lower biomass thresholds, which we believe are a key tool for management of forage fisheries, and discuss why maintaining adequate forage fish abundance is necessary to prevent excessive impacts on dependent predators.

Case Studies

In Chapter 4, we provide nine case studies, each of which focuses on one or more predominant forage fish species in a particular ecosystem (see map, page 31). The case studies are not meant to be comprehensive but rather were intended to illustrate a variety of forage fish species and the ecosystems in which they occur, as well as the wide range of issues surrounding their management. Three of the ecosystems examined (California Current, Humboldt Current, and Benguela Current) occur within major eastern boundary current upwelling systems and exemplify forage-fish dominant, “wasp-waist” attributes (Cury *et al.* 2000). Forage fish catch rates in these systems are among the highest in the world (Alder and Pauly 2006). Two of the case studies consider ecosystems situated in high latitudes (Antarctic and Barents Sea), the former representing a diverse system with krill (*Euphausia superba*) as the foundation prey for many higher-level dependent predators, and the latter representing a low-diversity system in which capelin (*Mallotus villosus*) plays the central role in a tightly coupled food web. The other four case studies include a semi-enclosed sea where there has been considerable fishing effort over many years (North Sea); a large estuary where forage fisheries conflict with the ecosystem services provided by forage fish (Chesapeake Bay); a brackish sea that represents an “impoverished” environment (Baltic Sea); and a large, semi-enclosed embayment (Gulf of Maine) in which forage fish provide critical support for the lobster (*Homarus americanus*) fishery, which is the dominant socioeconomic driver in the region. In all, these case studies illustrate key concepts in forage

fishery management that the Task Force found relevant and provide broad context and insight into the issues we investigated in other sections of the report.

Quantitative Methods

At the outset of the project, it was clear that meeting the Task Force's mission would require going well beyond a synthesis of existing theory and practice of forage fishery management. In order to provide specific management advice, we developed and applied methodologies that would both advance scientific understanding of the role of forage fish in marine ecosystems and enable us to examine the relative performance of alternative management strategies. We used two types of food web models of marine ecosystems in our analyses. The first, Ecopath (Polovina 1984, Christensen and Pauly 1992), is the most widely used food web model in fisheries (Essington 2007), with more than 200 models developed as of 2010 (Fulton 2010). Ecopath creates static models or "ecosystem snapshots" (Christensen *et al.* 2005), which can be used to analyze the biomass of ecosystem elements and the flow of energy between these elements. The second model, Ecosim (Walters *et al.* 1997), was developed in 1997 to be used in conjunction with Ecopath. The Ecopath with Ecosim (EwE) software allows for time dynamic modeling and is commonly used to explore the impact of fishery management strategies on ecosystem elements (Christensen *et al.* 2005). Each of the specific Ecopath or EwE models used was obtained from the published literature or from the scientific team that developed it.

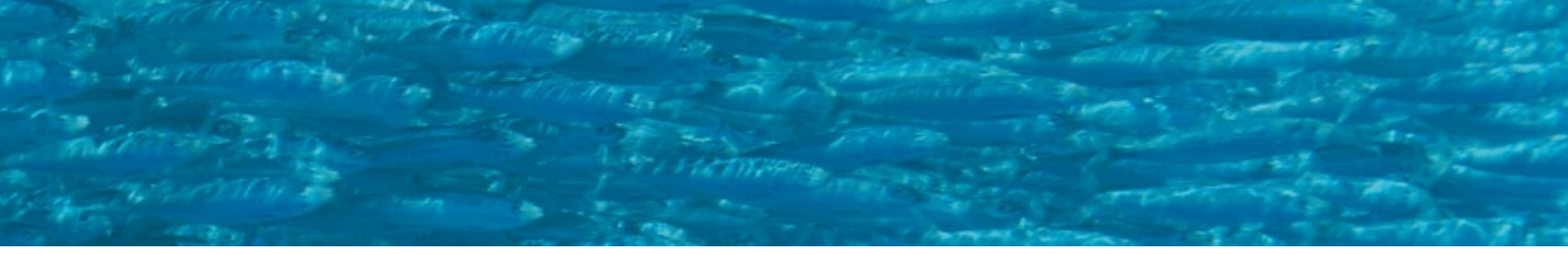
By conducting an analysis of more than 70 Ecopath models, we were able to quantify the value of forage fish both as an economic commodity and as ecological support for other species in the ecosystem. In our use of EwE models, we simulated what happens to forage fish and their predators under a variety of fishing strategies. The methods and results for each of these analyses are

provided in detail in Chapters 5 and 6, respectively. This original research undertaken by the Task Force provides significant scientific advances in support of ecosystem-based management of forage fisheries.

Developing Conclusions and Recommendations

We drew upon a variety of information sources when developing our conclusions and recommendations. We synthesized existing literature, examined current and past management practices for forage fish, and generated novel quantitative modeling approaches and results. We also compiled empirical data to further insights into the impacts of fisheries on ecosystem dynamics and predator dependence on forage fish. We used this information and our informed scientific judgment to recommend both specific management measures and general rules that are operationally defined and thus can be implemented immediately.

We believe that the management advice presented in this report provides a set of robust, precautionary standards, management targets, and biomass thresholds that can be used broadly to support the maintenance of forage fish populations as an important feature of marine ecosystems. We understand that every ecosystem is unique and would benefit from tailor-made solutions that account for individual characteristics, management structure, and research capacity of each system. However, we believe that the guidance provided herein will prove widely useful in holistic management of forage fish fisheries because it is flexible enough to be applied in data-rich situations as well as low-information scenarios. The results and recommendations contained within this report advance scientific understanding and provide necessary and credible guidance for applying an ecosystem-based approach for management of forage fish species.



1

Introduction: Little Fish, Big Impact

Forage fish play a crucial role in marine food webs in many ecosystems (Box 1.1). These small and medium-sized pelagic species are the primary food source for many marine mammals, seabirds, and larger fish, transferring energy from plankton to larger predators. Forage fish are also important predators in marine ecosystems, feeding upon phytoplankton, zooplankton, and, in some cases, the early life stages of their predators.

Forage fish play an intermediary role in many marine ecosystems, including estuaries, shelf seas, upwelling, and open ocean systems occurring from the tropics to the Earth's poles. They constitute the majority of prey upon which some predators depend. Such highly dependent predators may be iconic or ecologically important, while others may be commercially or recreationally valuable fish species. In some cases, highly dependent predators may include threatened or endangered species. A reduction in available prey—because of fishing,



Forage fish help sustain many species of wildlife in the world's oceans and estuaries.

School of northern anchovies off California, © Mark Conlin/SeaPics.com. Minke Whale, background, © Brand X Pictures/Fotosearch.

KEY POINTS

- Forage species occupy a key position in marine food webs that links the energy produced by plankton to large-bodied fishes, birds, and mammals.
- Forage fish characteristics include small body size, rapid growth, schooling behavior, and strong population responses to environmental variability. The latter may include shifts in abundance, distribution, or both.
- Fisheries for forage species are among the largest in the world, and demand for products derived from forage fish is increasing.
- Because many animals and humans depend on forage fish, it is important to manage fisheries that target them in a precautionary manner that accounts for their high degree of variability and importance to the ecosystem.



Grey seal, coast of Norfolk, UK.

environmental conditions, or a combination of both—can have direct and lasting impacts and can fundamentally change the structure and functioning of an ecosystem.

In their role as prey, forage fish provide the underpinnings for many species of wildlife in our oceans and estuaries. They support the whales we delight in seeing, the seabird colonies we enjoy viewing, and the wild fish that provide recreational opportunities and food. A primary challenge for fisheries managers and policymakers is to determine a level of catch that accounts for the important ecological role that forage fish play in the larger marine environment. This is especially important because forage fish are an increasingly valued commodity and at the same time provide fundamental ecological support to many other species. It is imperative, therefore, that we take a holistic viewpoint when managing these fish.

Fishing a Moving Target

Before the advent of industrial fishing in the 20th century, massive shoals of forage fish—herrings, sardines, and anchovies—were obvious to sailors, fishermen, and even to casual observers. Their great numbers inspired the notion that these fish were so abundant that they were essentially beyond the capacity of humans to deplete (McEvoy 1986, MacCall 1990, Roberts 2007). However, observations of great numbers of forage fish at certain times can be deceptive (Box 1.2). Many forage fish species are capable of spawning multiple times during the year, thereby increasing the probability of producing eggs and larvae that hatch under favorable environmental conditions. Because forage fish are capable of responding quickly to such conditions, their populations cannot be expected to maintain a steady state or equilibrium condition. In fact, forage fish often display rather unstable dynamics (Schwartzlose *et al.*

Box 1.1

Task Force Definition of Forage Fish

Forage fish are most often defined as prey for upper trophic-level predators. Here, we define forage fish in terms of their functional role in providing a critically important route for energy transfer from plankton to higher trophic levels in marine ecosystems.

This functional group is composed of low trophic-level species—often, but not always, fish—that meet most of the following criteria or conditions:

- Forage fish provide the main pathway for energy to flow from very low trophic levels—plankton—to higher trophic levels—predatory fish, birds, and mammals. They transfer a large proportion of energy in the ecosystem and support or regulate a variety of ecosystem services.
- Few species are in this trophic role in marine food webs, but they are the largest vertebrate component of each system by number and weight.
- Forage fish retain their unique role in the food web from egg to adult.
- Forage fish can experience rapid population expansion because of their relatively small body size, fast growth, early maturity, and relatively high fecundity. However, their short life span can also lead to sudden population collapse when adult mortality rates are high.
- Forage fish population size is usually strongly environmentally driven and may exhibit large annual, interannual, or decadal-scale fluctuations.
- Forage species usually form dense schools, making them highly accessible to fishing.

1999, Cury *et al.* 2000, Chavez *et al.* 2003, Alheit and Niquen 2004). Hence, major fluctuations in forage fish abundance have been observed and recorded for centuries. Cushing (1988) recorded the waxing and waning of herring fisheries in northern Europe, and Baumgartner *et al.* (1992) reported fluctuations of sardine and anchovy populations in the California Current system occurring over thousands of years. These studies established that the abundance of forage fish at specific locales has varied dramatically with shifts in oceanic conditions and can fluctuate enormously over time (Box 1.2). Additional research conducted during the past three decades and numerous reviews of trends in abundance have reinforced the conclusion that shoaling pelagic fish exhibit strong decadal variability in abundance and respond sharply to shifts in ocean climate (Alheit *et al.* 2009).

Forage fish have the propensity to form large shoals. This behavior is believed to have evolved as a defense against natural predators, but it makes them easily detectable and catchable by modern fish spotting and catching technologies (Pitcher 1995, Alder *et al.* 2008). Aerial spotter aircraft, sonar mapping, and large pelagic trawls and purse-seine nets that surround and capture very large shoals, lead to fishing that is highly efficient and effective even after a population declines. As a result, the catch per unit effort is not an accurate indicator of forage fish population size. Shoaling pelagic fish are highly vulnerable to fishing (Beverton 1990). Overexploitation is common worldwide (Alder and Pauly 2006) and detrimental to their long-term viability, and fisheries management approaches responsive to these characteristics are not always consistently applied (Barange *et al.* 2009).

Current Demand for Forage Fish

Since the advent of modern fish-finding and capture technology after World War II, humans have become a major predator of forage fish. Global landings are currently about 31.5 million tonnes*¹ annually, about 37 percent of the global wild marine fish catch

* tonne=t=1000 kg

1. This estimate includes mackerels, which are not considered in this study.



Demand for forage fish in agriculture, aquaculture, and other industries will continue to increase pressure on wild forage fish stocks.

Anchoveta in a Peru processing plant, Lenfest Forage Fish Task Force.

(Alder *et al.* 2008). Rarely, however, do we see forage fish listed prominently on restaurant menus or in supermarkets. This is because 90 percent of the catch is processed, or “reduced,” to fish meal and fish oil, which are used primarily for agriculture, aquaculture, and industrial purposes (Alder *et al.* 2008). Fish meal is used in feeds for farmed fish, pigs, and chickens, and fish oil is used in feeds for farmed fish, as well as in nutritional supplements for people. Forage fish have been particularly important to the development of the aquaculture sector, which now supplies almost half of the total fish and shellfish for human consumption (Food and Agriculture Organization, 2010). In 2006, 88.5 percent of fish oil and 68.2 percent of fish meal produced globally were used by the aquaculture sector (Tacon and Metian 2008). Rapid growth in aquaculture production has resulted in greater demand, higher prices, and increased consumption of fish meal and fish oil by the aquaculture industry (Naylor *et al.* 2009). Demand for carnivorous farmed fish in industrialized and emerging nations will continue to be an important driver in the world market² and will therefore continue to increase pressure on wild forage fish stocks (Naylor and Burke 2005). Although forage fish are not typically consumed directly by most people in industrialized countries, they are present in everyday life as an important component of the diet of the meat and fish that we consume on a regular basis.

² Although market forces play an important role in the regulation of forage fisheries, examination of these economic factors is beyond the scope of this report.

The Need for Precautionary Management

Precautionary management (Box 1.3) is necessary for three fundamental, but not mutually exclusive, reasons:

- Forage fish abundance can be difficult to quantify, and they exhibit large natural variations in abundance over space and time (see Box 1.2).
- Forage fish are prone to booms and busts with large associated impacts on dependent organisms.
- Single-species quotas have shortcomings that are most apparent when applied to this group. For example, despite massive landings, even these apparently prolific fish are susceptible to population collapse when the effects of fishing and unfavorable environmental conditions act together (Pinsky *et al.* 2011).

Steep declines in forage fish populations have been frequently observed despite apparent stability of the catches (Mullon *et al.* 2005) and are often accompanied by marked changes in ecosystem structure (Cury and Shannon 2004), such as sharp decreases in marine bird and mammal populations that depend upon forage fish for food. Moreover, those changes have led, in several cases, to the outburst of competing species, such as jellyfish (Pauly *et al.* 2009; Utne-Palm *et al.* 2010), which

Box 1.2

Understanding Variability and Spatial Distribution in Forage Fish Populations

High biomass (and catch) variability appears to be one of the defining characteristics of forage fish, mainly because of their short life spans and the environmental dynamics of their habitats (see, for example, Steele 1985, Stergiou 1998). This variability is important for practical and commercial reasons, such as the need for a steady supply of raw material for fish meal or canning plants, and for scientific reasons, such as the need to extract a stock recruitment signal from seemingly chaotic time series data (Csirke 1980, Myers *et al.* 1999).

However, the extent of variability of forage fish populations may be overstated. In fact, some scientists argue that in order for their populations to have persisted for thousands of years, various homeostatic (or stabilizing) mechanisms must have been at play. In addition, relatively stable populations may be perceived as less interesting and consequently may be understudied and underreported (Ursin 1982).

Homeostatic mechanisms are also difficult to detect because field sampling in fisheries science is often fixed in space and thus does not account for changes in spatial distribution. A good example is provided by the famous accumulations of sardine scales in the anoxic sediment of the Santa Barbara basin in California, which

are less economically desirable. Anthropogenic 'regime shifts' in marine ecosystems, resulting from the collapse of forage fish populations, represent a present and long-standing danger to marine ecosystem health (Richardson *et al.* 2009).

The primary management approach that has been used to limit catches of forage fish is quota management with a specified annual total allowable catch (TAC) (e.g., Patterson 1992, Barange *et al.* 2009). This approach

were used to reconstruct a 2,000-year time series of fluctuating abundance of sardine (Baumgartner *et al.* 1992). However, very few, if any, of the citing references point out that the California stock of what is known as *Sardinops sagax* oscillates between California and Vancouver Island, off the Canadian coast, and that their occasional scarcity off Santa Barbara does not *ipso facto* imply reduced stock abundance.

The biasing effect of such fixed-point sampling on the perception of variability was emphasized by Samb and Pauly (2000) with respect to an analog of the Pacific sardine, the Northwest African sardinella (*Sardinella* spp). Here, successive hydro-acoustic surveys by the R.V. Fridtjof Nansen, off Morocco in the north, Mauritania in the center, and Senegal (including The Gambia) in the south from 1992 to 1998 yielded biomass estimates for a single population that varied far more in Morocco (coefficient of variation = 97%) and Senegal (CV = 84%) than in Mauritania (CV = 25%).

Thus the prevailing view of the extraordinary variability of forage fish abundance, based largely on measurements taken repeatedly at specific places, must be tempered by the confounding effect of likely substantial shifts in spatial distribution over time.

presents two problems. First, it has often been unsuccessfully applied and has not sufficiently limited catches. Second, it was not designed to take into account the variability in forage fish stocks, their unique life-history characteristics, and the role they play in the ecosystem. The realization of these factors and the need to take a more precautionary approach to management as a consequence was slow to come in the 20th century and occurred only after many of the world's major herring, sardine, and anchovy fisheries had collapsed

or declined to levels that made them uneconomical to exploit. Collapses of forage fisheries from the 1960s to the 1980s were examined by Beverton (1990), who concluded that fishing caused or exacerbated collapse in many cases. Although Beverton noted that some populations declined or collapsed even in the absence of fishing, presumably because of shifts in ocean productivity or other environmental causes, it is clear that many collapses of forage fisheries are associated with high fishing mortality (Patterson 1992, Barange *et al.* 2009, Pinsky *et al.* 2011). While management is becoming more precautionary for forage fish, it has mostly been concerned with conserving the managed stock itself and only tangentially with sustaining or improving ecosystem services provided by forage fish.

Ecosystem services are difficult to quantify, but empirical evidence from several upwelling ecosystems

around the world shows that changes in forage fish abundance—caused by fishing, the environment, or a combination of both—affect predators in various ways. For instance, in the California Current, Becker and Beissinger (2006) found that after sardines collapsed off the coast of California, the diet of the marbled murrelet (*Brachyramphus marmoratus*), a seabird, shifted to lower-quality prey. Decreased prey resources appear partly responsible for poor murrelet reproduction and may have contributed to its listing under the U.S. Endangered Species Act. In addition, the reproductive success of brown pelicans (*Pelecanus occidentalis californicus*), a near-obligate predator of the northern anchovy (*Engraulis mordax*) in this ecosystem, is also related to the availability and abundance of its prey (Sunada *et al.* 1981). In the Benguela Current ecosystem, Crawford and Dyer (1995) found that anchovy abundance was significantly related to breeding attempts by four

Box 1.3

Using Precaution in Fisheries Management

The precautionary principle encourages more conservative management decisions at times of high uncertainty about the ecological impacts of fisheries, and especially in relation to serious or irreversible harm, such as the extreme depletion or extinction of a species (Garcia 1994, Parkes 2000, Gerrodette *et al.* 2002). In a single-species context, this is often applied by estimating reference points or thresholds through which certain key indicators of the exploited population should not pass, and which, if passed, result in an abrupt change in management policy. The uncertainties around these key indicators are also included in the setting of harvest rates and other management actions so that there is a low probability of passing the reference points established. For instance, a harvest level may be set so that there is a 10 percent or smaller chance of exceeding a predetermined maximum fishing mortality rate, F_{LIM} . As uncertainty about the stock status and implementation outcomes increases, managers need to set a lower annual catch limit to ensure that the resulting exploitation rate has a low probability of exceeding the limit point.

Application of the precautionary principle is more difficult for forage fish management in an ecosystem context than for single-species fisheries management. First, the productivity of the stock is often more dynamic and less predictable than is the case for other species because of life-history characteristics that lead the fish to be sensitive to changing environmental conditions. It may be difficult to quantify this uncertainty in terms of estimated population biomass levels. Second, because the ability to catch forage fish may increase at low stock sizes, fisheries can push stocks to collapse (Csirke 1989). Thus, risk-averse policies need to be implemented unless detailed information is available on the spatial pattern of fisheries that allows pending collapses to be recognized well in advance. Third, information on the status of forage fish predators and their dependence on particular forage species is often limited and highly uncertain.



Brown pelican in full breeding colors with a fish in its bill, California, © Hal Beral/V&W/SeaPics.com.

seabirds in South Africa: African penguin (*Spheniscus demersus*), Cape gannet (*Morus capensis*), Cape cormorant (*Phalacrocorax capensis*), and swift tern (*Sterna bergii*). They also found that when anchovy declined, so did the number of breeding individuals and, in some cases, success of chicks fledged. More recently, Crawford *et al.* (2007) found that the carrying capacity for African penguins in this ecosystem decreased by 80 to 90 percent as a result of increased competition for food with purse-seine fisheries and fur seals. And in the Humboldt ecosystem off the coast of Peru, Crawford and Jahncke (1999) found several linkages between forage fish and seabird predators. Numbers of Guanay cormorants (*Phalacrocorax bougainvillii*) are significantly related to the biomass of anchovy, with reproductive success decreasing in periods of anchovy scarcity. Numbers of Peruvian pelicans (*Pelecanus (occidentalis) thagus*) are significantly related to the combined biomass of anchovy and sardine, and decreases in the Humboldt penguin (*Spheniscus humboldti*), classified as vulnerable under International Union for Conservation of Nature (IUCN) criteria, can be partially attributed to competition with fisheries for food. Jahncke *et al.* (2004) also note that declines in abundance of guano-producing seabirds—Guanay cormorants, Peruvian pelicans, and Peruvian booby (*Sula variegata*)—are probably the result of competition for prey with the large anchoveta fishery in this ecosystem. These examples highlight instances

of predator impacts in upwelling ecosystems; however, examples of forage fish abundance affecting higher trophic levels can be found in other ecosystem types (see, for example, Springer and Speckman 1997).

In addition to empirical studies, the important ecological role of forage fish has been the focus of a multitude of modeling studies (for reviews, see Hollowed *et al.* 2000, Fulton *et al.* 2003, Plagányi 2007, Hollowed *et al.* 2011). For example, MULTSPEC (Bogstad *et al.* 1997) is a length-, age-, and area-structured simulator for the Barents Sea that includes cod, capelin, herring, polar cod, harp seal, and minke whales, and BORMICON (a boreal migration and consumption model) is an area-structured approach for the multi-species modeling of Arcto-boreal ecosystems (Stefansson and Palsson 1998). Numerous multi-species modeling studies have been employed to investigate the direct and indirect effects of common minke whales (*Balaenoptera acutorostrata*) on the cod, herring (*Clupea harengus*), and capelin fisheries in the Greater Barents Sea (e.g., Schweder *et al.* 2000). The projections from ecosystem models are generally highly uncertain, and much work remains to improve and validate these approaches (Plagányi and Butterworth 2004, Rose *et al.* 2010, Fulton 2010). However, their utility is increased if multiple models give qualitatively the same result (Plagányi and Butterworth 2011). For this reason, we used as many peer-reviewed Ecopath and EwE models as possible and integrated our results across these.

Using both empirical evidence and results from modeling studies is important in developing an ecosystem-based approach to fisheries management. Dependent predators are often affected by changes in prey abundance or distribution, and traditional methods of setting catch limits are insufficient to account for predator needs (Link 2005, Link 2010). In our modeling results (Chapter 6), we show how greater forage fish depletions can increase impacts on individual predators and species groups. Similarly, a modeling study by Smith *et al.* (2011) found that reducing exploitation rates on low trophic-level species resulted in much lower ecosystem impacts while still achieving a high percentage of maximum sustainable yield. Such studies can be used to estimate impacts on predators that would result from various

levels of fishing, which in turn can help guide management advice. We believe that accounting for dependent species is an important component of ecosystem-based management of forage fish, and we incorporate this notion in our recommendations in ways that can be operationally implemented.

Statement of Problem

Conventional wisdom has suggested that forage fish populations are resilient to fishing-induced and environmental changes because they function more like weeds than trees. That is, forage fish are capable of reproducing (or replenishing themselves) at a young age, and their biomass can quickly rise to high levels. Some populations have rebounded even after rapid and large declines. However, studies (Beverton 1990, Patterson 1992, Pinsky *et al.* 2011) have demonstrated that small, low trophic-level fish species are just as likely to collapse as long-lived, upper trophic-level species when fished at unsustainable levels.

It is now clear that the resilience of forage fish populations has been overestimated, and the effects of their depletion on other species have generally been ignored. Much of the previous scientific research and management advice has centered on maintaining the forage population alone without explicitly addressing the ecosystem impacts that may result from their removal. Even in cases where forage fish are well-managed from a single-species perspective (the stock is not overfished; overfishing is not occurring), depleted abundance of forage fish may negatively affect the ecosystem (Pikitch *et al.* 2004). This phenomenon has been called ecosystem overfishing and occurs when the harvesting of prey species impairs the long-term viability of other ecologically important species (Murawski 2000, Coll *et al.* 2008). In simple terms, a strategy that would seem optimal for managing one fish population may be insufficient when accounting for ecosystem considerations such as predator-prey interactions. With a few exceptions, such as in South Africa (Barange *et al.* 2009) or Antarctica (Constable *et al.* 2000, Reid *et al.* 2005), an ecosystem-based approach that considers ecosystem overfishing in the management of forage fish has yet to be applied.

Forage fish depletion may also cause top-down effects on lower trophic levels, which may have implications for the wider food web. For example, Frank *et al.* (2011) propose that high levels of forage fish in the northwest Atlantic, caused by the overfishing of large-bodied demersal species, have outstripped their zooplankton supply and are now decreasing, while demersal species are again increasing. We recognize that forage fish play a broader role in marine ecosystems and that they can act as ecosystem engineers through top-down effects on zooplankton and phytoplankton. However, information on top-down effects is far more scarce than that for the bottom-up effects of forage fish. We focus here on the links between forage species and their predators, and the implications for ecosystem-based management, while also considering top-down effects insofar as they are expressed in our modeling analyses.

Ecosystem-based fishery management of forage fish is especially important because they are strongly interconnected with so many other species and because their dynamics often closely track the climate-driven, biophysical environment in which they reside. Forage fish abundances fluctuate naturally in step with changes in environmental variables, notably ocean temperature. Accounting for such factors in devising management strategies can provide a buffer against overfishing during periods when populations are naturally low. And because forage fish play such a central role in marine food webs, even minor removals of a forage species may cause ripple effects, especially to highly dependent species (Smith *et al.* 2011; Chapter 6).

Scientific interest in the dynamics of forage fish and their role in marine ecosystems is not new (Alaska Sea Grant 1997). However, clear management guidance has been lacking on how to set catch limits for forage fish in a manner that considers their ecological role. One of our primary objectives is to offer a set of standards developed by consensus of the Task Force for the holistic, ecosystem-based management of forage fish. We aim to provide guidance to managers and policymakers that is clear and specific and can be immediately implemented.

2

Biological and Ecological Characteristics of Forage Fish and their Implications for Fisheries Management

In this chapter, we provide an overview of key ecological and biological characteristics of forage fish that should be considered in their management. We regard the following factors as particularly relevant to formulating management approaches for forage fish:

1. Catchability.
2. Age-structure truncation and conservation of fecundity.
3. Assessment of the resilience and recovery potential of a population.
4. Steepness of the stock-recruitment relationship.
5. Sources of mortality and management implications.
6. Sustainability of other ecosystem components.
7. Localized depletion.
8. Accounting for interacting species.



Schools of forage fish can remain highly catchable even when their abundance declines. This increases their susceptibility to collapse.

Menhaden, © Mark and Carol Archambault.
Background © Shutterstock.

KEY POINTS

- Catchability of forage fish stocks can remain high despite decreases in population size, leading to a greater chance for collapse.
- Managing forage fisheries to maintain adequate numbers of large, fecund fish can conserve a population's ability to grow and avoid collapse.
- Although forage species are highly productive, their short life spans can result in sudden changes in population size. When fishing mortality is high, a larger spawning stock must be maintained to minimize the risk of collapse.
- Forage fish mortality from nonhuman sources is variable because of changes in predation and plankton production. Natural mortality rate should be monitored, and even in a single-species context, a ratio of fishing mortality to total mortality (F/Z) of greater than 0.4 is unsustainable for forage fish.
- Depletion of forage fish can affect predators that depend on them as prey, particularly at local scales; this predation requirement must be taken into account when estimating allowable fishery catches.

1. Catchability—Forage fish have the propensity to form large shoals. This behavior is believed to have evolved as a defense against natural predators, but it makes them easily detectable and catchable by modern fish spotting and catching technologies (Pitcher 1995, Alder *et al.* 2008). From the 1950s onward, after sharp declines in numerous populations of small pelagic fish were observed (Alder and Pauly 2006), managers identified a major reason for their susceptibility to collapse: variable catchability. Catchability, defined as the level of fishing mortality attributable to a unit of fishing effort, traditionally had been assumed to be constant with respect to stock size in fisheries assessments but was found to be inversely proportional to abundance in several shoaling pelagic stocks (MacCall 1976, Ulltang 1976, Csirke 1988, Beverton 1990). Thus, as population size declined, the remaining but highly visible schools of forage fish were very vulnerable, even at low levels of abundance.

A classic example of this phenomenon involved Pacific sardines (*Sardinops sagax*) after World War II (McEvoy 1986). Catch per unit effort (CPUE), the traditional metric used to track relative abundance, did not decline as forage fish abundances declined. Improvements in technology, including spotter planes, which could locate schools near the surface, and acoustic equipment, which could find them at depth, further increased fishing efficiency. Thus, shoals of forage fish remained easily detectable to fishermen at low abundance, leading to increases in their catchability that eventually drove stocks to collapse.

2. Age-structure truncation and conservation of fecundity—Management of fisheries often includes measures to protect young and small fish through gear regulations, time closures, and spatial closures (Fréon *et al.* 2005). The intent is to increase yield per recruit (YPR) by allowing young fish to grow and adult

fish to reproduce. Regulations that protect small fish can increase fishing mortality of larger fish, leading to truncation of age structure and to a substantial reduction in the abundance of older age classes (Hsieh *et al.* 2010). For short-lived forage fish with few reproducing age classes, the consequences of age-structure truncation can be serious. Limiting catches of the oldest and largest individuals can conserve fecundity, because these individuals have the highest reproductive potential, and hence protect against collapse of a stock. These limited catches can be difficult to achieve, however, in forage fisheries where relatively unselective fishing gears such as purse seines or mid-water trawls are employed. Decades ago, Murphy (1967) noted the benefits of protecting age structure and fecundity in forage fish in his analysis of the dynamics of Pacific sardine. Although seldom instituted in the past for management of forage fish, conserving fecundity is now often an explicit management objective. As an example, target and limit fecundity reference points are provided in the assessment of the Atlantic menhaden (*Brevoortia tyrannus*) fishery (ASMFC 2006). Although conserving fecundity is a management objective in this fishery, no explicit regulations have yet been implemented to protect fecundity or to conserve age structure of Atlantic menhaden.

3. Assessment of the resilience and recovery potential of a population—Recruitment (the number of new young fish entering the population each year) is highly variable in most marine fish, but relatively strong density-dependent regulation provides some resistance to collapse. In clupeid stocks (herrings, sardines, anchovies), there may be less ability to regulate abundance through density-dependent mechanisms than for other bony fishes with higher fecundity, which places clupeids at risk when fishing mortality is high. Cushing (1971) fit simple power models $R = kP^b$ to relate recruitment, R , and spawning population size, P . The parameter b is an index of density dependence. Cushing found that some clupeid stocks (herrings and sardines) had values of b that were greater than 0 but less than 1, meaning that recruitment decreases as adult stock size decreases. If k is sufficiently small, this implies a high probability of collapse at low spawning-stock sizes, otherwise known as an Allee effect. Because b implies unstable population regulation,

clupeids may have a low ability to regulate abundance in the face of environmental stresses. Moreover, for small k , $b < 1$ implies that there is a population size below which the population will collapse. This reinforces the idea that precautionary management measures need to be taken to prevent fishing levels that reduce spawning stock biomass below this critical threshold.

4. Steepness of the stock-recruitment relationship—Over the past 20 years, it has become common in stock assessments to describe the density dependence of stock-recruitment relationships (SRRs) in terms of steepness, h , which is defined as the recruitment one obtains at 20 percent of the unfished biomass (Mace and Doonan 1988; see Rose and Cowan 2003, Mangel *et al.* 2010 for review). Myers *et al.* (1999) treated steepness as a purely statistical concept and found that steepness of clupeid stocks was approximately 0.5 (that is, recruitment was reduced by 50 percent after an 80 percent reduction of spawning biomass), making it fairly low. A low steepness has a number of important implications, perhaps most importantly that a larger spawning stock is needed to reduce the chance of population collapse. There is evidence that highly variable species such as prawns are characterized by low steepness (Dichmont *et al.* 2003, Punt *et al.* 2010). Myers *et al.* (2002), in another statistical analysis of steepness and reproductive longevity, showed that species falling into the low steepness category are those with an early age at maturity (< 2 years), high natural mortality (> 0.3 /year), and relatively low fecundity ($< 100,000$ eggs/year per individual). Although a stock characterized by an SRR with high steepness can produce “pretty good yields” at even a low spawning biomass, stocks with low steepness are predicted to produce high sustainable yields only at much larger spawning biomass levels and have low resilience to fishing (Hilborn 2010).

However, in light of the recognition that the biomass of forage fish fluctuates considerably, it is more appropriate to think of steepness conditioned on the environmental regime (e.g., Munch and Kottas 2009, and references therein) rather than as a purely statistical concept (i.e., related to a theoretically unfished population and its recruitment in a steady state); also see Shelton and

Mangel (2011). The implication for management is that maintenance of relatively high spawning stock sizes in herrings, sardines, and anchovies is necessary to avoid the path to progressive declines in recruitment that is highly probable if spawning stocks are fished down. For more on how steepness is represented in terms of biological parameters, see Appendix A.*

5. Sources of Mortality and Management

Implications—Forage species are a critical food source for a wide variety of predators. Given the variability in forage fish populations, natural mortality rates, M , may fluctuate with changes in environmental conditions and predation rates. On the whole, natural mortality is relatively high for prey populations. For example, in the Gulf of Maine/Georges Bank area, predators can consume substantial quantities of Atlantic herring, often greater than amounts harvested by the fishery (Overholtz *et al.* 2008). When fisheries and predators both remove significant amounts of biomass of the same prey size, there is a heightened potential for prey stock declines (Overholtz *et al.* 2000).

After the collapses of numerous fisheries, some rules of thumb emerged for management of marine fisheries that lowered the risk of failure. The most fundamental of these is that the fishing mortality rate, F , should not exceed the natural mortality rate, M (i.e., $F/M \leq 1$; Beverton 1990, Thompson 1993). With total mortality expressed as $Z = M + F$, this implied that exploitation rates, F/Z , should be ≤ 0.5 . Patterson (1992) examined data on collapsed fisheries for shoaling pelagic species (i.e., forage fishes) and found that sustainability was associated with exploitation rates that did not exceed $F/Z = 0.4$ (or $F/M \leq 0.67$), indicating that fishing mortality rates for sustainability in forage fisheries should be substantially lower than natural mortality rates. Note that these observations consider only sustainability of the target species and do not explicitly address effects of fishing on the ecosystem.

It has also been suggested that total allowable catches (TACs) should be set to control and stabilize total mortality, Z , rather than fishing mortality, F , to account for variable predation mortality, M (Collie and Gislason 2001).

Predation mortality often makes up the largest part of the natural mortality rate and can be highly variable (Tyrrell *et al.* 2011). Acknowledging that M is variable (and scaled to predator abundances)—and considering it in estimating fishing mortality and stock biomass targets and thresholds—provides the basis for a precautionary, ecosystem-based approach to maintain adequate forage fish biomasses. For example, Overholtz *et al.* (2008) found that biological reference points for Atlantic herring are significantly different when predation mortality is included; maximum sustainable yield (MSY) harvest levels were lower than those estimated from the single-species assessment in which predation effects were not explicitly accounted for. Stephenson (1997) proposes including a “forage F ,” which would consist of a composite of key predator-prey relationships. Furthermore, although there may be intention to achieve a specific target fishing mortality, the actual fishing mortality rate may differ from that intended (Patterson 1999, Mangel 2000b). Reasons for differences between intended and actual fishing rates include discards and incidental take of forage fish, the inability to control catches accurately, and errors in estimating biomass. An example where actual fishing mortality exceeded a target is illustrated in the North Sea (Chapter 4).

6. Sustainability of other ecosystem components—

Although little attention was given to the ecosystem effects of forage fish depletion during the early stages of industrial fishing, there was awareness that fisheries removed biomass once eaten by predators (other fish, seabirds, and marine mammals). Production models initially applied to assess the potential of the Peruvian anchoveta (*Engraulis ringens*) fishery indicated an MSY level of 10 million tonnes (Schaefer 1970, Murphy 1977), which in retrospect was a level too high to sustain. Catches at that level in the 1960s had already resulted in major declines in seabird populations dependent on anchoveta (Schaefer 1970). Anchoveta stock abundance was further eroded by fishing and then collapsed in the early 1970s from the combination of high fishing mortality and low stock productivity under El Niño conditions at the time. Stock assessments had not provided managers with information sufficient to manage the fishery sustainably or to maintain other components

* www.lenfestocean.org/foragefish



Atlantic menhaden are thought to be locally depleted by the purse seine fishery in the Chesapeake Bay.

Purse seining on the Chesapeake Bay, NOAA.

of the ecosystem at desirable levels in the highly variable Humboldt upwelling system. A minimum biomass threshold was recently implemented in this system to avoid a recurrence of collapse and to ensure sufficient anchoveta for ecosystem predators (Humboldt case study, Chapter 4).

7. Localized depletion—Forage fish are vulnerable to localized depletion, which is a reduction, through fishing, in abundance or biomass in a specific area. Localized depletion occurring in key foraging areas and at critical feeding times may have a major effect on predators that have little ability to find more distant patches of abundant prey (Hewitt *et al.* 2004, Watters *et al.* 2008, Hill *et al.* 2009, Plagányi and Butterworth 2011).

In the United States, Atlantic menhaden are thought to be locally depleted by the purse seine fishery in the Chesapeake Bay (Chesapeake Bay case study, Chapter 4), although no metric has been developed to characterize the situation (Maryland Sea Grant 2009, ASMFC 2010). In this case, localized depletion is believed to negatively affect food demand of important predators such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), osprey (*Pandion haliaetus*), and bald eagles

(*Haliaeetus leucocephalus*). In parts of the North Sea, localized depletion of sand eel (*Ammodytes marinus*) has led to diminished reproductive output and population abundances of seabirds, notably black-legged kittiwake (*Rissa tridactyla*) (Rindorf *et al.* 2000, Daunt *et al.* 2008). New harvesting technologies have the potential to locally deplete Antarctic krill (*Euphausia superba*), a special cause for concern given the sensitivity of the Antarctic ecosystem (Kawaguchi and Nicol 2007; Antarctic case study, Chapter 4).

8. Accounting for interacting species—An ecosystem-based approach to management involves addressing bycatch, predator-prey interactions, and the multiple fisheries that occur within an ecosystem. It is common for species of forage fish to shoal together, causing a potential bycatch problem. The following are examples of situations in which multi-species interactions have occurred and are being managed. There are other circumstances in which these types of interactions are not managed, but we highlight three noteworthy cases.

Mixed schools of shoaling fish: Anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the Benguela Current—Mixed schools of shoaling pelagic

fish present a management dilemma common to all mixed fisheries. In South Africa, both sardine and anchovy are targeted by a purse-seine fishery; the anchovy fishery is currently healthy, but sardine have declined in recent years. Unfortunately, it is not possible to catch anchovy without an accompanying bycatch of juvenile sardine (De Oliveira and Butterworth 2004) because juveniles of both species can shoal together. South Africa, like many other mixed fishery management regimes that more commonly involve groundfish fisheries, has implemented a total allowable catch for anchovy along with a total allowable bycatch for sardine (Benguela Current case study, Chapter 4). In effect, this limits the anchovy harvest if the sardine total allowable bycatch has been taken.

When the predator becomes the prey: Sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) in the Baltic Sea—Filter-feeding fish, such as many forage fish species, often prey on fish eggs and larvae. In some circumstances, the eggs consumed can include a species' own young (i.e., cannibalism) or even those of fish that may become their predators later in life. In most cases, a balance is established in which both predator and prey can coexist. However, changes in the abundance of one of the species in the complex interaction, as has happened with cod in the Baltic, can lead to the development of a different balance of relative species abundances. In this case, released from predation by cod, sprats have proliferated and are preventing cod from recovering by consuming their eggs and larvae. Addressing these trophic interactions may involve both decreasing catches of the predator species and increasing catches of the prey species (Baltic Sea case study, Chapter 4).

The need for bait: Herring (*Clupea harengus*) and lobster (*Homarus americanus*) in the Gulf of Maine—Many fisheries rely on fresh bait from forage fisheries or other sources, but few are as dependent upon bait as is Maine's lobster fishery, which began in the mid-1800s at a time of high finfish landings and diversity. Over time, however, the abundance of all groundfish species (e.g., cod, hake, haddock, flatfish, and halibut) declined because of fishing while the abundance and landings of lobsters increased (Appendix C, Figure 5A).* Increased

lobster landings may well be the result of the extirpation of their predators (Butler *et al.* 2006), but the loss of groundfish also increased the fishing pressure and demand for bait. As groundfish were extirpated, the most abundant of Maine's fish, Atlantic herring, took on an increasingly important role as lobster bait. Today, 70 percent of New England's herring catch is used for lobster trap bait (Grabowski *et al.* 2010). Over the past half-century, the proportion of Maine's landings from herring declined while the proportion from lobsters increased (Appendix C, Figure 5B).* Remarkably, in 2009, a larger tonnage of lobsters was landed than herring. From a socioeconomic perspective, humans—especially the lobster fishermen—may be most dependent on forage fish in this system and ultimately the largest driver of fishing on them. In addition, the apparent dietary dependence of lobsters on bait from traps has resulted in a major revamping of the main food web in the Gulf of Maine (Atlantic herring case study, Chapter 4).

Summary

A number of management lessons can be learned from an examination of the ecological characteristics of forage fish. Certain characteristics, such as the propensity to shoal and the low steepness of the stock recruitment curve, make forage fish vulnerable to overfishing. Forage fish may also have a lower potential to rebound after overfishing or environmental factors have caused stocks to decline. In addition, forage fish can be locally depleted as a result of intense exploitation, and this depletion can have drastic effects on predators reliant on a local food source. Some management ideas have emerged that begin to take these factors into consideration. First, the maximum sustainable yield can be calculated using total mortality (fisheries and natural mortality) so that it takes predation into account and treats fisheries as another predator in the system. History has also shown that exploitation rates $F/Z > 0.4$ are associated with collapse of forage fish stocks, and thus lower levels are needed to ensure sustainability. The following chapter presents approaches to management of forage fisheries that illustrate many of the ideas discussed here.

* www.lenfestocean.org/foragefish

3

Approaches and Strategies for Forage Fish Management: Lessons Learned

In practice, precautionary, comprehensive, ecosystem-based management of forage fish and other fisheries is still relatively rare. As a consequence, forage fish and predator populations have been impacted. Here, we review management strategies that have been used or suggested for forage fisheries, drawing from the fisheries literature and other sources. We highlight measures that have been taken to address ecosystem concerns, and present a new concept for setting forage fish harvest limits based on an approach developed to manage incidental mortality of marine mammals (Wade 1998). We include examples for which ecosystem-based approaches were implemented without abundant data or sophisticated ecosystem-level models. These illustrations are important considering the history of forage fish population collapses and the poor understanding of ecosystem-level processes.



A recent comprehensive study found that when forage fish fall below a third of their maximum biomass, seabird reproductive success is negatively affected.

Puffin carrying sand eels for its chick, Faroe Islands,
© Shutterstock. Anchovies, background, © iStockphoto.com/J Tan.

KEY POINTS

- Examples of precautionary and ecosystem-based management measures exist for some forage species.
- Efforts to link management thresholds to observed changes in predator abundance or reproductive rates are proposed for Antarctic krill fisheries.
- Ecosystem considerations such as predator needs can be incorporated into single-species stock assessments, although the result may be a simple buffer to the allowable catch.
- Fishery harvest limits based on MSY for single species may not be appropriate for forage species due to their high variability and effects on dependent predators.
- More sustainable forage fish management has been achieved with minimum biomass thresholds (or “cutoffs”) for forage fish fishing. Using graduated fishing mortality for stock sizes above the threshold (“hockey stick” control rule) may be even more effective.
- Harvest guidelines could be based on a simple maximum removal equation that incorporates the population growth rate of the forage species and the number of predators that strongly depends on it.
- Management measures that restrict fishing in time and/or space may be useful tools to reduce the potential for local depletions of forage fish that affect sensitive predator species.

Management Based on Precaution: Moratoriums

Occasionally, scientists and managers have determined that the importance of forage species to predators and fisheries outweighs the potential for profitable exploitation of the resource. Harvest bans for capelin in Iceland and the Barents Sea and sand eels in Scotland have occurred during periods of low stock abundance. The U.S. Pacific Fishery Management Council banned the harvest of krill in 2006, before a fishery was established, and the North Pacific Fishery Management Council prevents directed fishing on some groups of forage fish.

Management Based on Empirical Reference Points

In the absence of a robust stock assessment and the considerable information required to derive reference points, simple rules to guide the harvesting of forage

fish may have utility. A basic consideration in fisheries management is whether or not a change in fishing effort (i.e., increasing or decreasing) is warranted; empirical indicators can be used to address this question. Some of these indicators are described below. However, unless they are accompanied by functional linkage to exploited biomass, either through a population dynamics model or through an empirical relationship derived from experience, they are no more than a general guide to the future exploitable biomass, and they need to be treated with commensurate precaution.

Prey length and age—Adjusting allowable catches to achieve a desired average length or age has been proposed as a simple foundation for fisheries management (Froese 2004), although precise thresholds and reference points need to be determined for each species and for different environmental conditions. For example, a decline in the average length of fish in the catch is often a consequence of high fishing mortality that

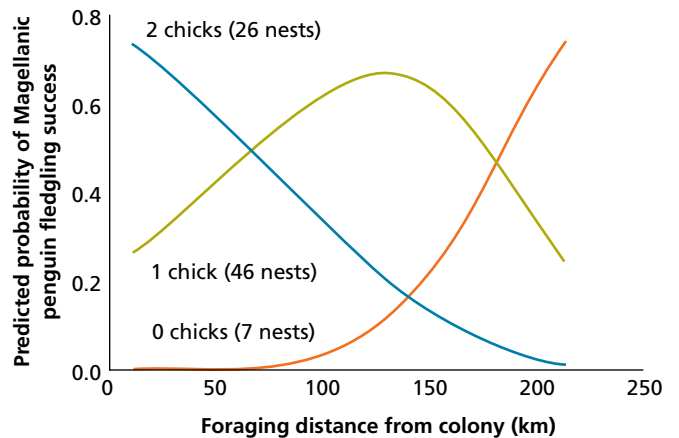
truncates the age and size distributions of a population. Decreased mean size may also be due to size-selective fishing mortality, focused on larger fish, and potentially can lead to evolutionary change over relatively short time scales, especially for short-lived species such as forage fish (Conover *et al.* 2005). However, recruitment of large numbers of young fish as a result of a strong year class can also reduce mean age or length of the catch. Thus, including recruitment data in length-based management rules is important. Age-specific body size might be used to measure density-dependent growth responses (Lorenzen and Enberg 2002) and might thereby be a useful basis to develop an empirical indicator of stock status.

Reproductive output—When reproductive conditions for forage fish are poor, fishing effort may need to be reduced to prevent population collapse. Stock biomass by itself may not be a reliable indicator of probable recruitment, particularly under shifting environmental conditions. Generally however, a reduction in egg production (e.g., gonadal mass), maturity, physiological condition, and egg quality are indicators of poor conditions for reproduction. Therefore, monitoring the condition of adults and their offspring can provide information that may be of use in predicting recruitment, and therefore future stock status.

Predator condition and reproductive success—If a measure of the condition of predators (e.g., fat reserves or mass per length) declines, then predators are undernourished and, in general, fishing effort on forage species should be reduced. Similarly, if predator reproductive success is declining, then predators may be stressed because of a shortage of food, and fishing effort on their prey should be reduced (see Box 3.1 and Appendix B* for a more detailed description of how these relationships can be quantified and applied to management).

Studies have shown that seabirds are particularly sensitive to changes in food supply and can be indicators of the health of local fish stocks (Cairns 1987, Davoren and Montevecchi 2003, Velarde *et al.* 2004). Decreased food availability (Boersma 1978, Cury *et al.* 2011), or an increase in foraging distance (Boersma and Rebstock

Figure 3.1
Foraging-trip distance predicted Magellanic penguin reproductive success in Punta Tombo, Argentina. (Boersma and Rebstock 2009.)



2009) can result in a decline in seabird reproductive success. For example, Magellanic penguins in Punta Tombo, Argentina, exhibit a decrease in mean reproductive success as foraging trip distance increases (Figure 3.1). Fisheries can also act as a direct competitor of seabirds, reducing their prey. Bertrand *et al.* (2010), using vessel monitoring data and electronic tracking of Peruvian booby and guanay cormorants, showed that seabirds forage farther and longer to mitigate the effects of fisheries competition, and may even abandon their nests if competition with a fishery is intense. Fisheries afford benefits to some species (kleptoparasites and scavengers), but exact both direct and indirect costs to others (pursuit-divers) (Wagner and Boersma 2011).

A recent empirical analysis using the most comprehensive global database yet assembled quantifies the effect of long-term fluctuations in food abundance on seabird breeding success (Cury *et al.* 2011) around the world. Based on a meta-analysis that included 438 years of observation, the authors identified a threshold in prey abundance (sardine, anchovy, herring, capelin, and krill, termed “forage fish”) of one-third of the maximum prey biomass observed in the long-term studies. Below the computed threshold, the 14 seabird species examined

* www.lenfestocean.org/foragefish

Box 3.1

How Do Predators Respond to Declines in Prey?

Predator response to a change in prey abundance depends on a variety of factors in the predator-prey relationship. Some of these include the amount of time and energy a predator uses to find, capture, and consume prey; the ability to adapt foraging strategies in response to lower prey abundance; and whether prey are easier or harder to capture as they become more scarce. Quantifying these relationships remains a challenge. An alternative approach is to examine the relationship between prey density (or total biomass) and predator population characteristics which are linked to foraging success, such as reproductive and survival rates, growth rate, or the size of a breeding population.

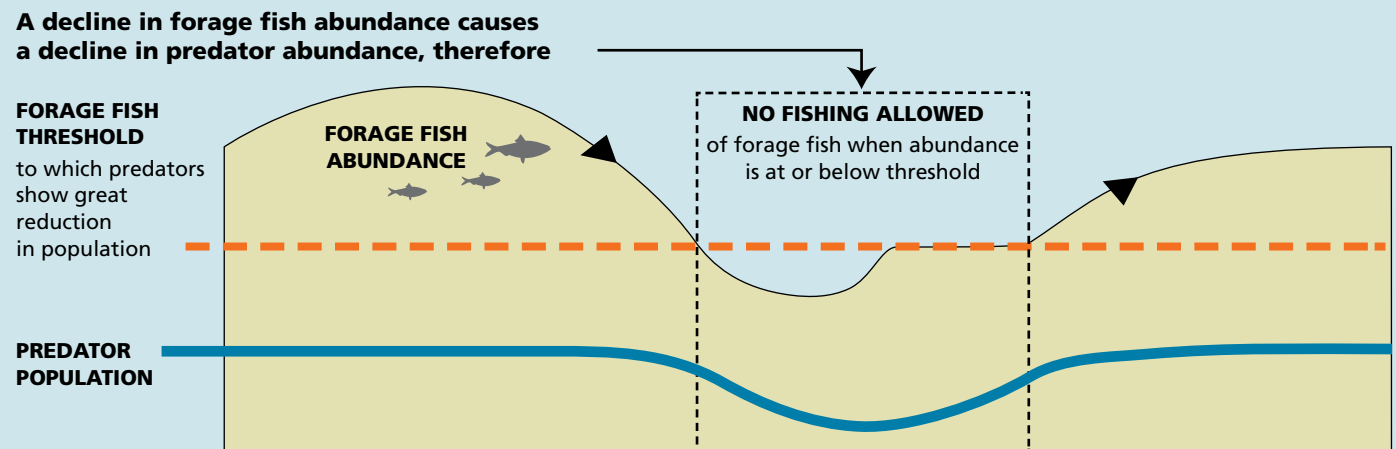
Evidence is mounting that a few generalized types of “functional responses” first presented by Hollings (1959) are playing out in the real world. Fast-growing, short-lived predators generally respond to more prey in a basic linear fashion—increasing with the increase in prey availability. Long-lived predators with few offspring show increases in key population parameters as prey biomass increases up to a point where either prey saturation or predator adaption takes effect. Saturation

can occur when prey biomass reaches a point where predators no longer have the capacity to take advantage of the additional prey by growing or reproducing more. Predator adaptation results in a similar response but for a different reason. In this scenario, predators are able to adapt their foraging strategies as prey biomass decreases from a theoretical high, allowing them to maintain foraging success in the face of declining prey numbers up to a point when their adaptations can no longer compensate for the decline in prey.

Given our increased understanding of these relationships, it becomes possible to introduce new management options that take these responses into account. Many of the functional responses measured with respect to forage fish indicate that forage biomass falls to fairly low levels before a significant decline in predators is observed, but that the predator decline is dramatic when it does occur (Figure 3.2). By establishing a forage fish biomass harvest threshold above the point of major predator declines, fisheries could be managed in an ecosystem context that responds to real-world predator-prey relationships. Further explanation can be found in Appendix B.*

Figure 3.2

This kind of threshold could be used to decide whether or not fishing should be allowed when the management objective of the fishery is to maintain populations of other species in the ecosystem that depend upon a forage fish species.



experienced consistently reduced and more variable productivity. This response appears to be common to all 7 ecosystems investigated within the Atlantic, Pacific, and Southern Oceans.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) considers the needs of dependent predators when setting quotas for krill. Interpretation of dependencies from long-term monitoring of upper trophic-level predators is typically complicated by issues of scale and environmental influences, but changes in krill abundance are reflected in broad ecosystem responses (see Reid *et al.* 2005). However, it should be recognized that predator condition has drawbacks as an indicator of forage fish overfishing. There are often multiple causes of reproductive failure, and overfishing of one forage fish species could be masked by the increased abundance of an alternative prey species for the predators. In general, size, reproductive output, and predator performance indicators can be influenced by factors outside of the fishery and can be easily confounded by local effects. Although they need to be developed with care, indicators of predator condition have the potential to be precautionary indicators through which fisheries could be managed when there is little alternative information available about fish biomass. In addition, they are implicitly an ecosystem-based approach to management because they manage the fishery with respect to its effects upon components of the ecosystem other than the exploited species.

Management Based on Reference Points from Stock Assessments

Stock assessments underlie most current approaches to fisheries management. Conducting stock assessments involves fitting time-series data, usually reflecting some important subset of the population to a quantitative model of the fish population, allowing estimations of the stock size and how it has changed through time. By their nature, these models are retrospective and the extent to which they can predict future trends is therefore limited. The predictive power of models is influenced by uncertainty about vital rates (survival rate, reproductive rate, growth rate) and how they vary with

other factors, including the state of the environment, the size of populations of other species that compete for food, the number and diversity of natural predators of the focal forage fish population, and the abundance of alternative forms of prey the natural predators have available to them. In addition to these factors, which are often unknown, often unquantified, and rarely taken in to account, there is uncertainty in the data used to derive the dynamics of a forage fish population. This type of uncertainty is often dealt with using sub-models describing the dynamics of the stock, the observation process (e.g., accuracy and precision of survey data), and the catch processes (e.g., type and timing of fishing and monitoring of catch). Although these models are generally used to predict the response of a population and the catches it will yield over time as a consequence of a given harvest strategy (for reviews see Hilborn and Walters 1992, Walters and Martell 2004; for a specific example see Alonzo *et al.* 2008), the uncertainties they contain when used in a predictive context are often greatly underestimated. However, despite their underlying problems, they often form the basis for sets of rules used to manage fish stocks that are exploited (e.g., reference points and control rules).

Reference points based on age-structured approaches—As techniques to estimate the age of individual fish in catches advanced, stock assessments initially relied on abundance-at-age and age-specific fishing mortality rates as reference points for stock and fishery status. These reference points were commonly derived from catch-at-age models, such as virtual population analyses (VPAs), which use catch data to reconstruct the dynamics of individual cohorts as they pass through a fishery. The assessments and management advice for most of the world's major forage fisheries are now conducted using age-structured approaches (Barange *et al.* 2009). Age-structured approaches typically result in quotas that are lower than were historically determined from assessments lacking age-structure. However, this is a single-species approach to fisheries management that does not account for ecosystem effects.



Fish drying on a net in Canary Islands, Spain, © Shutterstock.

Constant targeted yield or fishing mortality: MSY approaches—One of the most common goals of fisheries management has been to obtain maximum sustainable yield (MSY) as a target or limit (maximum) level of catch, calculated on the basis of specific reference points derived from a stock assessment. In circumstances where catch stability is highly desired, a maximum constant yield strategy may be adopted. In this approach a constant amount of catch is taken each year, regardless of fluctuations in target species population size. Thus a constant yield strategy can be quite risky, particularly for forage fish. If the constant catch level selected is too high for some periods, a rapid population collapse can follow. An alternative, commonly used strategy is to use a fixed fishing mortality rate (F_{MSY}) that gives the theoretical long-term MSY (e.g., Clark 1991). A constant F_{MSY} approach harvests the same fraction of the population each year, requiring annually updated assessments, and thus the amount of harvest can vary across years due to interannual variability in productivity. Modified constant yield or fishing mortality approaches that are conditioned on the environment as originally defined by Ricker (see Mangel *et al.* 2002 for further

detail) may provide less risky and more appropriate harvest strategies for forage fish, which are known to fluctuate in concert with environmental factors. In the California Current (Chapter 4), while fishing beyond the productivity of the stock likely contributed to their collapse, both sardine and northern anchovy show marked cycles of abundance that are likely tied to environmental variability (Baumgartner *et al.* 1992; also see Box 1.2 on variability). The inclusion of predation in population and ecosystem models is another advance that typically results in more conservative estimates of biological reference points such as MSY (Worm *et al.* 2009, Tyrell *et al.* 2011).

Spawning potential approaches—An alternative to MSY-based approaches is to set reference points based on the target species' spawning potential. This approach³ is an extension of the Beverton and Holt (1957) yield-per-recruit approach which uses information about growth rates, the natural mortality rate, and spawning biomass per recruit (which is how fisheries science often summarizes the fecundity rate used in the context of classical population dynamics). Historically, a common choice for target yield from an exploited fish

³. In this approach, Y_e and F_e denote the targeted yield and fishing mortality, respectively and $SPR(F)$ the spawning biomass per recruit (i.e., the average mass of spawning fish, taking growth and survival into account) when fishing mortality is F . Applying these methods generally requires estimates of unfished biomass B_0 and natural mortality M , which are estimated from separate analyses such as stock assessments.

stock is based upon the idea that the fishery should take only a small proportion of the amount of fish that die naturally each year (Equation 1).⁴ A further consideration for the choice of fishing mortality is to find the appropriate value for the proportion of natural mortality that can be taken by a fishery such that the reproductive capacity of the population is not reduced as a result of fishing (Equation 2).⁵ Alternatively, fishing mortality can be set as a fraction of the natural mortality rate (Equation 3)⁶ without considering the biomass of the stock. However, one problem with the latter approach is that when natural mortality increases, fishing mortality should be reduced to maintain total mortality below a target level (Equation 4).⁷

Both these approaches (fishing level set relative to absolute natural mortality or fishing level set relative to the natural mortality rate) require very good information about natural mortality, which may vary by age and over time. Except in very specific circumstances this is difficult to obtain, and the natural mortality rate is often a best guess. Sometimes, it can be estimated from stock dynamic models such as VPA, but in these circumstances it remains sensitive to biases in other parameters within the models.

Variable F determined from a biomass-fishing mortality control rule—This involves the use of a control rule that adjusts fishing mortality based on the current stock status relative to a target level and that appropriately limits fishing to ensure that the stock does not fall below a threshold level (Figure 3.3). Typical control rules are:

- There is no fishing if the fish stock biomass is below a threshold biomass.
- The fishing mortality rate increases (perhaps linearly, as with a “hockey stick” control rule; see Chapter 6) toward the target fishing mortality rate when the fish stock biomass is below a target biomass and presumably above the threshold biomass.

- The fishing mortality rate is set at the target fishing mortality rate when the fish stock biomass is at or above the target biomass.

The challenge is to select appropriate threshold and target biomass levels, as well as target and threshold levels of fishing mortality (Hilborn 1985, Hilborn and Walters 1992, Walters and Martell 2004, Clark 2006). A strong criticism of this approach is that setting thresholds and targets still requires use of the same kind of information—often insufficient—needed for other approaches. However, this approach has the advantage that it is possible to set the thresholds and targets in a precautionary way, and it can be refined based upon experience of managing a fishery. A commonly applied set of rules is to fix the lower biomass threshold ($B_{\text{threshold}}$) at one-fifth (20 percent) of the predicted biomass when there is no fishing (B_0); and to set the target biomass (B_{target}) between 40 percent and 60 percent of B_0 . F_{target} is the fishing mortality rate required to achieve B_{target} , and does not exceed F_{MSY} (Witherall 1999 and NMFS 1998). Restrepo and Powers (1999) recommend a target rate of fishing mortality of 75 percent of F_{MSY} .

In Australia, fisheries managers use B_{MEY} as the target (the stock size required to produce maximum economic yield, with a proxy of $B_{\text{MEY}} = 1.2 B_{\text{MSY}}$). The default biomass limit (threshold) reference point is $B_{\text{LIM}} = 0.2 B_0$ (AFMA 2007). In the U.S., the Magnuson-Stevens Fishery Conservation and Management Act does not require the use of biomass thresholds as a precautionary tool, but they are often used in individual fishery management plans (see, for example, the California Current case study, Chapter 4).

Recently, Froese *et al.* (2011) proposed harvest control rules that use a target biomass of $1.3 B_{\text{MSY}}$ (corresponding to about 65 percent B_0) and a limit of $0.5 B_{\text{MSY}}$, where a TAC is set to achieve the target and is reduced linearly if the stock is below B_{MSY} . The authors suggest that for forage fish, a more precautionary biomass target

4. Equation 1: $Y_t = \epsilon MB_0$ Suggested ϵ ranges for this proportion are from 0.15 to 0.5 (Gulland 1983, Clark 1991, Dorn 2002).

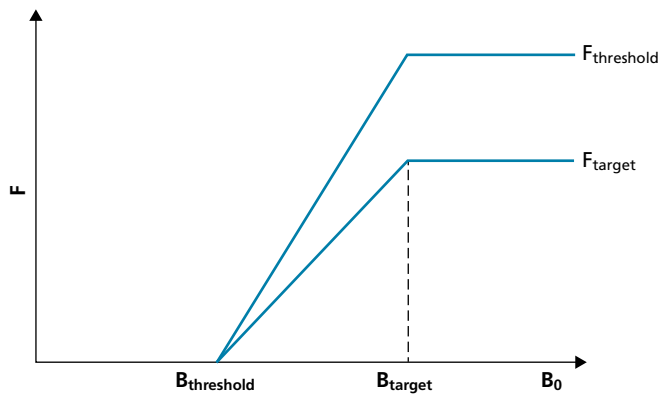
5. Equation 2: $SPR(F_t) = \epsilon SPR(0)$ with the same range of values on (Clark 1991).

6. Equation 3: $F_t = \epsilon M$

7. Equation 4: To keep total mortality constant at a target level, while natural mortality changes, the fishing mortality in year t when natural mortality is $M(t)$ is given by $F(t) = \max[Z_{\text{tar}} - M(t), 0]$.

Figure 3.3

Diagram of a harvest control rule that specifies the fishing mortality as a function of the stock size. Fishing mortality is zero below $B_{\text{threshold}}$ and linearly increases to $F = F_{\text{target}}$ as the population increases to B_{target} .



of $1.5 B_{\text{MSY}}$ (representing 75 percent of unexploited biomass) is probably needed. Further, Froese *et al.* (2011) state that, if implemented, these rules could have prevented the collapse of the North Sea herring in the 1970s and could have dealt with strong cyclic variations in recruitment for species such as blue whiting.

Management Based on the Use of Biomass Thresholds

A harvest threshold system in which a minimum stock biomass must be present before a fishery can occur—or which halts a fishery when that level is approached—has been used to manage a number of forage fisheries. Such a system protects forage fish and dependent predators when biomass is low. Other “simple” biomass thresholds are based on values of spawning stock biomass that have been observed to cause declines (see the Humboldt Current and Barents Sea case studies, Chapter 4), while others are more complicated, with thresholds coupled to variable metrics, such as egg biomass and temperature (examples below). We find biomass thresholds⁸ to be an

important management tool that can be derived from a variety of methods (see Table 4.1) and can provide precaution to account for ecosystem concerns.

Krill in the Antarctic: The use of precautionary biomass thresholds—The first, and perhaps most well-known example of the use of a precautionary biomass threshold was implemented in the Antarctic by CCAMLR for krill (see Antarctic case study, Chapter 4). As the major forage species in the Antarctic, it is managed to preclude depletion below 75 percent of its unfished biomass. Managers chose this threshold because it is considered conservative, falling halfway between 50 percent depletion (which is a biomass level associated with MSY yields for simple population models) and unfished levels (i.e., total precaution). The rationale for setting a conservative threshold included consideration of very poor information about the biomass of krill, with a survey conducted about once every 10 years, and the relatively poor understanding of the distribution and movement of the stock.

Herring in Alaska: The use of a harvest threshold biomass based on egg surveys—Herring (*Clupea harengus*) are unusual among forage fish because of their spawning aggregations. A combination of egg surveys on the spawning grounds and knowledge of body mass-egg production relationships, sometimes coupled with acoustic surveys, can provide an estimate of spawning biomass that has some level of cross-validation. Southeast Alaska herring fisheries are managed using a harvest threshold system; a minimum stock biomass must be present before fishing can take place. The minimum threshold biomass necessary for a fishery varies among herring stocks and is based on estimates of historical abundance (e.g., Carlisle 1998) with the intention of keeping the stock within the historical bounds of variation. For example, thresholds for the six sac-roe fisheries in Southeast Alaska vary between 2,000 and 25,000 tonnes of spawning biomass. Estimates of current herring spawning biomass are derived from annual surveys of herring abundance and

⁸ Even though biomass thresholds are often used, it is important to clarify that in many cases biomass is estimated without validation, and estimates of error within surveys is often confined to particular sources, such as the error that can derive from acoustic backscatter. Many other sources of error, which can produce biased estimates of biomass, are poorly described. A common problem with operational fisheries management is that it normally has to proceed under the assumption that the estimates of biomass made independent of the fisheries is unbiased.



Cormorant diving for herring.

age- and size-composition. Forecasts of the next year's spawning stock biomass are derived from age-structured analysis (for stocks with sufficient historical data) or biomass accounting methods (for stocks with little historical data). If the estimated biomass is below the minimum threshold B_{TH} , no fishery occurs. If biomass is above the threshold, allowable harvest is calculated on a sliding scale between 10 and 20 percent of the forecasted spawning stock biomass. When spawning stock biomass is at the minimum threshold level, a 10 percent harvest is allowed. Allowable harvest increases linearly with forecast spawning population size. In this case, the harvest level is allowed to reach a maximum of 20 percent when the biomass is six times the threshold level. Stocks with more than six times the threshold biomass are harvested at 20 percent. Larger, migratory herring populations in this region appear to be sustainable, but some smaller populations are closed to fishing due to low stock levels, although it is unclear whether these levels are a result of the environment or fishing.

Sardines in California, Oregon, and Washington: The use of a harvest biomass threshold with an explicitly coupled environmental variable—The catch for sardines (*Sardinops sagax caerulea*) in the California Current off the continental United States is also regulated by a threshold harvest system (California Current case study, Chapter 4). For the next year, the harvest is set as the current biomass minus an offset of 150,000 tonnes, which is the lowest level of estimated biomass at which harvest is allowed. This is reduced further by a factor that is empirically defined because of

the established relationship between water temperature and sardine biomass. The total is then reduced again to account for the amount of fish in the population that is outside the jurisdiction of the management regime, and this is assumed to be a constant. This approach is thought to provide the fishing mortality associated with MSY (Hill *et al.* 2009). Thus, the sardine harvest guideline is explicitly coupled to changing sea surface temperature, to which responses of fish have been documented (MacCall 1990). Recently, an analysis of the correlation between recruitment and temperature showed that temperatures have been much higher overall, and temperature is no longer a good indicator of productivity (McClatchie *et al.* 2010). The Pacific Fishery Management Council's Coastal Pelagic Species Management Team is currently planning an evaluation of alternative models for setting ecosystem-based cutoffs for forage fish harvest.

Management Based on Potential Biological Removal Principles

Given the many uncertainties around the fisheries management approaches described so far, we offer a new theoretical approach that may prove useful for forage fish management. This approach is adapted from Potential Biological Removal (PBR) methodology and is referred to as the "Forage Fish Control Rule." Unlike most other approaches, which require considerable amounts of information about fish stocks and the factors affecting fish stock dynamics, the PBR methodology has the advantage that it requires estimates of relatively

few parameters (growth rate, biomass, and the number of major dependent predators). It was conceived during the renewal of the U.S. Marine Mammal Protection Act in the mid-1990s as a means to address incidental take of marine mammals by fisheries (Wade 1998), and was developed as a tool for guiding management decisions where there is little specific information about the size or dynamics of the population. However, the PBR method lends itself to a more general application in resource management, and in the last dozen years it has been used to limit the number of marine animals that can be taken from a population as a direct result of a broad range of human activities. Unlike most of the other fisheries management approaches that start from a presumption of maximizing yields, PBR starts from a presumption of precaution.

The methodology built around the PBR approach and that is suggested here has a number of features that make it attractive for use with forage fish:

1. incorporates biological realism,
2. accounts for predators of the forage species, including humans,
3. prevents a population from falling below its observed natural range of variation,
4. includes parameters that can be estimated,
5. allows for the incorporation of uncertainty, and
6. is simple.

This new harvest rule—designated the “Forage Fish Control Rule”⁹ Y_{FFCR} —embodies the same kind of properties as PBR, but is designed to deal with the specifics of forage fish. It sets the harvest level for a particular year relative to the apparent amount of fish available at the time which is specified by establishing the difference between the current biomass and the lowest biomass that has been measured or could be expected through history. This amount of fish is then converted to a notional exploitable biomass by establishing how much it is likely to grow in the next year.

⁹. Equation 5 specifies the harvest Y_{FFCR} , where $Y_{FFCR} = \max\left(0, \frac{C_u}{N+1} \times \frac{r}{2} \times (B - B_{\min})\right)$

In this equation, C_u is a conservation factor, between 0 and 1, that accounts for uncertainty in the other parameters. N is the number of predator species for which the focal forage fish is a major component (i.e., 50%) of the diet, r is the maximum per capita growth rate (so that $r/2$ is per capita growth rate half of carrying capacity for a logistically growing population), B is the minimum estimate of current biomass, and B_{\min} is the minimum estimate of biomass through history due to natural fluctuations. If $B < B_{\min}$, then the catch rule sets the yield equal to 0.

In many ways, this is similar to determining the maximum sustainable yield, although the philosophy being proposed is one of minimizing risk rather than maximizing yield. This exploitable biomass is then reduced by a “conservation factor” which is a proportion between 0 and 1 (C_u). This can be chosen based upon simulations (Wade 1998) showing the different levels of risk associated with each choice of value for the conservation factor. However, we also suggest that, as part of this process of choosing the value of the conservation factor, it should be reduced (increased precaution) in accordance with the number of other predators that feed upon the exploited fish species, and perhaps weighted by the biomass of each predator. This would mean that the greater the number and biomass of predatory species that depend upon forage fish for at least 50 percent of their dietary energy, the smaller the catch of the exploited species should be.

The combination of the number of predators and the lower limit of stock biomass are the most important innovations in this approach. They capture notions of Fowler (2009) that humans should be considered as another predator and that the population should not fall below its natural range of variation. The main drawbacks of this approach are the sensitivity to the population estimates, the fact that the growth rate (r) may change over the long term due to ocean conditions (or other environmental factors) and to the depletion of top predators, and the difficulty in determining an appropriate choice for the parameter C_u . The appropriate value of C_u to achieve fishery production combined with protection of dependent predators can be explored by simulation testing. While this testing has not yet been conducted for the Forage Fish Control Rule, experience with the PBR approach has shown that low values of C_u (i.e., <0.5) should be used when there is large uncertainty associated with estimates of the other parameters.

Management Based on Temporal and Spatial Approaches

Temporal and spatial management refers to any action that limits fishing activities based on season or location. Temporal and spatial quotas can limit total catches within a time period or region, while time and area closures prohibit fishing during specified time periods and/or in certain regions. Spatial closures that permanently prohibit directed fisheries or other harmful activities are often called no-take reserves. No-take reserves can be used as a way to manage fishing effort in circumstances where other controls (e.g., gear restrictions, days at sea, quota management) are not feasible (Mangel 2000a). When temporal and spatial management (and no-take reserves, in particular) limit fishing mortality, they may provide a hedge against inaccurate stock assessments that can lead to unsustainable harvest quotas. Spatial and temporal management of this type also has the advantage that it can be simpler, cheaper, and more effective to enforce because it helps to focus enforcement effort in time and space.

There is a rich and largely theoretical literature on how permanent spatial closures might benefit fisheries by offering protection against overfishing (e.g., Beverton and Holt 1957, Demartini 1993, Mangel 1998, Crowder *et al.* 2000, Gerber *et al.* 2003, Moffitt *et al.* 2009). A central point of discussion has been the size and structure of reserve networks that best meet fisheries objectives and how these depend on population dispersal characteristics (Botsford *et al.* 2003, Gaines *et al.* 2010). Temporal and spatial management can be used to prevent strong selectivity of fishing fleets for particular sizes or sub-populations that have unique life history traits. For example, catch or effort quotas can be defined for individual regions and/or time periods so that fishing effort is not focused intensively on particular stocks or during time periods when populations are particularly vulnerable to fishing gear (e.g., spawning aggregations). This latter point is particularly relevant for forage fish, whose spatial ranges often expand when populations are large and contract when populations are small (MacCall 1990, Fréon *et al.* 2005) so that fleets may maintain high catches—and unsustainable exploitation

rates—on small populations by focusing effort on the core areas of population ranges.

Some predators depend upon the availability of dense aggregations of forage fish and invertebrates during critical life history stages. Fishing activities in feeding grounds can have multiple adverse impacts on predators. First, fishing can cause local depletion of populations whenever exploitation rates greatly exceed the dispersal and local production capacities of forage fish populations. Second, the process of fishing (e.g., purse seining, mid-water trawling) can cause fish aggregations to disperse, or otherwise diminish predator feeding opportunities (although there are situations in which these also increase predator food intake rates because some predators opportunistically exploit the activities of fisheries). Temporal and spatial management to preserve the ecological roles of forage fish may be required in cases where predators are deemed to be dependent on localized prey resources and when fishing is suspected of causing localized depletion of forage fish.

Key considerations in using temporal and spatial management include:

- What is the capacity of fishing activities to reduce foraging opportunities of dependent predators (at appropriate ecological time scales)? Are dispersal and local production rates of forage fish populations sufficiently low that temporal or spatial management would enhance prey availability near critical habitats at ecologically relevant time scales?
- How dependent are forage fish predators on the local density of forage fish, specifically as manifest in population numerical (demographic) responses?
- How might a fishery redistribute fishing effort in time or space in response to time-space restrictions and what might be the consequence of that effort reallocation to the forage fish population and fishery?

Only through careful scientific assessment can these questions be answered to ascertain if temporal or spatial management will succeed for the case of interest. However, temporal and spatial management can also be used as a precautionary management tool when the



Requiring a minimum biomass of forage fish, and implementing temporal and spatial management measures, are ways to protect both the forage base and dependent predators.

Steller sea lions, California, NOAA.

above information can't be determined, or to regulate fishing effort in fisheries when quota management advice might be imprecise or ineffective. Below, we offer four examples of temporal and spatial management that have been implemented to protect the forage base or dependent predators.

*Steller Sea Lions (*Eumetopias jubatus*) in the Aleutian Islands and eastern Bering Sea*—The western population of Steller sea lions was listed as endangered under the U.S. Endangered Species Act in 1997, following declines mainly during the 1980s. There are multiple hypotheses to explain the decline and continued low population status and these are still actively debated (National Research Council 2003, Wolf and Mangel 2008, Boyd 2010). One hypothesis put forth is that shifts in the fish community, coupled with directed fishing for walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) in the vicinity of rookeries and haulouts might be reducing foraging opportunities and inducing nutritional stress. Several changes to fisheries management were introduced in 2002 to reduce the possibility of fishing operations affecting sea lions (National Marine Fisheries Service 2003). These included prohibitions on fishing during specific times and in specific locations and the protection of near-shore areas that might be critical foraging areas for juvenile sea lions and for mothers during the early stages of pup rearing. The Steller Sea Lion Conservation Area (SCA) was established, a large region north of the Aleutian Islands in the Bering Sea, where harvest limits for walleye pollock are set at conservative levels.

It has been difficult to evaluate the success of these temporal and spatial management measures on Steller

sea lion recovery. Rates of decline of the western population of Steller sea lions have slowed since conservation measures were introduced and populations continue to increase in other regions where there are no specific spatial and temporal fisheries management measures to protect sea lions. There continues to be a robust debate regarding the evidence for nutritional stress as a causative agent in the population decline and the extent to which fishing closures have had a detectable impact on local prey availability. For example, if nutritional stress is present, it is not clear if it is due to high levels of pollock in the diet (Wolf and Mangel 2008) or too little of something else (e.g., herring). This is a case in which careful scientific inference is needed before one can assess the effects of spatial management (Mangel 2010). It also remains likely that, in this case, spatial management is being introduced as a precautionary measure when the underlying causes of Steller sea lion decline may well lie elsewhere.

*African Penguins (*Spheniscus demersus*) in the Benguela*—Sardine and anchovies are important prey items for African penguin populations off Namibia and South Africa (Crawford *et al.* 2006, Underhill *et al.* 2006); field measurements in the vicinity of Robben and Dassen islands off the west coast of South Africa indicated that about 82 percent of their diet is comprised of these two forage species (Hockey *et al.* 2005). An increase in penguin numbers during 2000–2004 occurred simultaneously with a period of high pelagic fish abundance (Crawford *et al.* 2006). However, following recent apparent reductions in overall fish biomass (de Moor *et al.* 2011) and an eastward shift in sardine biomass, there have been substantial reductions in the numbers of penguins in most of the South African colonies. African



Ecosystem-based management of forage fish will likely require a blend of strategies and greater precaution when knowledge is limited.

African penguins, South Africa, © C. Whitley.

penguins may be particularly sensitive to changes in abundance and distribution of prey because of their land-based breeding requirements (e.g., Crawford *et al.* 2006); severe decreases of African penguins occurred in Namibia due to an altered distribution of prey (Crawford *et al.* 2001). A lack of available food is thought to be the main cause of higher adult mortality and lower breeding success in recent years.

In response to the deteriorating status of African penguins, the Dassen Island region was experimentally closed to purse-seine fishing (20 km radius) in 2008 and 2009, and the Robben Island region was left open to fishing to examine the differences in the response of penguins in the two regions. In addition, St. Croix Island, where there were also breeding colonies of penguins, was closed to purse-seine fishing (20 km radius) during 2009 and 2010, and a nearby penguin colony at Bird Island, where there was no fishery closure, served as the control. Pichegru *et al.* (2010) found that foraging effort decreased by 30 percent within three months of the closure at the start of 2009, and they concluded that small no-take zones might have immediate benefits for breeding penguins. Coetzee (2010) and Butterworth *et al.* (2011) suggest that this result is premature because there was very little fishing around St. Croix in 2008 (before the area was closed), hence differences in foraging effort may have reflected natural variability rather than impacts from the fishery, and that even though Dassen Island was closed in 2008 and 2009, penguins declined, in contrast to Robben Island where numbers remained stable despite the presence of fishing. Ryan *et al.* (2010) responded that birds at Dassen Island may suffer more from reduced prey availability for a number of reasons and that even “low levels” of commercial fishing may be enough to affect fish abundance and

hence availability to penguins. Thus, in the short term, it may be difficult to clearly demonstrate the costs of a fishery to competing predators even using experimental approaches. In fact, the underlying problem of studying these effects is well illustrated by this study and the inconclusive outcome. The apparent treatments where fishing was excluded or allowed were almost certainly so different that the chances of discerning an effect in just two years were probably unrealistic. It is likely that experiments of this type would need to be conducted over time scales of decades and also at much larger spatial scales in order to understand the interaction between seabirds, such as penguins, and fishing.

North Sea Sand Eel (*Ammodytes marinus*)—The sand eel fishery expanded rapidly in the North Sea beginning in the early 1970s, reaching 800,000 mt/year by 1977, and fluctuated around that level until it was closed in 2009 (see the North Sea case study, Chapter 4). The apparent dependence of several seabird populations on sand eels, as measured through correlations between breeding success and local sand eel density (Monaghan *et al.* 1989, Rindorf *et al.* 2000, Richerson *et al.* 2010) suggests the potential for competition between the fisheries and seabirds. At the scale of the entire North Sea, the sand eel population exhibited an increasing trend, expanding nearly two-fold from 1975 to 2000 (Furness 2002). During that same period, counts of breeding numbers for multiple seabird populations also increased (Furness 2002).

In 1999 and 2000, a large region of the North Sea along the coast of Scotland was closed to sand eel fishing. Daunt *et al.* (2008) documented changes in sand eels age 0+ and 1+ in this region, as well as changes in the consumption of sand eels by seven species of seabirds. They

noted a strong increase in age 1+ sand eel populations beginning in 2000 and a general trend of increasing consumption of sand eels by seabirds. Annual breeding success of black-legged kittiwake, a species known to be highly dependent on sand eels (Furness and Tasker 2000), was positively related to sand eel abundance (Daunt *et al.* 2008). Daunt *et al.* concluded that the fishery closure had positive ecological effects but noted that it was difficult to attribute the entire response to fishery closures, as environmental changes leading to strong sand eel recruitment could also have played a role.

A key feature of sand eel biology is their dependence on patchily distributed sand substrate that creates the potential for low dispersal among post-settlement individuals. Thus, fisheries can potentially induce localized depletion, despite having relatively minor effects at the entire stock scale (synchronous patterns of recruitment suggest high rates of larval and pre-recruit dispersal). The fishery largely targets age 1 and older sand eels and occurs mainly during late spring when seabirds may depend on age 0 sand eels near breeding locations (Rindorf *et al.* 2000, Frederiksen *et al.* 2004). Sand eel populations are also highly sensitive to climate variability (Arnott and Ruxton 2002, Frederiksen *et al.* 2004), so it is important to distinguish between bottom-up and fishery-induced top-down effects (Munch *et al.* 2005).

Antarctic Krill (*Euphausia superba*)—The Antarctic krill is a critically important species in the Southern Ocean. CCAMLR manages the krill fishery and has adopted an ecosystem-based, precautionary approach (Reid *et al.* 2005; also see Antarctic case study, Chapter 4). A key management principle of CCAMLR is that the effects of the krill fishery on predators should be reversible on a reasonable time scale, such as two or three decades. Annual catch limits are currently far below the estimated total krill biomass. Catch limits in the South Atlantic, southeast Indian Ocean, and southwest Indian Ocean sectors are 4.0 million mt, 0.44 million mt, and 0.45 million mt, respectively, while biomass estimates are 44.3 million mt, 4.83 million mt, and 3.9 million mt, respectively (Croxall and Nicol 2004; more details at www.ccamlr.org). The intention of such catch limits is to minimize the potential for ecosystem-wide depletion of the krill.

Current catches of krill are low; however, the demand for krill is predicted to increase. The precautionary catch limit set by CCAMLR aims to meet the needs of dependent predator populations, but there remains concern about the impact that an expanding fishery may have on krill predators especially with regard to space. Consequently, CCAMLR has recognized the need to subdivide the precautionary catch limit in the south Atlantic sector of the Southern Ocean into small-scale management units (SSMUs) to minimize the impact that the krill fishery has on krill predators (Hewitt *et al.* 2004) and to address concerns of localized depletion.

Summary

This chapter has described a wide variety of assessment and management tools that have been suggested and/or applied to forage fish fisheries. The choice of management tools to achieve ecosystem-based management of forage fish in a given situation will depend upon data availability and the associated level of uncertainty, for both target and dependent species. In general, management needs to be more precautionary as the level of uncertainty increases (Table 7.1, Chapter 7). Targets and limit reference points for forage fish need to be more precautionary than those that have been relied upon in the past (such as maximum sustainable yield); some new approaches described in this chapter (such as the Forage Fish Control Rule) may prove useful. In some of the cases described above, measures such as biomass thresholds or buffers were implemented because of a past observation of fishery collapse, and to prevent similar occurrences in the future. Consequently, we believe that establishment of a minimum biomass threshold is an essential element of sustainable forage fish management. Later in this report (Chapter 6) we explore the ramifications of using minimum biomass thresholds of various magnitudes, as well as other reference points using quantitative analyses of food web models. We found that temporal and spatial measures are also important tools for protecting forage fish and their predators. Ecosystem-based management of forage fish will most likely require a blend of strategies to ensure that policies are sufficiently risk-averse, and to prevent significant impacts to both the forage fish population and dependent predators.

4

Case Studies of Forage Fisheries

Strategies for forage fisheries management most often rely on a single-species approach and do not account for the vital role these fish play in marine ecosystems. However, some fisheries are exceptions. We have identified case studies and examples of fisheries that exercise precaution or illustrate ecosystem concerns. In some ecosystems, measures such as biomass thresholds or buffers were implemented because of a past observation of fishery collapse. In other cases, concerns have been raised that management is insufficient to address ecosystem needs.

The case studies are not intended to be comprehensive, exhaustive reviews of each marine system but rather are meant to highlight particular elements most relevant to the mission of the Task Force while providing a reasonable amount of background information for context. All figures for this chapter can be found in Appendix C.*

* www.lenfestocean.org/foragefish



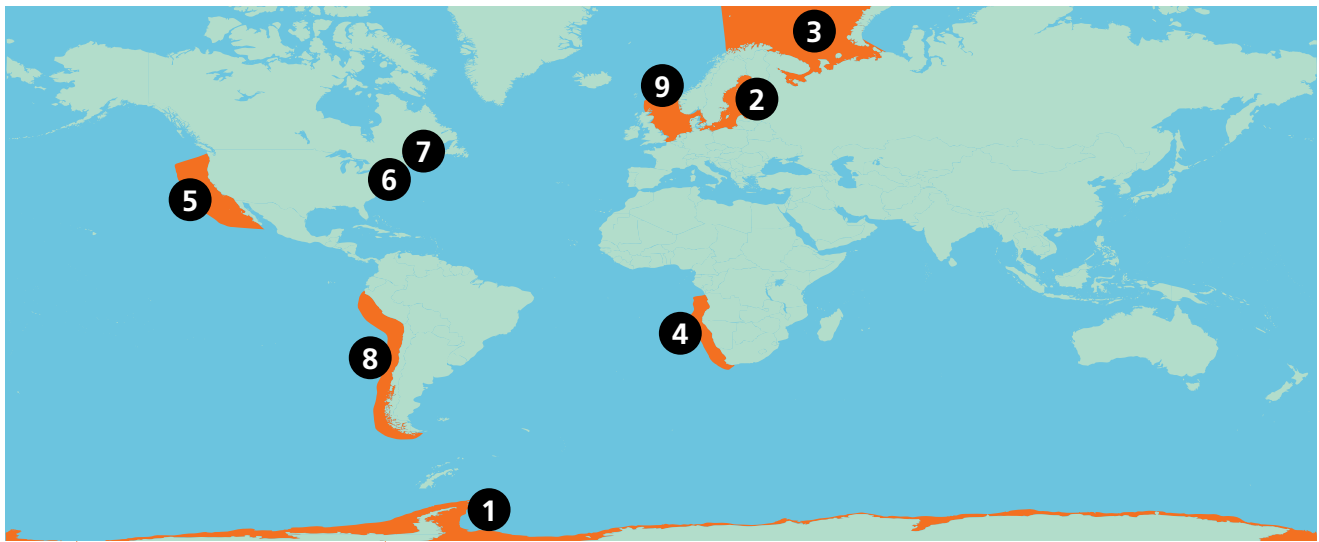
Case studies can provide useful information on lessons learned from past management mistakes, and on which measures are most effective for forage fish populations.

Humpback whale, © DAJ/Getty Images. Sardine shoal, background, © shutterstock.com.

KEY POINTS

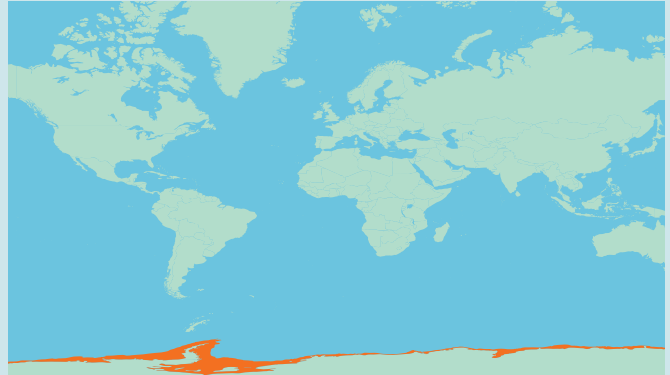
- Nine case studies illustrate the diversity of forage fish and their dependent predators.
- Some precautionary management is in place, but many fisheries lack strong regulation and monitoring.

Case Studies



Ecosystem	Lessons and concerns	Example Forage Species
1 Antarctic	Precautionary minimums at work: An international agreement requires krill biomass to be maintained at 75 percent of the estimated biomass without fishing in order to ensure there is food for penguins, seals, and other predators.	Krill 
2 Baltic Sea	Too much of a good thing: Proliferation of a forage fish called sprat has triggered a “trophic cascade,” allowing phytoplankton to increase. This has reduced oxygen levels, harming hatching of fish. Baltic nations are considering deliberate reduction of sprat.	Sprat 
3 Barents Sea	An effective threshold: To protect the world’s largest stock of cod, Norway and Russia prohibit capelin fishing if its biomass falls below 200,000 tonnes. Capelin collapses have not been repeated, and many fish stocks are now abundant.	Capelin 
4 Benguela Current	Effective catch limits: South Africa has set conservative catch limits for anchovy and sardines, and yields are now stable. On the other hand, the sardine population has collapsed off Namibia, where overfishing still occurs.	Anchovy 
5 California Current	A buffer against future crashes: Allowable catch of Pacific sardine based on maximum sustainable yield, but with a buffer of 150,000 tonnes. Pacific sardine crashed and then rebounded during the 20th century.	Pacific sardine 
6 Chesapeake Bay	Greater precaution needed: In 2011, menhaden fishing was limited to a level that would maintain 15 percent of maximum spawning potential, but more conservative measures are likely required to preserve menhaden’s crucial role as prey for striped bass, bald eagles, and others.	Atlantic menhaden 
7 Gulf of Maine	Rebuilding Atlantic herring: Atlantic herring declined precipitously in the 1970s but has increased since the early 1990s. Managers continue to reduce allowable catch to further rebuild the population.	Atlantic herring 
8 Humboldt Current	Impoverished but productive: The Peruvian anchoveta fishery, the largest in the world by volume, has recovered from collapses in 1972 and 1983. Managers now halt fishing if biomass falls below 5 million tonnes, but earlier anchoveta declines and other human activity have left the ecosystem greatly impoverished.	Peruvian anchoveta 
9 North Sea	Limits are not enough: While scientific advice is considered when setting catch limits, illegal fishing and discarding of herring at sea have pushed actual catch above the limit.	North Sea herring 

Antarctic Ecosystems: The Central Role of Krill



Ecosystem

Although the Antarctic marine ecosystem is remote, it shares with other regions a long history of over-exploitation of many of its marine resources (Constable 2004). Changes appear to be taking place at all levels in the ecosystem, from primary production to apex predators (Ducklow *et al.* 2007). Climate warming, a major driver in this system, appears to be happening more rapidly here than at lower latitudes and may be causing ecosystem changes (Boersma 2008, McClintock *et al.* 2008, Plagányi *et al.* 2011). Recent evidence of climate change includes consistent decreases in sea ice (IPCC 2007, Smith and Stammerjohn 2001, Stammerjohn *et al.* 2008 a, b), changing patterns of precipitation (Turner *et al.* 2005), and possible effects on krill-dependent species (e.g., Loeb *et al.* 1997, R.C. Smith *et al.* 1999, Croxall *et al.* 2002, Clarke *et al.* 2007, Ducklow *et al.* 2007, Murphy *et al.* 2007, Trathan *et al.* 2007).

Krill are critically important foundation prey that support large and diverse populations of seals, seabirds, whales, and other higher-level predators in this system. Krill life history is closely tied to the annual advance and retreat of sea ice around the Antarctic continent. During the winter months, krill survive on algae that grow on the underside of sea ice, and during the summer, they feed on plankton that blooms as the ice melts and they locate their nursery areas close to the

ice. As sea ice declines, krill habitat is shrinking. Many krill-dependent predators are also being affected by increased temperature and a loss of sea ice, though probably mostly through effects on their food supply. Penguins—important sentinels of environmental variation (Boersma 2008, Boersma *et al.* 2009)—are experiencing changes in spatial distribution, phenology, and predator-prey interactions (Forcada and Trathan 2009, Chapman *et al.* 2010, Trivelpiece *et al.* 2011). For example, there are indications that macaroni penguins (*Eudyptes chrysolophus*) may not be able to adapt rapidly enough to changes in climate and krill fishing (Cresswell *et al.* 2008). A recent study (Trivelpiece *et al.* 2011) has also shown that chinstrap penguin (*Pygoscelis antarctica*) populations may continue to decline as krill populations decrease in the Scotia Sea around their breeding areas in the West Antarctic Peninsula.

The Antarctic system is characterized by marked spatial and temporal patchiness in krill abundance (see, for example, Murphy *et al.* 1998) that is reflected in the reproductive success of krill-dependent predators (Reid 2001, Trivelpiece *et al.* 2011). Food availability is important to the many predators in the Antarctic. Changes in vital population parameters of marine mammals, as observed in the Southern Ocean, imply that their populations may be limited by food supply (Plagányi and Butterworth 2005). For example, if food availability falls below a certain threshold, seal and seabird populations



Antarctic krill, © Flip Nicklin/Minden Pictures.

are likely to exhibit increased juvenile natural mortality largely because of reduced body condition (see, for example, Boyd *et al.* 1995). Predators appear to selectively target krill even when it is present only at low levels (Boyd and Murray 2001). In addition, female Antarctic fur seals increase the duration of foraging trips in response to reduced availability of prey (Boyd 1999).

Fisheries

Krill have a fairly long but sporadic history of being harvested. Krill catches fell from peak levels (about 350,000 tonnes) when the Soviet Union split up in 1991 and subsidies ended. Since then, catches have remained around 100,000 tonnes, though there appears to be a small but consistent increase in recent years (Kawaguchi and Nicol 2007). Since the 1996–97 season, the fishery has operated only in the south Atlantic sector (Kawaguchi and Nicol 2007).

The fishery has also been limited to some degree by petroleum prices, which have swayed the economic balance between huge travel costs and a fairly low-value product. However, recent improvements in fishing technology and improved product value have given rise to concerns that an expanding krill fishery might harm the recovery of previously over-exploited populations such as large baleen whales and penguins.

Management

Fisheries in the Southern Ocean are managed by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). This international fishing agreement was the first to acknowledge the importance of maintaining the ecological relationships between harvested, dependent, and related populations of marine species. To account for the needs of predators in the system, a conservative reference level was set, where 75 percent of the pristine krill biomass is required to be maintained. This level represents a compromise between the optimal depletion level (50 percent, when assuming logistic growth) and the pristine level (100 percent, with no fishery).

Spatial catch limits have also been implemented. A precautionary catch limit of 4 million tonnes has been set for one particular area (Area 48); however, to prevent localized depletion, there is an additional cap of 620,000 tonnes, which cannot be exceeded until the catch is spatially subdivided. CCAMLR is engaged in research on the subdivision of the precautionary catch limit among 15 small-scale management units in the Scotia Sea to reduce the potential impact of fishing on predators (Hewitt *et al.* 2004, Hill *et al.* 2009). In this system, the policies enacted illustrate how the main forage species is valued as ecological support and not simply as a resource to harvest.

The Baltic Sea: An Impoverished Ecosystem



Ecosystem

The Baltic Sea is a brackish-water sea at the center of a large basin in north-central Europe. The fresh water forms a stable layer over the deeper, saltier water, which prevents mixing and results in a very low-oxygen environment in the central, deeper part of the sea. Such conditions are not conducive to high biodiversity, so the Baltic has lower biodiversity than the adjacent North Sea (Elmgren and Hill 1997).

The Baltic also suffers from human-induced eutrophication, documented since the onset of the 20th century, that has presented problems and challenges for the nine countries bordering the system (Elmgren 2001). In the southwestern Baltic, the lack of oxygen caused by this eutrophication has gradually reduced the areas suitable for successful hatching of marine fish eggs. Accordingly, successful recruitment of cod (*Gadus morhua*) is now linked with the occasional influx of marine water coming from the narrow waterways of the Skagerrak Strait, which links with the North Sea via the Kattegat Bay (Köster *et al.* 2005).

The simplified food web characteristics of the Baltic are caused by both natural and anthropogenic processes. The phytoplankton => zooplankton => sprat (*Sprattus sprattus*) => cod food chain is now dominant in the

southern Baltic. Sprat, a small clupeid, is a typical forage fish that, even though it is preyed by cod, also eats the eggs of cod. This sets up complex population dynamics in which each interacting species can be both predator and prey, depending upon the stage of the life cycle. Herring (*Clupea harengus*) sometimes play a role similar to that of sprat (Casini *et al.* 2008) in this food web, and they also eat cod eggs.

The recruitment of cod appears to be increasingly erratic and is linked to occasional influxes of North Sea water. Adult cod are subjected to an intense fishery, which has led to a decline in predation of the zooplanktivorous sprat by cod. As a result, sprat have proliferated, especially since the 1990s, leading to a multi-level cascade, documented empirically (Casini *et al.* 2008) and straightforwardly reproduced in simulations (Österblom *et al.* 2007). Here, the human-induced changes to higher trophic levels led to a reduction of grazing pressure



Baltic Herring, © Henrik Larsson/Shutterstock.



German fishing port, Baltic Sea, © Shutterstock.

on the phytoplankton, leading to an environment where eutrophication, already strong in the Baltic, was intensified.

Fishery

The fisheries of the Baltic Sea have recently been reviewed by Zeller *et al.* (2011) with an emphasis on previously unaccounted catches, which appear to have been 35 percent higher than officially reported from 2000 to 2007. Fishing has a major impact on the resources of the Baltic Sea. For example, cod and Gulf of Riga herring were considered overfished (ICES 2008), but more recently the status of the cod stocks has improved slightly, and catches are considered to be set in accordance with scientific advice (ICES 2010).

Management

The countries surrounding the Baltic Sea appear to be strongly committed to reducing eutrophication in this ecosystem and are contemplating various policy interventions to reduce sprat populations, which would allow the zooplankton population to increase and thus increase grazing on phytoplankton. Potential interventions include intensified direct exploitation, alone or in combination with a strong reduction of fishing mortality on cod, which would in turn result in intensified predation on sprat. The policy that is chosen

This example is unique in that there is an attempt to examine forage fish in the context of their predators, and policies may involve intentional reduction of forage fish.

(if any) would involve the deliberate reduction of the biomass of a forage fish—one of the few cases where such a measure might be considered beneficial to the ecosystem as a whole. This example is unique in that there is an attempt to examine forage fish in the context of their predators, where multi-species assessments account for changes in forage fish density (sprat and herring) based on predator abundance (cod).

Barents Sea: The “Capelin Limit Rule”



Ecosystem

The Barents Sea is a shelf-sea ecosystem in the Arctic, bordering the Norwegian Sea to the west and the Arctic Ocean to the north. It is a moderately productive, ice-edge ecosystem, strongly influenced by variable Atlantic Ocean inflow, alternating climate regimes, and ongoing climate change (Hunt and Megrey 2005, Gaichas *et al.* 2009, www.indiseas.org). Strong Atlantic inflow variability associated with shifts in phase of the North Atlantic Oscillation and Atlantic Multidecadal Oscillation translate into recruitment variability in herring (*Clupea harengus*) and cod (*Gadus morhua*) and variable levels of predation on capelin (*Mallotus villosus*) (Olsen *et al.* 2010, ICES 2010b). In years of high inflow from the Atlantic Ocean, temperatures are relatively warm, and cod and herring recruitment is favored (ICES 2010b). Ongoing climate change and warming also are associated with shifts in components of the ecosystem, such as the recent invasion of the Barents Sea by blue whiting (*Micromesistius poutassou*) from the Norwegian Sea (www.indiseas.org). Emerging oil and gas exploration in the Barents is an issue of concern (Olsen *et al.* 2007). Ecosystem-based management plans for the Barents and its resources have been developed recently that take into account expanding economic and exploitative activity (e.g., petroleum exploration) (Olsen *et al.* 2007).

The fish community in the Barents Sea is relatively low in diversity, consisting of approximately 200 species (www.indiseas.org). Atlantic cod, capelin, and herring are a key triad of species in this ecosystem, linked by prey-predator relationships (Gjøsæter *et al.* 2009, Olsen *et al.* 2010). Capelin is the most abundant forage fish in the Barents Sea, and its total stock biomass was estimated at 3.71 million tonnes in 2011 (ICES 2011). Cod preys primarily on capelin but also on herring and smaller cod. Herring, when abundant, is an important predator of capelin larvae. Haddock (*Melanogrammus aeglefinus*), now at high abundance in the Barents, is also an important predator of capelin. When abundant, these predators exercise strong top-down control on capelin abundance and, when combined with fishing, can lead to decline or collapse of the capelin stock (Gjøsæter *et al.* 2009, Hjermann *et al.* 2004). Such collapses have precipitated trophic cascades, resulting in nutritional stress and cannibalism in cod and mortality or emigration from the Barents Sea by starving mammals and birds (Hamre 1994). It also results in serious economic losses to a cod fishery that is unproductive when capelin is in low abundance.



Trawler, © Hlynur Ársællsson/Shutterstock.

Fisheries

Major fisheries have been pursued in the Barents Sea by Norway and Russia for more than a century. Catches increased until the 1960s and 1970s but then declined dramatically under the combined effects of unfavorable climate and overfishing. Recently, the situation has improved, attributable to effective management and favorable climate. The cod fishery is the most valuable in the Barents Sea, which now supports the world's largest stock of cod (www.indiseas.org). Landings of cod ranged from 400,000 to 640,000 tonnes from 2000 to 2006. Catches of capelin peaked at nearly 2.5 million tonnes in the 1970s (ICES 2011), then collapsed in the 1980s, with reverberations throughout the ecosystem (Hamre 1994, Gjøsæter *et al.* 2009, Appendix C, Figure 1).*

Management

Overfishing, exacerbated by poor climate conditions, caused collapse of Barents Sea capelin in the 1980s, but the two subsequent collapses are primarily attributed to environmental causes (Gjøsæter *et al.* 2009). The capelin stock is managed by the Joint Norwegian-Russian Fisheries Commission that sets quotas scaled to a "Capelin Limit Rule," under which the catch is 0 when

spawning stock biomass (SSB) falls below 200,000 tonnes (ICES 2010a, <http://assessment.imr.no/>). A moratorium on capelin fishing was in effect from 2004 to 2008 when SSB was below this level, demonstrating effective use of a biomass threshold. Most recently, capelin SSB was estimated at 504,000 tonnes (ICES 2011), and the catch was set at 320,000 tonnes for 2012. Temporal, spatial, and minimum landing size regulations are also in effect.

Many fish stocks are at high abundance in the Barents Sea, but managers must remain vigilant, because fishing and predation pressure on capelin are at high levels as well. History has demonstrated how shifting climate, fishing, and predation pressure can act to destabilize this ecosystem; capelin, the primary forage species, is the lynchpin and requires precautionary management to ensure resiliency of the Barents Sea ecosystem. To this end, the Joint Commission responds quickly to adjust capelin catches or declare moratoriums when abundance is low (ICES 2010a, <http://assessment.imr.no/>). Multispecies and ecosystem models are an integral part of stock assessments to evaluate how changes in abundance of capelin and that of its predators affect ecosystem diversity and productivity.

* www.lenfestocean.org/foragefish

The Benguela Upwelling System: A Tale of Two Fisheries



Ecosystem

The Benguela system is one of the world's four major eastern boundary upwelling systems and supports large forage fish populations. There are substantial differences between the northern Benguela coastal upwelling system off Namibia, with currently depleted fish stocks, and the wind-driven southern Benguela upwelling region off South Africa, which supports large fisheries.

The dominant forage fish species are the anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), which exert “wasp-waist” control in these systems (Cury *et al.* 2000). Observations and modeling studies predict pelagic fish decreases to have substantial effects on both higher and lower trophic levels (Shannon *et al.* 2009, Crawford *et al.* 2008). A number of fish, such as snoek (*Thyrsites atun*); seabirds, such as African penguins (*Spheniscus demersus*),¹⁰ Cape gannets (*Morus capensis*), and Cape cormorants (*Phalacrocorax capensis*); and cetaceans, such as Bryde's whale (*Balaenoptera brydei*), long-beaked common dolphins (*Delphinus capensis*), dusky dolphins (*Lagenorhynchus obscurus*), and Heaviside's dolphins (*Cephalorhynchus heavisidii*), depend on these forage fish species. The shelf areas off Namibia, the west coast of South Africa, and the Agulhas Bank make up the major nursery areas for pelagic spawners (Hutchings *et al.* 2009). Eggs and larvae spawned on the Agulhas Bank are advected northward in a strong shelf-edge jet, and

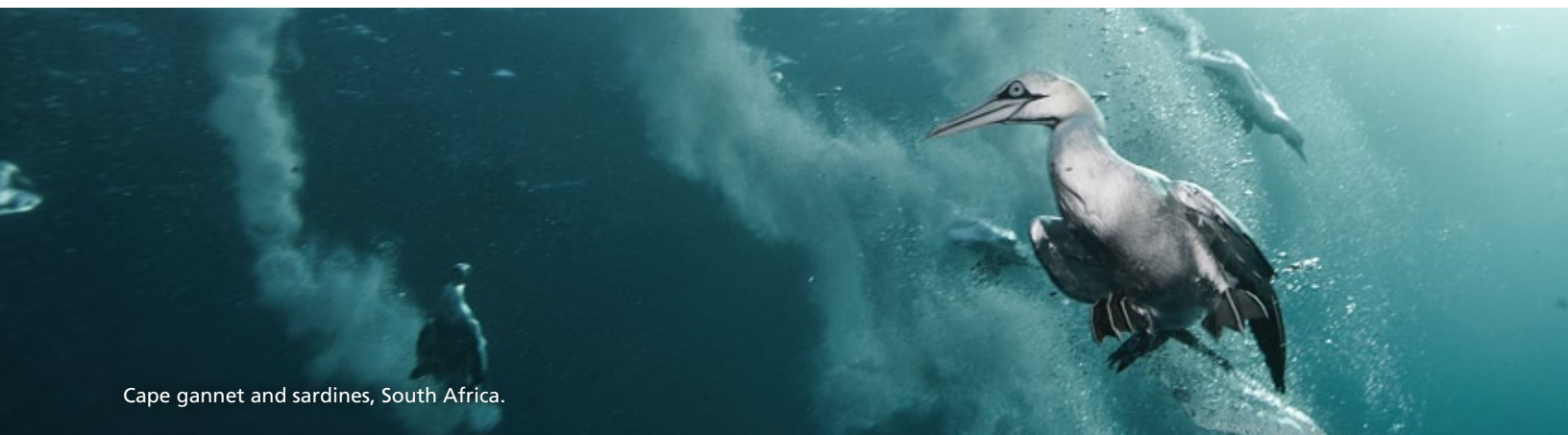
pre-recruits then move inshore to feed in west coast nursery grounds.

Fisheries

Anchovy and sardine are targeted in both the northern Benguela (Namibia) and the southern Benguela (South Africa). In Namibia, sardines were dominant from 1950 to 1975 but collapsed in the mid-1970s, probably because of over-exploitation and under-reporting of catches (Butterworth 1980). Subsequent recovery was impeded by a combination of low-oxygen events and heavy fishing pressure during poor recruit years (Boyer *et al.* 2001). To date, stocks are totally depleted, and a small “socioeconomic” quota has been set in Namibia that may prevent sardine and anchovy populations from recovering. Sardine and anchovy in this system appear to have been replaced by gobies (*Sufflogobius bibarbatus*), horse mackerel (*Trachurus trachurus*), and jellyfish (Bakun and Weeks 2006, Utne-Palm *et al.* 2010). Although seabirds have declined in the northern Benguela, fur seal population numbers are still high albeit variable (Kirkman *et al.* 2007). Increases in the trophic level of the catch in this system reflect the collapse of small pelagic fish (Shannon *et al.* 2009).

In South Africa, the recruit-driven anchovy fishery started in the 1940s, and landings rose to 300,000 to 500,000 tonnes from the 1970s to the end of the century. Sardine and anchovy numbers peaked from 1999

¹⁰ More information on the dependence of the African penguin on forage fish can be found in the main text.



Cape gannet and sardines, South Africa.

to 2003 (Appendix C, Figure 2).^{*} The anchovy fishery is currently healthy, but sardines have subsequently declined, and there has been an eastward shift in their distribution (van der Lingen *et al.* 2006, Coetzee *et al.* 2008). Although not yet fully understood, this shift has been partly attributed to an abrupt change in environmental forces influencing the relative favorability of eastern and western spawning locations (Roy *et al.* 2007). Because fish-processing facilities are located on the west coast of South Africa, this has had a negative impact on fishery stakeholders (Coetzee *et al.* 2008) and dependent species.

Management

Historically, sardine and anchovy were managed separately in South Africa. However, since 1991, the South African anchovy fishery has been regulated using an Operational Management Procedure (OMP) approach (analogous to a Management Strategy Evaluation or MSE), which is an adaptive management system that is able to respond rapidly (without increasing risk) to major changes in resource abundance, as occurred around 2000 (de Moor *et al.* 2011). The first joint sardine and anchovy OMP was implemented in 1994 (De Oliveira *et al.* 1998), with subsequent revisions (De Oliveira and Butterworth 2004, de Moor *et al.* 2011). The necessity for joint management of sardine and anchovy is a result of the operational interaction between the two fisheries; it is not possible to catch anchovy without an accompanying bycatch of juvenile sardine (De Oliveira and Butterworth 2004), because juveniles of both

species can shoal together. Total allowable catches (TACs) are calculated based on abundance estimates from hydroacoustic surveys of recruitment each May and of spawning biomass each November (De Moor *et al.* 2008). Recommendations for both target TAC and total allowable bycatch (TAB), respectively, are provided. An initial conservative anchovy TAC, associated with an initial sardine TAB, is specified at the start of the season based only on the results from the November spawning biomass survey (de Moor *et al.* 2011). These limits may be increased later in the year based on results from the annual May recruitment survey.

The stability of South African pelagic yields has been attributed largely to effective and conservative management, with comparatively low catch rates (8 percent average for sardine; 30 percent average for anchovy) applied to the major forage species. In contrast, the collapse of sardine in the northern Benguela (Namibia) has been attributed to a) exploitation rates that were too high, b) underestimation of actual exploitation rates because of under-reporting of catches, c) growth overfishing after a change from sardine to anchovy nets with smaller mesh size, and d) the interplay of unsustainable fishing levels under environmental change (Butterworth 1980, Boyer and Hampton 2001). In South Africa and Namibia, an attempt at ecosystem-based management is also being made through the use of spatial closures to protect African penguins and other seabird foraging areas (see main text on the use of temporal and spatial management). However no improvement is expected in Namibia until the sardine and anchovy stocks recover.

^{*} www.lenfestocean.org/foragefish

The California Current: Supporting Multiple Forage Fish and Invertebrates



Ecosystem

The California Current is a temperate upwelling ecosystem spanning the coastal waters from the Baja California peninsula to British Columbia. It is characterized by a narrow shelf and steep slope that produce sharp offshore gradients in groundfish communities and also by distinct physical coastal features that are associated with unique biogeographic boundaries. The ecosystem consists of two major eco-regions, delimited at Point Conception, CA. Like many other upwelling ecosystems, the California Current is characterized by environmental variability at multiple scales (Huyer 1983, Checkley and Barth 2009). Seasonally, the system is defined by the transition from net downwelling of coastal water from poleward winds in winter to net upwelling produced from equatorial winds in spring (Bograd *et al.* 2009). Interannually, the ecosystem displays marked variation in the timing of the spring transition to upwelling (Barth *et al.* 2007). Warm- and cold-phase El Niño-Southern Oscillation (ENSO) events have strong effects on the ecosystem and food web, with predictable shifts in species composition associated with the warm-phase ENSO that brings subtropical or tropical species into the ecosystem (Bograd *et al.* 2009). At longer time scales, decadal-scale shifts in ocean conditions (Pacific Decadal Oscillation, or PDO) are thought to underlie patterns of zooplankton diversity and forage fish productivity, affecting the entire food web (Francis *et al.* 1998).

The California Current supports multiple species of forage fish, chiefly Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulus mordax*), Pacific herring (*Clupea pallasii*), eulachon (*Thaleichthys pacificus*), whitebait smelt (*Allosmerus elongates*), and Pacific sand lance (*Ammodytes hexapterus*). Euphausiids (*Thysanoessa spinifera*, *Euphausia pacifica*, *Nyctiphanes simplex*) are the key invertebrate forage species. Other species that may play similar ecological roles include juvenile hake (*Merluccius productus*) and salmon (*Oncorhynchus* spp.), Pacific (*Scomber australasicus*) and jack mackerel (*Trachurus symmetricus*), bonito (*Sarda chiliensis lineolata*), and market squid (*Loligo opalescens*) (Field and Francis 2006). The abundances of many forage fish populations are not routinely estimated, but long-term records from scale deposition suggest that sardine and anchovy undergo oscillating patterns of abundance, with sardines exhibiting the most wide-ranging fluctuations (Baumgartner *et al.* 1992, but see Box 1.2 on variability). Sardines are thought to be more productive during warm phases of the PDO, and anchovy productivity is greater during cold phases (Chavez *et al.* 2003).

Several fish species of special concern, such as coho and Chinook salmon (*Oncorhynchus kisutch* and *Oncorhynchus tshawytscha*), and some rockfish (*Sebastes*) species prey on forage fish but do not appear to specialize on them. Forage fish are also consumed by commercially important marine fishes such as lingcod (*Ophiodon elongatus*), Pacific hake (*Merluccius productus*), Pacific halibut (*Hippoglossus stenolepis*), and spiny



California least tern, © Shutterstock.

dogfish (*Squalus acanthias*). A large number of seabird species rely on forage species as well, particularly during the nesting season (Sydeman *et al.* 2001); the reproductive success of the endangered marbled murrelet (*Brachyramphus marmoratus*) is tied to the availability of Pacific krill (Becker *et al.* 2007). Terns (family *Sternidae*) and cormorants (family *Phalacrocoracidae*) prey mainly on marine fish, and some species may specialize on particular species of forage fish. The federally endangered California least tern (*Sternula antillarum*) feeds on northern anchovy, and its reproductive success may depend on local anchovy densities (Elliott *et al.* 2007). Marine mammals such as Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), small-toothed whales (*Odontocetes*), and killer whales (*Orcinus orca*) all consume significant quantities of forage fish (Field *et al.* 2006).

Fisheries

The largest forage fishery in the California Current, by weight of landings, is the Pacific sardine (Field and Francis 2006), which underwent a dramatic rise and fall in the first half of the 20th century and peaked at just over 700,000 tonnes annually. Although fishing beyond the productivity of the stock probably contributed to its collapse, both sardine and northern anchovy show marked cycles of abundance that are probably tied to environmental variability (Baumgartner *et al.* 1992; see

Box 1.2 on variability). Currently, the coastwide sardine catch is about 60,000 tonnes; recent sardine assessments suggest a 50 to 80 percent decline in predicted biomass from the peak abundance that followed the rebound of the stock in the 1970s.¹¹ Northern anchovy is caught occasionally and is considered an underutilized stock. Pacific herring are caught seasonally during their spawning season and are managed by individual states. Eulachon smelt are caught primarily in estuaries and have declined dramatically.¹² Fisheries for squid and mackerel may affect the forage base for a number of higher trophic level species.

Management

Fisheries in the U.S. portion of the California Current are managed by the Pacific Fishery Management Council, which has jurisdiction over the exclusive economic zone off Washington, Oregon, and California. The sardine assessment and recommended catch are updated annually as part of the Coastal Pelagic Species Fishery Management Plan, which also includes a formal assessment for Pacific mackerel but only monitors northern anchovy and Pacific herring as ecosystem component species. Sardine catch recommendations are coastwide, but the assessment includes spatially and temporally variable estimates of natural mortality and growth. Allowable catch is based on an MSY calculation modified by expected productivity (temperature dependent) and reduced by a buffer of 150,000 tonnes to account for uncertainty and ecosystem needs. The council traditionally has taken a conservative approach to management and generally follows the recommendations of its Science and Statistical Committee. Concern over declines in stock status indicators for sardine, not declines in catch rates, are driving current reductions in allowable catch. In 2006, the council voted to prohibit Pacific krill fishing within its jurisdictional waters as a precautionary measure to protect forage for commercially important stocks. A substantial barrier to effective management of forage fish throughout the California Current is uncertainty about stock movement and connectivity, and response to environmental variance.

¹¹ www.pcouncil.org/wp-content/uploads/PFMC_2008_CPS_SAFE_App1_Sardine.pdf

¹² http://www.nmfs.noaa.gov/pr/species/fish/pacific_eulachon.htm

Chesapeake Bay: Undervalued Forage Species and Concerns of Localized Depletion



Ecosystem

The Chesapeake Bay, the largest estuary in North America, is home to many ecologically and economically important fish and shellfish and is a nursery for larvae and juveniles that eventually recruit to the coastal ocean. In the local Native American language, the Chesapeake is the “Great Shellfish Bay,” and historical harvests of oysters and blue crabs support that description. The bay is stressed by a multitude of human activities, however. Overloads of nutrients, shoreline and riparian habitat modifications, and sediment loading have led to eutrophication, hypoxia, declines in sea grasses, and loss of habitat. There is heavy fishing effort by commercial and recreational sectors, and stocks of several species have collapsed under multiple stresses. The eastern oyster, an icon in the bay’s history, is nearly gone; shortnose and Atlantic sturgeons are nearly extirpated; and four alosine species (shad, river herring) have been reduced to small fractions of their former abundance. On a positive note, the once-depleted striped bass stock was rebuilt, and piscivorous birds, such as osprey and bald eagles, have rebounded and are abundant.

Atlantic menhaden (*Brevoortia tyrannus*), a small, herring-like fish that is key prey for piscivores, is the most important forage species in the bay. The Chesapeake supports a large biomass of age 1–2 menhaden and a large contingent of age 0 juveniles, which recruit to the bay as larvae from ocean spawning. Historically, the bay supplied more than 65 percent of menhaden recruitment

to the migratory coastal population (Menhaden Species Team 2009). Recruitment of menhaden to the bay has been consistently low for the past two decades.

A second key forage species is the bay anchovy (*Anchoa mitchilli*), a short-lived species that is the most abundant fish along the Atlantic coast of North America from Cape Cod to Yucatán (Able and Fahay 2010). Bay anchovy is not fished but is important prey for virtually all piscivores. Numbers of bay anchovy in the Chesapeake Bay total in the tens of billions (Jung and Houde 2004). Other small pelagic fishes, such as atherinids, are abundant but not fished. Shad and river herring juveniles (*Alosa* spp.) historically were abundant and provided important alternative forage but have declined precipitously in recent decades.

A diverse assemblage of predators consumes key forage species in the bay. Predators include striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) as well as osprey (*Pandion haliaetus*), bald eagle (*Haliaeetus leucocephalus*), double-crested cormorant (*Phalacrocorax auritus*), gannets (*Morus* spp.), loons (*Gavia* spp), terns (*Sternidae*), gulls (*Laridae*), and herons (*Ardeidae*) (Menhaden Species Team 2009). The bay’s carrying capacity for forage fish is unknown, as are the amounts of these fish required to sustain predators at high levels of abundance.

Interannual variability in level of freshwater flow into the bay plays a critical role in determining its

productivity and its variable abundances of estuarine fishes. Atlantic menhaden historically has the highest recruitment of age 0 juveniles in years with relatively low freshwater flow and warm temperatures during winter and spring, at the time menhaden larvae enter the bay (Kimmel *et al.* 2009, Wood and Austin 2009).

Fisheries

The bay has a long history of fishing, with reported landings (commercial and recreational) of fish and shellfish exceeding 300,000 tonnes annually in the 20th century (CBFEAP 2006).

Landings of many species declined progressively in the late 20th century. Catches became dominated by blue crab (*Callinectes sapidus*) and Atlantic menhaden (Appendix C, Figure 3),* which is key prey for piscivorous fish and birds. Menhaden are targeted by the bay's biggest fishery (by volume), in which they are reduced to fish meal and oil or are used for bait in other fisheries. The reduction fishery, once coastwide, has contracted in the past half-century to center in the Chesapeake Bay, where a single factory processes the catch. This reduction fishery, conducted by purse-seine vessels, yielded more than 100,000 tonnes annually through much of the 20th century (Smith 1999).

Management

The single, migratory, coastwide population of Atlantic menhaden is managed by the Atlantic States Marine Fisheries Commission (ASMFC), which for years had judged menhaden to be neither overfished nor experiencing overfishing. However, management now acknowledges that overfishing of the coastwide stock occurred in many years during recent decades (ASMFC 2010, 2011a), precipitating a call for action and a plan to lower the coastwide target and threshold fishing mortality rates for Atlantic menhaden. Menhaden abundance within the bay itself has not been estimated, but heavy fishing has led to concerns by recreational fishermen, managers, and the public regarding localized depletion of menhaden and their attendant losses of ecosystem services as prey and filterers (Menhaden Species Team 2009).

Historically, few regulatory measures to control landings and fishing mortality guided the menhaden fishery (ASMFC 2010). Purse-seine fishing, allowed within the bay only in Virginia's waters, is regulated by seasons and mesh-size standards. A cap of 109,020 tonnes, the average catch in the bay over the previous five years, was placed on the fishery in Virginia's waters of the bay in 2006 in response to public outcry over localized depletion, despite ASMFC's assurance at the time that the coastwide stock was not overfished or experiencing overfishing (Menhaden Species Team 2009, ASMFC 2010). The coastwide stock assessment does not consider dynamics, demographics, or depletion of menhaden at local scales such as in the Chesapeake Bay. Hence, there is no spatially explicit estimate of menhaden abundance, and it is unknown whether current levels of menhaden fishing within the bay are sustainable.

In 2011, the Menhaden Management Board of the ASMFC proposed a draft addendum to the menhaden management plan requiring a threshold fishing mortality rate that would set F at a level to maintain 15 percent of maximum spawning potential (MSP), with a target F of 30 percent MSP (ASMFC 2011b). The recent average level of $F = 9$ percent MSP is now recognized as too risky for sustainable fishing and may compromise menhaden's role as prey in the coastal ecosystem. The proposed amendment was approved (ASMFC 2011c). More conservative management by the ASMFC is needed, because the most recent stock assessments indicate that fishing is a bigger factor than previously thought (ASMFC 2010) and there is no management mechanism to reduce fishing mortality to appropriate levels. In recent years, many stakeholders believed that management entities have insufficient appreciation of ecosystem services provided by menhaden. The newly proposed regulations still do not include specific measures for the Chesapeake Bay beyond maintaining the current cap on reduction fishery landings. Making menhaden assessment and management more spatially explicit, and gaining a greater understanding of menhaden's role as prey, would help address localized depletion concerns in the bay and ensure that menhaden's ecosystem services are not compromised.

* www.lenfestocean.org/foragefish

Gulf of Maine: A Trophic and Socioeconomic Cornerstone



Ecosystem

The Gulf of Maine is a semi-enclosed embayment with counter-clockwise circulation (Xue *et al.* 2000) and slightly, but significantly, diluted seawater resulting from the inflow of myriad rivers. Its seaward boundary is Georges Bank. Both of these subarctic ecosystems are productive, but contain low species diversity. There are 120 species of fish in the Gulf of Maine and 54 percent of those are groundfish (Bigelow and Schroeder 1953). Nevertheless, forage fish are important and abundant in the large marine ecosystems that comprise this area. Among the Gulf of Maine's nine species of clupeids, only four attain any degree of abundance and ecological or economic importance to qualify as forage fish (Collette and Klein-MacPhee 2002). They include Atlantic herring (*Clupea harengus*), river herring (alewife [*Alosa pseudoharengus*] and blueback herring [*A. aestivalis*]), and Atlantic menhaden (*Brevoortia tyrannus*). Of these, Atlantic herring is the only species that has maintained a relatively high abundance.

Atlantic herring is the most abundant and important consumer of zooplankton, while river herring and menhaden are much less abundant and differ in the habitats they use. Nevertheless, all of these species can be pooled as forage fish in a single functional group. These clupeids are relatively small and oily, making them the preferred food of numerous predators. As a group they are preyed on by fish and sharks including:

sand lance (*Ammodytidae*), cod (*Gadus morhua*), pollock (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), white hake (*Urophycis tenuis*), striped bass (*Morone saxatilis*), mackerel (*Scomber scombrus*), bluefin tuna (*Thunnus thynnus*), sculpins (*Myoxocephalus sp.*), winter flounder (*Pseudopleuronectes americanus*), dogfish (*Squalus acanthias*), porbeagle sharks (*Lamna nasus*), and skates (*Rajidae*) (Bigelow and Schroeder 1953, Reid *et al.* 1999). Herring and other clupeids are also eaten by marine birds (gulls, gannets, alcids, and cormorants), as well as by northern shortfin squid (*Illex illecebrosus*), seals, porpoises, dolphins, and whales (especially minke whales, [*Balaenoptera acutorostrata*]). In this long list, it is possible that seals are most dependent on herring and others in this functional group (Bowen and Harrison 1996). Atlantic herring are by far most abundant and have been the most important of the forage fishes in the Gulf of Maine since humans first arrived more than 5,000 years ago (Steneck *et al.* 2004). Herring and alewife bones were commonly found in Native American middens dating between 4,500 to 400 years ago (Spiess and Lewis 2001). Thus, the link to humans has deep roots and profound impacts.

Atlantic herring are also a significant source of nutrition for lobsters. In the 1980s, a study of lobster gut contents determined fish bait comprised 80 percent of lobster diets (Steneck unpublished data). More recently, stable isotope analyses of lobster flesh in heavily fished and



Northern lobster, Gulf of Maine, © Andrew J. Martinez/SeaPics.com.

unfished regions of Maine determined that herring comprises the majority of their diet, and lobsters fed herring bait grew more rapidly than those living in unfished regions (Grabowski *et al.* 2010). Currently, the herring harvest effectively feeds lobsters as a farming operation (Steneck *et al.* 2011).

Over the last half-century, patterns of distribution and abundance of Atlantic herring have shifted. Maine state inshore and National Marine Fisheries Service offshore trawl surveys over the past three decades have shown that herring were largely absent from much of the coastal area with historically high abundance (Appendix C, Figure 4;* Reid *et al.* 1999, Maine DMR inshore trawl surveys). However, other areas, such as Georges Bank, Massachusetts Bay, and Cape Cod that had been singled out as largely devoid of herring from 1919 to the 1950s (Bigelow and Schroeder 1953), contain the highest concentration of adult herring in recent decades (Appendix C, Figure 4;* Reid *et al.* 1999, Maine and Massachusetts inshore trawl surveys).

Such discrete population dynamics are, in part, the result of distinct local stocks of Atlantic herring, which create a metapopulation. Evidence for this includes asynchronous population dynamics (Overholtz 2006), tag and recapture studies (Kanwit and Libby 2009), and genetics (Stephenson *et al.* 2009). Early studies identified five distinct stocks for the western North Atlantic (from Newfoundland to New Jersey; Iles 1972), which have

since been refined into even smaller units. Clearly distinct spawning times and locations along with evidence for greater larval retention (Iles 1971) suggest small-scale connectivity (Stephenson *et al.* 2009), qualifying this species as having “complex stock structure.”

Fisheries

Atlantic herring comprised over half of Maine’s harvested biomass for much of the time after 1950, with the other forage fish species comprising only 1 to 2 percent. However, nearly all forage fish in New England declined precipitously beginning in the 1970s. This provides an important insight into what drives the abundance of forage fish. It also illustrates recruitment consequences of these changes.

Despite the metapopulation structure of Atlantic herring (coastal and Georges Bank stocks) and anadromous forage fish (with local stocks requiring specific estuaries), landing declines of both groups were remarkably synchronous. NOAA’s *Species of Concern* document for river herring (NOAA 2009) identifies five “factors of decline”: dams and other impediments, habitat degradation, fishing, bycatch, and striped bass predation. However, a recent study (Spencer 2009) that examined four rivers in Maine with distinctly different watershed and dam chronologies demonstrated a synchronous and precipitous decline in alewife abundance during the 1970s. Therefore, Spencer (2009) concluded that ocean

* www.lenfestocean.org/foragefish



Lobster boats, Portsmouth, NH, © Shutterstock.

mortality was the most likely explanation for Maine's alewife decline. Striped bass predation is also an unlikely driver of the forage fish declines in the Gulf of Maine and Georges Bank, because the increase in striped bass began in the 1990s, well after the forage fish decline of the 1970s. In fact, Atlantic herring recovery has accelerated since the 1990s with increases in spawning stock biomass, recruitment, and juvenile herring abundance (Reid *et al.* 1999, Overholtz 2006).

Despite their different life-history habitat requirements, anadromous and ocean-dwelling forage fishes live together along the eastern seaboard of the United States and Canada where they are vulnerable to large-scale fishing. In the late 1960s distant-water fleets from Cuba, Bulgaria, Germany, the Netherlands, Poland, Spain, and the former Soviet Union fished and reported landings of river herring and Atlantic herring from 1966 to 1977 and then again from 1984 through 1989 (NOAA 2009). The general landings decline during that period and the recovery in Atlantic herring during the 1977–1984 hiatus, suggests offshore fishing may be the largest cause of depletion for forage fish in the Gulf of Maine.

Of significant note is the interaction between the herring and lobster fisheries. As lobster fishing intensified over time, the demand on herring increased and its supply declined. Today, Maine's herring landings cannot supply local demand for bait (horizontal line in Appendix C, Figure 5c).* As a result, the price of herring

has skyrocketed (Appendix C, Figure 5d).* In the past few years, alewife and menhaden harvesting for bait has increased. In 2006, menhaden comprised 7 percent of Maine lobster bait, but by 2008, it had increased to 19 percent (Maine Lobstermen's Association data). Despite these and other sources of bait, the supply remained short of the needs of the lobster industry. This is a unique fisheries crisis in Maine because it is entirely economic. Lobster stocks are booming (Appendix C, Figure 5a),* but because of the complete dependence of this fishery on herring bait, which has risen from \$15/tonne to nearly \$250/tonne since 1950, the cost of doing business now threatens the profitability of the lobster fishery. This presents an interesting example of how a regional fishery can act as a driver of a forage fishery in the same ecosystem.

Management

Forage fish in the United States are managed locally (each state regulates river herring harvests), inter-state (Atlantic States Marine Fisheries Commission—ASMFC) and federally (National Marine Fisheries Service). The mix of these management agencies has changed over time. Atlantic herring were managed by the International Commission for the Northwest Atlantic Fisheries from 1972 to 1976, at which point the United States withdrew and began to develop its own herring management plan. The U.S. federal Fishery Management Plan (FMP) was adopted in 1978 to manage the Gulf

* www.lenfestocean.org/foragefish



Atlantic puffin with fish, © twildlife /iStockphoto.com.

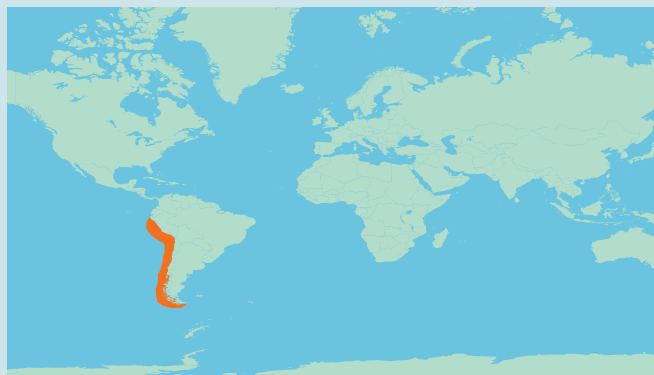
of Maine and Georges Bank stocks (separately) and to rebuild spawning stock biomass. From 1976 to 1978 the National Marine Fisheries Service (NMFS) developed a preliminary management plan to regulate the foreign fishing fleet.

However, in 1982 NMFS rescinded the 1978 Herring FMP because it conflicted with state regulations. In 1999 a compromise FMP was implemented that used a quota system with hard TACs. When 95 percent of the quota is caught, the area is closed until the next year. About the same time, the ASMFC developed seasonal spawning closures in the Gulf of Maine for the fall months. Three closures span nearly the entire U.S. coast of the Gulf of Maine.

Management measures for Atlantic herring may be effective. Spawning stock biomass, recruitment and juvenile abundances have all increased since the early 1990s (Overholtz 2002). The same is not the case for river herring, which remains depressed today. Nevertheless, despite claims of recovery in Atlantic herring by NMFS (Overholtz 2002), the New England Fishery Management Council has steadily reduced the TAC. For example, the coast of Maine (fisheries management area 1A) had a quota of 60,000 tonnes from 2000 to 2006, but since then it has been steadily reduced to 26,546 in 2010 (a 56 percent decrease). This reduced quota is intended to further rebuild the spawning stock biomass in Atlantic herring.

Other forage species have not recovered in this ecosystem, although Atlantic herring biomass has increased. Even so, Maine's herring landings cannot meet the local demand for bait.

The Humboldt Current and the World's Largest Fishery



Ecosystem

There are four eastern boundary current systems: the Canary and Benguela current systems off northern and southern Africa, respectively, and the California and Humboldt Current systems off of North and South America, respectively. These ecosystems share similar features such as strong upwelling, comparable flora and fauna, and a parallel history of exploitation (Parrish *et al.* 1983, Jarre-Teichmann and Christensen 1998). However, the Humboldt Current system, and more particularly its northern part in the waters of Peru, differs in important ways from other classical upwelling systems (Faure and Cury 1998), and indeed from any other system in the world, because of its enormous production of fish biomass, notably of the forage fish known as Peruvian anchoveta (*Engraulis ringens*) (Appendix C, Figure 6).*

This high productivity manifested itself, until the middle of the 20th century, in tremendous populations of guano-producing seabirds which relied, as did the numerous marine mammals and larger fish, on abundant anchoveta schools. Cormorants (Spanish 'guanay,' *Phalacrocorax bougainvilli*) were the most abundant seabirds off Peru, with a mean population of 12.6 million individuals from 1955 to 1964. This species declined to just 1.34 million (11 percent of historical numbers), presumably because 96 percent of its diet consisted of anchoveta (Muck and Pauly 1987). Within the same

period, Peruvian booby ('piquero'; *Sula variegata*) and pelicans ('alcatraz'; *Pelecanus thagus*) also declined from 1.86 million to 1.50 million and from 0.34 million to 0.18 million (81 percent and 52 percent of historical levels), respectively. A smaller decline in gannets and pelicans possibly occurred because they could more easily switch to an alternative prey such as sardine (*Sardinops sagax*).

Fishery

Until mid-century, Peru had a diversified coastal fishery, whose targets included fish for local consumption (e.g., various species of croakers) and offshore fisheries for tunas and tuna-like fish, notably the bonito *Sarda chilensis*, which were all compatible with the guano industry. However, this pattern of exploitation changed in 1953, with the onset of an industrial anchoveta fishery to supply an export-oriented fishmeal industry. The direct exploitation of anchoveta made the ecosystem less resilient to El Niño events, and the first of these after the onset of this fishery in 1965, saw the massive decline of the huge seabird populations (Appendix C, Figure 7),* which had until then maintained the large Peruvian guano industry.

The anchoveta fishery was largely unaffected by the 1965 El Niño event, and expanded further, peaking in 1971 with an official catch of 12 million tonnes (Tsukayama and Palomares 1987) and an estimated actual catch of 16 million tonnes (Castillo and Mendo

* www.lenfestocean.org/foragefish



Anchovies, © Nikontiger/iStockphoto.com.

1987). In 1972, a strong El Niño event concentrated anchoveta in a few pockets of cold water from which immense catches were realized before the fishery was closed after the population collapsed. The anchoveta recovered, but dropped again due to the long-lasting El Niño of 1983 and its follow-up effect lasting until the 1990s, which included a warm period favoring sardine rather than the anchoveta.

Management

The anchoveta population has recovered since, and now yields an annual catch of about 5 million to 8 million tonnes, despite more frequent El Niño events. This is in part because of a new management regime that closes the fishery when the biomass declines below 5 million tonnes. This limit is based on the observation that anchoveta recruitment tended to drop markedly in years when observed adult biomass was below 4 million tonnes (Renato Guevara, Instituto del Mar del Perú [IMARPE] Research Director, unpublished data; see also contributions in Bertrand *et al.* 2008).

The Humboldt Current ecosystem is greatly impoverished in comparison to its state prior to the onset of the anchoveta fishery: bird populations are extremely reduced and marine mammals, notably sea lions (*Otaria flavescens*) and fur seals (*Arctocephalus australis*), have not recovered from direct hunting early in the 20th century and the devastating El Niño of 1983. It may be

Although the anchoveta population has recovered, predators such as seabirds and marine mammals are still at extremely reduced levels.

possible to rebuild the earlier diversity of this ecosystem without forgoing long-term anchoveta yields. Such a transition, especially if it accompanies an increase in the fraction of anchoveta catch that is devoted to direct human consumption—currently about 2 percent—would ensure a sustained supply of seafood. Achieving such a transition may be particularly important as the Humboldt current system is one of the few low latitude marine ecosystems considered unlikely to decline due to global warming (Bakun 1990; Cheung *et al.* 2010) and whose relative contribution to global fisheries catches will likely increase in the coming decades.

The North Sea: Lessons from Forage Fish Collapses in a Highly Impacted Ecosystem



Ecosystem

The North Sea is a shallow, semi-enclosed region bounded on the west by the British Isles and on the east by continental Europe. This ecosystem has relatively high primary productivity (McGinley 2008) and supports fisheries for haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), cod (*Gadus morhua*), saithe (*Pollachius virens*), plaice (*Pleuronectes platessa*), sand eels (*Ammodytes marinus*), and herring (*Clupea harengus*), as well as for Norway lobsters (*Nephrops norvegicus*). In addition to sustaining fishing pressures, the North Sea receives outflow from rivers draining major industrial and agricultural regions in northern Europe, and is subject to intensive use for transport, oil and gas extraction, and marine renewable energy. As a result, the North Sea is one of the most impacted large marine ecosystems on the planet (Halpern *et al.* 2008).

Sand eels and juvenile herring are the principal prey for many diving seabirds and some marine mammals in the North Sea. The reproductive success of black-legged kittiwakes (*Rissa tridactyla*) is especially sensitive to the abundance of sand eels (Wanless *et al.* 2007), but other species may exhibit different levels of sensitivity to forage fish abundance (Furness 2003, Frederiksen *et al.* 2008). For instance, although both species of seals that occur in the North Sea (grey and harbor seals; *Halichoerus grypus* and *Phoca vitulina*, respectively) have high proportions of sand eels in their diets, there is no clear relationship between their population and sand eel

abundance. However, the availability of alternative prey and other possible causes of population change may mask the relationship. It is also likely that several species of cetaceans in the North Sea feed principally on herring and sand eels, but there are few data about cetacean diets from this region and there is no information about the functional relationship between vital rates of North Sea cetaceans and the abundance of forage fish.

Fisheries

The main forage fish that are commercially exploited are North Sea sand eels and herring. The sand eels consist of 5 different species, although 90 percent of commercial catches are made up of the lesser sand eel (*Ammodytes marinus*). Sand eel populations have declined in the past 10 years to less than 50 percent of biomass levels prior to 1983. Patterns of sand eel abundance and exploitation levels show similarities to those observed in North Sea herring during the 1970s. Declining abundance was accompanied by sustained levels of exploitation until 2003, when rates decreased, leading to an eventual closure of the fishery in 2008.

A different type of process is evident for herring, which shows much less inter-year variance in total biomass but also shows long-term variability. Increasing herring exploitation through the 1970s, combined with declining abundance, led to the collapse of the pelagic fishing industry in the late 1970s. A similar but less dramatic change recurred in the mid-1990s and may also be under way.



Even if TACs are set according to scientific advice, actual catches can well exceed the limit, as evident in the North Sea herring fishery.

Black-legged kittiwake, Norway.

Management

While the TACs for herring appear to be set according to the scientific advice, catches are considerably greater than the TAC (Appendix C, Figure 8).^{*} This is probably caused by discarding and “high-grading,” but has also been associated with illegal landings and illustrates the general principle that fishing mortality can be a target but may not be well controlled (Mangel 2000b). These data suggest that estimates of fishing pressure are likely to represent the low end of the possible range of fishing pressures exerted on these forage fish populations.

For the North Sea herring fishery in the 1970s there is evidence that overfishing during a period of natural decline probably caused the collapse of the stock. However, there is also evidence from more recent similar events that the management system appears to be able to adjust fishing pressure sufficiently fast to prevent a repeat of the experience of the late 1970s. The fishery for sand eels has not been active for as long as that for herring and has probably not developed a sufficiently well-tuned adaptive approach to allow an effective response (in terms of speed and magnitude) to the early signs of stock vulnerability. However, some of the highest exploitation rates for sand eels occurred immediately before the recent decline in population biomass. Overall, there is evidence that high levels of exploitation may have exacerbated the recent decline of North Sea sand eels.

^{*} www.lenfestocean.org/foragefish

TABLE 4.1

Case Studies Examined by the Lenfest Forage Fish Task Force

Ecosystem Name	Ecosystem Type	Major Forage Species	Research or Management Element	Implications and Lesson(s) Learned
Antarctic	High Latitude	Krill (<i>Euphausia superba</i>)	Biomass threshold (75% B ₀)	Implemented to prevent excessive krill depletion to ensure predators have sufficient food; while not computed through a quantitative model, appears to be a conservative threshold
			Spatial TACs	Under development to prevent localized depletion
Baltic Sea	Enclosed sea	Sprat (<i>Sprattus sprattus</i>) Herring (<i>Clupea harengus</i>)	Multi-species assessments	Accounts for changes in forage fish density (sprat and herring) based on predator abundance (cod)
Barents Sea	High latitude	Capelin (<i>Mallotus villosus</i>) Herring (<i>Clupea harengus</i>)	Biomass threshold/"capelin limit rule" (TAC is set to zero when SSB falls below 200,000 tonnes)	Implemented to maintain forage fish and to prevent repeat collapses
			Multi-species and ecosystem models	Accounts for shifting climate, fishing, and predation pressure that can destabilize the ecosystem Implemented to evaluate how changes in abundance of capelin and its predators affect ecosystem diversity and productivity
Benguela Current	Upwelling	Anchovy (<i>Engraulis encrasicolus</i>), sardine (<i>Sardinops sagax</i>)	In South Africa, operational management procedure with adaptive feedback implemented; conservative TACs based on seasonal surveys	Anchovy TAC can increase only following the results of mid-season recruitment surveys
			In South Africa, joint management of forage fish; total allowable bycatch (TAB) of sardine coupled with anchovy TAC	Accounts for schooling of anchovy and sardine to limit bycatch
			Experimental closed areas in South Africa	Closures are being implemented to quantify forage fish depletion effects on penguins
California Current	Upwelling	Pacific sardine (<i>Sardinops sagax</i>), northern anchovy (<i>Engraulis mordax</i>), Pacific herring (<i>Clupea pallasii</i>), eulachon (<i>Thaleichthys pacificus</i>), whitebait smelt (<i>Allosmerus elongates</i>), Pacific sandlance (<i>Ammodytes hexapterus</i>) Euphausiids (<i>Thysanoessa spinifera</i> , <i>Euphausia pacifica</i> , <i>Nyctiphanes simplex</i>)	TAC is reduced below MSY by a "buffer" of 150,000 mt and is modified by expected productivity (temperature dependent)	Instituted to account for uncertainty related to forage fish populations and ecosystem variability/predator needs; while not computed through a quantitative model, provides a buffer thought to be precautionary
			Prohibition of Pacific krill fishing	Instituted as a precautionary measure to ensure prey availability

Ecosystem Name	Ecosystem Type	Major Forage Species	Research or Management Element	Implications and Lesson(s) Learned
Chesapeake Bay	Estuary	Atlantic menhaden (<i>Brevoortia tyrannus</i>) Bay anchovy (<i>Anchoa mitchilli</i>)	Coastwide stock assessment only for menhaden; no spatially explicit assessment information	Menhaden abundance within the Chesapeake Bay has not been estimated; therefore management within this area needs to be more precautionary to avoid localized depletion
			Purse-seine reduction fishery quota for menhaden in the Chesapeake Bay is based on past average catches rather than a level shown to sustain forage fish population or ecosystem needs	Menhaden fishing mortality has exceeded the threshold in recent decades; Management changes in 2011 constrain fishing mortality to maintain 15% maximum spawning potential Management of menhaden fishing does not consider predator needs in Chesapeake Bay or coastwide
Gulf of Maine	Semi-enclosed embayment	Atlantic herring (<i>Clupea harengus</i>) Alewives (<i>Alosa pseudoharengus</i>), blueback herring (<i>A. aestivalis</i>), Atlantic menhaden (<i>Brevoortia tyrannus</i>)	Hard TAC for herring with a buffer; fishery closes when 95% of quota is caught. Seasonal spawning closures for herring in the fall	Implemented to rebuild spawning stock biomass of herring
Humboldt Current	Upwelling	Peruvian anchoveta (<i>Engraulis ringens</i>)	Biomass threshold (anchoveta fishery is closed when biomass falls below 5 million tonnes)	Instituted to ensure that anchoveta recruitment is maintained
North Sea	Semi-enclosed sea	Herring (<i>Clupea harengus</i>) North Sea sand eels (<i>Ammodytes</i> spp.)	Herring TACs set according to scientific advice	However, catch has exceeded recommended levels, showing that fishing mortality may not be controlled even when TACs may be appropriate
			Spatial closures for sand eel fishery	Implemented to ensure prey availability for kittiwakes and to prevent their decline

5

Direct and Supportive Roles of Forage Fish

Forage fish constitute a large and growing fraction of global wild marine catch (Alder *et al.* 2008). Most studies of forage fish have focused on their role as a directly harvested commodity, and have virtually ignored the other important roles they play both ecologically and economically. The value of their supportive functions within ecosystems is much less easily quantified than their direct value, however. Consequently, the overall global importance of forage fish has likely been significantly understated.

As described in Chapter 1, forage fish play a critical role in the ecosystems they inhabit by transferring energy from low to upper trophic levels (Cury *et al.* 2000, Fréon *et al.* 2005). Strong dependence on forage fish as prey has been described for a wide range of marine species including other fish, seabirds, and marine mammals. The supportive role of forage fish is clearly both an ecologically and economically important one. Many species that consume forage fish are caught in commercial fisheries. This creates the potential for trade-offs between fisheries that target forage fish directly, and those that target species for which forage fish are important prey.



Forage fish contribute an estimated total of \$16.9 billion USD to global fisheries annually.

Striped bass, © Doug Stamm/SeaPics.com. Off-loading of anchovies, background, Lenfest Forage Fish Task Force.

KEY POINTS

- We performed an analysis of 72 ecosystem models to measure the importance of forage fish to marine systems and economies. We examined direct catch value, indirect support of non-forage fish fisheries, as well as forage fish importance to other ecosystem predators.
- Forage fish contribute an estimated total of \$16.9 billion (ex-vessel value in 2006 USD) to global fisheries annually. According to our analysis, the direct catch value is approximately one-third of that total.
- The economic value of forage fish is highest in upwelling ecosystems, with the largest catch and value generated by the Humboldt current where the Peruvian anchoveta fishery occurs. Catch and catch value generally decreased at higher latitudes.
- The value of forage fish as supporters of other commercially fished species is also highest in upwelling ecosystems and exceeds the value of direct catch in 30 of the ecosystems we studied.
- Forage fish provide the largest proportion of their support value to ecosystem predators in high latitude systems (>58° North and South).

In this chapter we describe the methods and results of an analysis of food web models that was aimed at providing a global view of both the supportive and direct contributions forage fish make in modern-day ecosystems. We compare and contrast the results for different types of ecosystems, and elucidate patterns observed. Finally, we present estimates of the economic value of forage fish to commercial fisheries, first by ecosystem type, and then extrapolated to provide the first estimate of the economic value of forage fish globally.

Methods

We used Ecopath models that were published and/or provided to us by the investigators who originally developed them. Ecopath models are food web models which contain information on the major species or functional species groups within an ecosystem and their respective trophic linkages and energy flows (Polovina

1984, Christensen and Pauly 1992). Of the more than 200 Ecopath models that have been published, we selected 72 for our analysis, based on availability, geographic coverage, and temporal coverage. Only models that described the period from 1970 or later were included. The Ecopath models used (Appendix E, Table 1)* spanned a wide geographical range and provided relatively good global coverage of most coastal ocean areas and marine ecosystem types, with the exception of the Indian Ocean region, which is poorly studied compared with others (Figure 5.1). Organisms were considered to be forage fish if they met the criteria developed by the task force (see Box 1.1). However, in some cases where important forage fish species had been combined into model groups by the original investigators, the entire group was included in the forage fish category (see Appendix D* for details on this methodology). A comprehensive list of forage fish species included in the models is provided in Appendix E, Table 2.*

* www.lenfestocean.org/foragefish

Figure 5.1

Approximate locations of the 72 Ecospath models used in this analysis



We recognize that using Ecospath models, as for any mathematical representation of an ecosystem, has certain limitations. Ecospath models provide only a single spatial and temporal snapshot of an ecosystem, which means that they do not capture changes in ecosystem dynamics and fishing effort over space and time. Models are constructed based on the investigator's understanding of the ecosystem and research objectives, so model complexity varies. For instance, some Ecospath models lack predators that are known to prey on forage fish,¹³ and in other cases, investigators pooled individual predator species together into a single trophic group. Aggregating predators results in an averaged percentage of forage fish in the "diet dependency" for the model group, and may mask high diet dependency for one or more individual species in that group. In addition, averaging diet dependence for a single species over a large geographic area may mask high diet dependencies that may occur on smaller spatial scales. "Ground-truthing" every model to determine how well it represents its respective ecosystem

was beyond the scope of this analysis. However, our approach enabled us to use a large number of models over a wide range of ecosystems, and it provides a relatively rapid way of assessing the importance of forage fish in marine ecosystems around the world.

Importance of forage fish to predators—We used the Ecospath models to identify forage fish predators and to measure the degree of dependence of each predator on forage fish. A species was considered a forage fish predator if its diet contained any forage fish (i.e., diet of > 0 percent forage fish). We denoted species whose diet was comprised of $\geq 50 < 75$ percent forage fish as "highly dependent," and those for which forage fish comprised 75 percent or more of their diet as "extremely dependent"; we then calculated the number of highly and extremely dependent predators in each model. We also developed a pooled frequency distribution of predator dependence (percent of forage fish in the diet) by combining data from all models.

¹³ Nearly 30 percent (21 out of 72) of the models in our study did not include any seabird model groups, while 33 percent (24 out of 72) did not have a marine mammal group. Consequently, our results may be viewed as conservative since we were not able to capture the importance of forage fish to predators not included in those models.

Calculating the direct and supportive roles of forage fish to commercial fisheries—To facilitate comparison across ecosystems, estimates were standardized to the same units. The annual catch weight or “volume” per unit area (t/km²/yr) was calculated for each commercially important fishery species in each ecosystem model. To estimate the direct value of forage fish catch in each ecosystem (in USD/km²/yr), catch volume was multiplied by species-specific ex-vessel price per tonne (Sumaila *et al.* 2007) and summed over all forage fish species. The supportive value of forage fish to other fisheries was calculated by determining the fraction of catch for each predator species that was supported by the consumption of forage fish, and then multiplying the result by the total catch volume of the predator species. This was then multiplied by the ex-vessel value for each predator species and summed across all species (Hunsicker *et al.* 2010). Further details on calculations and equations used are provided in Appendix D.* Data obtained for each ecosystem model were grouped by ecosystem type and latitude to determine whether there were patterns in direct, supportive, or total value among categories.

Global estimate of forage fish economic value to fisheries—To provide a global picture of the contribution of forage fish to total commercial fisheries value, we used the estimates of the direct and supportive values of forage fish by ecosystem model and then extrapolated the results to derive global estimates. Details of the procedures used are provided in Appendix D.* Briefly, we worked at the scale of Exclusive Economic Zones (EEZ) or High Seas Areas (HSA), for which catch value data by species and functional group (species that perform a similar role in the ecosystem) were available (courtesy of the *Sea Around Us* Project). When a single Ecopath model was situated within a given region, we assumed that this model provided a reasonable estimate of the supportive value of forage fish for the entire region. When multiple Ecopath models were available for a given region, we used average values weighted by the geographic area covered by each ecosystem model.

* www.lenfestocean.org/foragefish

¹⁴ Non-cephalopod invertebrates are excluded from these values.

Ecopath models were present in 25 percent (64 out of 257) of the world’s EEZs and HSAs, constituting 39 percent of the global marine catch value¹⁴ (2006 USD) and 53 percent of the global forage fish direct catch value¹⁴ (2006 USD) (Sumaila *et al.* 2007). An additional 86 EEZs and HSAs, which did not have Ecopath models, were included under the assumption that the Ecopath model in the EEZ or HSA immediately adjacent was representative of that neighboring EEZ or HSA. These EEZs and HSAs represented an additional 28 percent of the global forage fish direct catch value to fisheries. The remaining 107 EEZs or HSAs did not have Ecopath models or an adjacent neighbor with an Ecopath model (e.g. isolated islands) and represented only 19 percent of the global forage fish direct value to fisheries. In these EEZs or HSAs, we applied an “Ecopath value relationship” (see Appendix D),* or EVR, based on the average of EVRs from other Ecopath models in the same latitudinal group. EVRs are the ratio of supported predator catch value (i.e., predators that consume forage fish) to total fisheries catch value (i.e., predator catch value plus non-predator catch value). We calculated all values as ex-vessel real price values in 2006 USD and summed all support service values and forage fisheries catch values across all EEZs and HSAs. This produced our estimate of forage fish contribution to global fisheries value. We calculated value data as ex-vessel value in 2006 for all EEZs and HSAs and represented the sum of both the direct and supportive values of forage fish. For further details on the extrapolation method used, refer to Appendix D.*

Results

Extent of predator dependency on forage fish—Seventy-five percent (54 out of 72) of the Ecopath models had at least one predator that was highly (≥ 50 percent but < 75 percent of diet) or extremely dependent (≥ 75 percent of diet) on forage fish. Furthermore, 29 percent of the models included at least one predator with a diet consisting of 75 percent or more of forage fish (Figure 5.2a). Extremely dependent

Figure 5.2a

Percentage of Ecopath models (n = 72) with at least one predator with a forage fish diet of $\geq 50\%$.

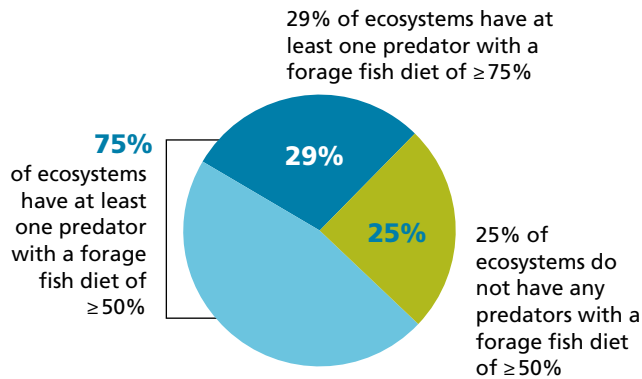
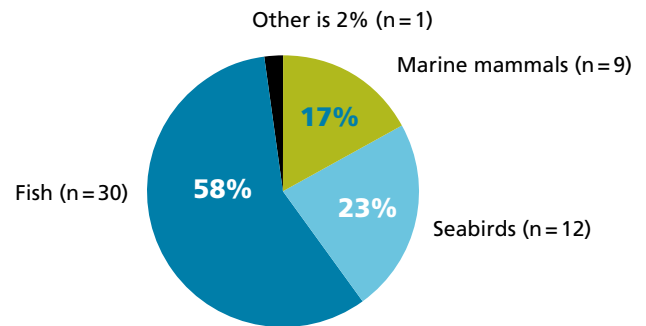


Figure 5.2b

Composition of predators (n = 52) with forage fish diets $\geq 75\%$, from all Ecopath models. ("Other" is Patagonian squid.)



predators included seabirds, marine mammals, large pelagic fish, and one species of squid (Figure 5.2b), and were found in all latitude groups and ecosystem types, with the exception of open ocean ecosystems. In general, extremely dependent predators were most commonly found in upwelling and Antarctic ecosystem types, where on average 2 and 5 extremely dependent predators were found in each model of these ecosystem types, respectively.

Pooled data across all models indicated that 49 percent of all predators relied on forage fish for at least 10 percent of their energy requirements (Figure 5.3), and that on average, 16 percent of all predators in an ecosystem were highly or extremely dependent on forage fish. Close to one out of five predator species in these models relies on forage fish to supply the majority of their energy requirements. There were some predators whose diets consisted of more than 90 percent forage fish, although they were rare, representing fewer than 5 percent of all predator species. Antarctic ecosystem models had the greatest percentage of dependent predators across all levels of forage fish dependency, while tropical lagoons had the lowest (Figure 5.4).

* www.lenfestocean.org/foragefish

¹⁵ We used all 72 Ecopath models to determine forage fish catch in weight; however only 56 Ecopath models could be used to determine value. This is because only 56 Ecopath models had full taxonomic information of all model groups, which is necessary to determine ex-vessel prices.

Importance of forage fish to commercial fisheries—

Direct forage fish catch and catch of other species supported by forage fish varied greatly among the Ecopath models examined, both in tonnage and value.¹⁵ In some Ecopath models, no forage fish catch was reported, while in other models forage fish catches were extremely large (Appendix E, Figure 5.1).^{*} Three Humboldt Current models, where the Peruvian anchoveta fishery operates, had the highest forage fish catches in this analysis. Of the Humboldt Current models, the Sechura Bay (Peru) model reported an extraordinarily high level of forage fish catch (81 t/km²/yr valued at \$35,497 USD/km²/yr). The two "northern Humboldt Current" models for El Niño and La Niña time periods had forage fish catches of 20 t/km²/yr (\$934 USD/km²/yr) and 39 t/km²/yr (\$2,020 USD/km²/yr), respectively.

Forage fish had an important supportive role for commercial fisheries catch in all models examined, including those in which there were no direct forage fish catches. Of the ecosystems we examined, the supportive service of forage fishes was most important to the catch of other commercial fisheries in central Chile (3.82 t/km²/yr), Prince William Sound (pre-oil spill: 3.58 t/km²/yr), and the northern California Current (3.04 t/km²/yr; Appendix

Figure 5.3

Frequency of predators of different dependency levels (percent of forage fish in diet) across analyzed ecosystems (n = 72) with standard deviation plotted.

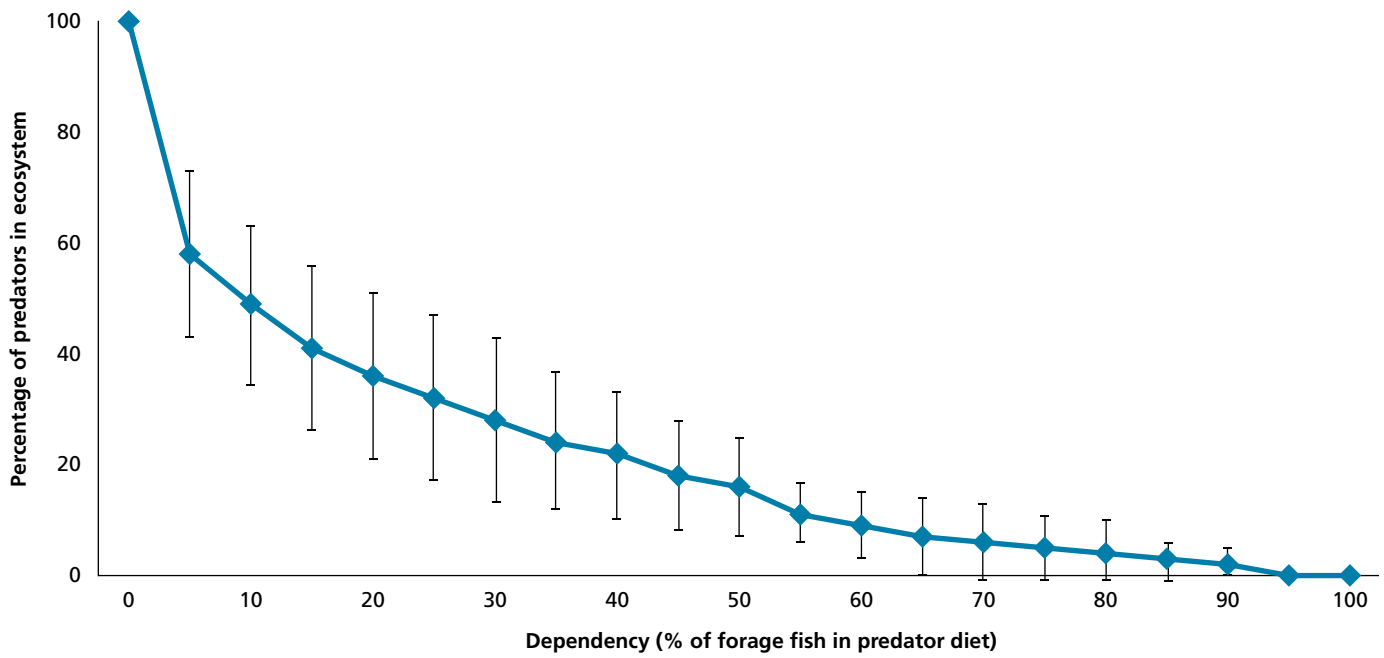


Figure 5.4

Comparison across ecosystem types of the percentages of predators within a given forage fish dependency level.

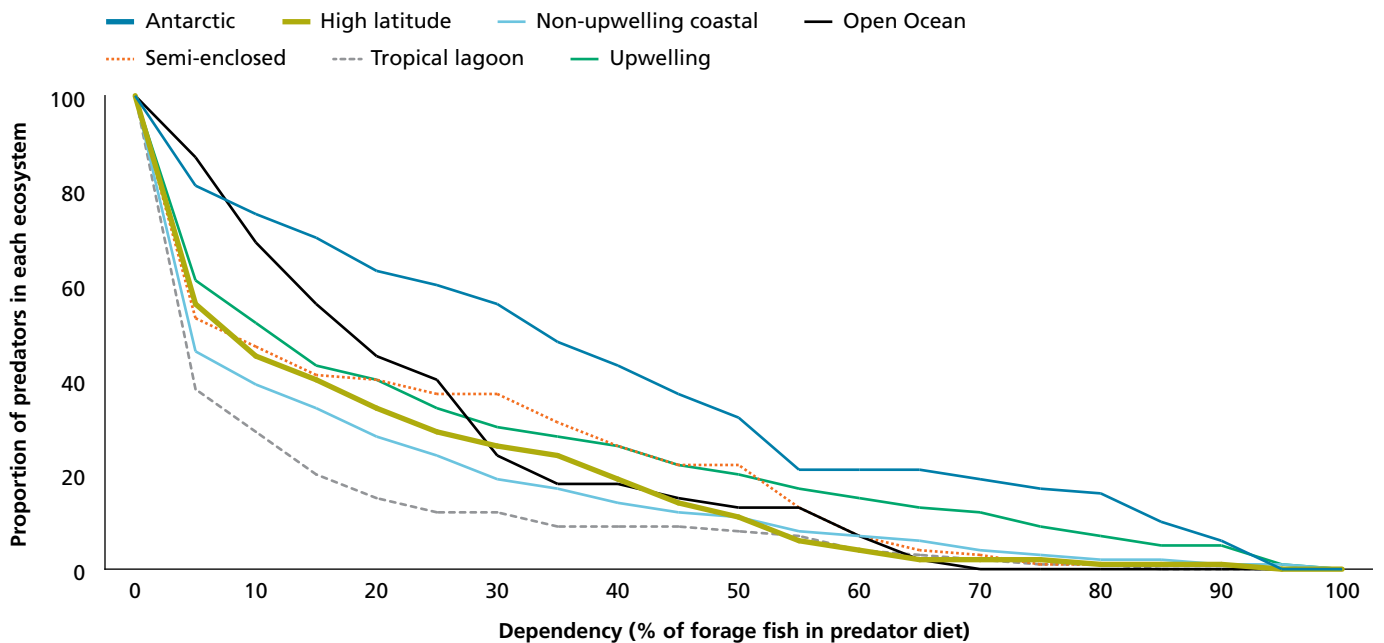
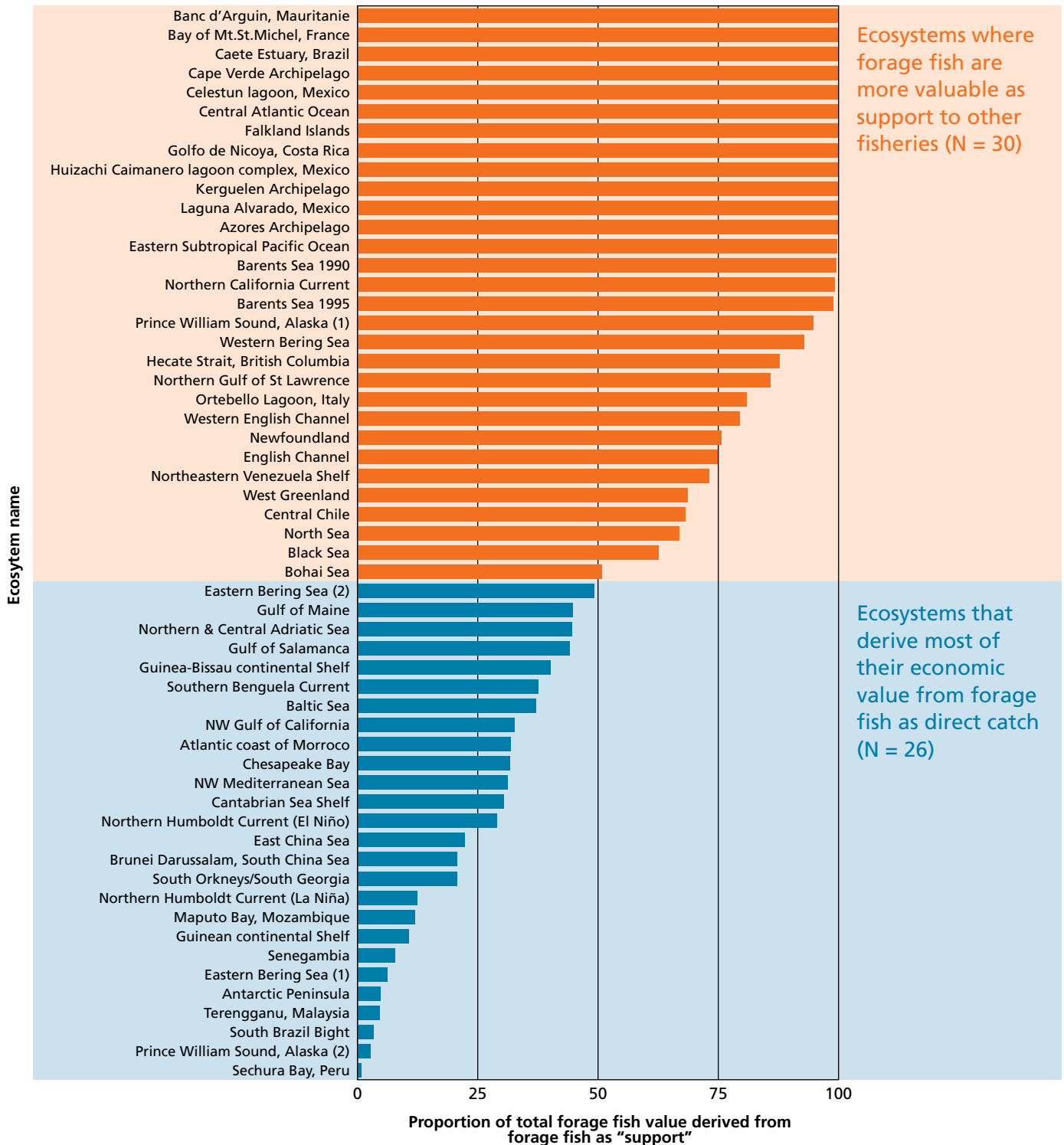


Figure 5.5

Cross-ecosystem comparison of support service value to total fisheries value (direct and supportive forage fisheries value).

This graph represents only a snapshot, and the ratio of support value to direct catch value will change with the expansion or reduction of fisheries for forage species.



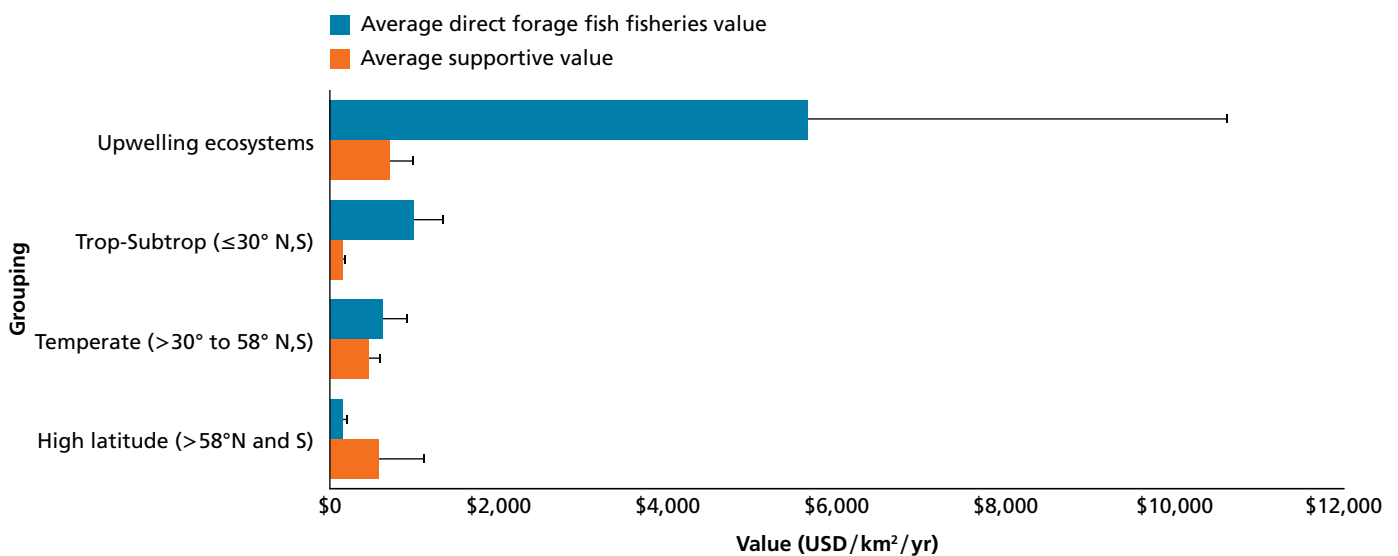
E, Figure 5.2).^{*} In terms of value, forage fish provided the greatest supportive contribution to fisheries in Prince William Sound¹⁶ at a value of \$5,942 USD/km²/yr, followed by the Chesapeake Bay at a value of \$2,966 USD/km²/yr. The high supportive value in these ecosystems is due to the large contribution of forage fish to the diets of salmon (*Oncorhynchus* spp., Prince William Sound) and striped bass (*Morone saxatilis*, Chesapeake Bay), both of which are relatively high-value species.

We calculated the relative amount of direct and supportive contributions of forage fish to fisheries in each Ecopath model to facilitate comparisons across models. In 13 out of 56 models, 100 percent of the total forage fish value was derived from the supportive service to other commercial fisheries (i.e., there were no direct forage fish fisheries in these 13 ecosystems; Figure 5.5).¹⁷ The ex-vessel value of the commercial fisheries catch supported by forage fish was greater than the value of forage fish catch in more than half of the models we examined (30 out of 56 models; Figure 5.5).

Latitudinal comparisons—The largest per-unit-area annual forage fish catches were found in the tropical-subtropical latitude group (4.95 t/km²/yr ± 2.5 SE) and decreased monotonically from the tropics to the polar regions. In contrast, the ecological support service of forage fish to other commercial fisheries catch was lowest in the tropical-subtropical latitude group (0.23 t/km²/yr ± 0.05 SE) and was greater in temperate (0.63 t/km²/yr ± 0.2 SE) and high latitude ecosystems (0.35 t/km²/yr ± 0.29 SE). When upwelling ecosystems were excluded, Ecopath models representing temperate regions had the highest direct forage fisheries catch amongst latitude groups (Appendix E, Figure 5.3).^{*} Direct catch value (excluding upwelling ecosystems) was greatest in the low latitude systems and diminished poleward (Figure 5.6). Forage fish support service to fisheries increased poleward so that it was nearly equal to direct catch (Appendix E, Figure 5.3)^{*} or exceeded the value of direct catch (Figure 5.6) in high latitudes.

Figure 5.6

Catch value of forage fish (blue bars) and mean contribution of forage fish to other commercial species' catch value (orange bars), by latitude. Upwelling groups were separated out to more clearly demonstrate latitudinal patterns, with standard error plotted.



^{*} www.lenfestocean.org/foragefish

¹⁶ Prince William Sound, pre-oil spill model created by Dalsgaard and Pauly (1997).

¹⁷ Our analysis is based on the time period for the respective Ecopath models and does not reflect changes in fisheries effort or new fisheries that may have occurred since the model was created.

Comparisons across ecosystem-types—Forage fish catch volume (per unit area per year) was highest in upwelling ecosystems (Figure 5.7a), exceeding that of all other ecosystem types combined by a factor of four. Forage fish direct catch volume exceeded the volume of catch from supported fisheries for all ecosystem types (Figure 5.7a). Similarly, forage fish were most economically valuable (in terms of direct catch) in upwelling ecosystems at \$5,657 USD/km²/yr ± \$4,980 SE (Appendix E, Figure 5.4).^{*} Other ecosystem types had substantially lower average direct forage fish values, each contributing less than \$830 USD/km²/yr. The value of forage fish catches was smallest in the high latitude Arctic and Antarctic ecosystems (\$171 USD/km²/yr and \$149 USD/km²/yr, respectively). In contrast, the supportive value of forage fish was greatest in the Arctic ecosystem (mean = \$786 USD/km²/yr)—over 4.5 times greater than the value of the direct forage fish catch for that ecosystem type (Appendix E, Figure 5.4).^{*}

^{*} www.lenfestocean.org/foragefish

Global estimate of forage fish value to fisheries—We estimated the total ex-vessel value of forage fish to global commercial fisheries to be **\$16.9 billion** (2006 USD), using the estimation methods described in Appendix D.^{*} This estimate combines the direct forage fish fishery value of \$5.6 billion (33 percent, 2006 USD) with a supportive service value to non-forage fish fisheries of \$11.3 billion (67 percent, 2006 USD). Importantly, we found that the value of fisheries supported by forage fish (e.g., cod, striped bass, salmon, etc.) was twice the direct value of forage fish fisheries at a global scale (Figure 5.8). We note that the estimated total ex-vessel value of \$16.9 billion dollars annually is likely an underestimate, because it does not take into account the contribution of forage species to early life history stages of predators that are not yet of commercial catch size (e.g., juvenile cod, juvenile striped bass). In this analysis we did not include forage fish species that are only forage fish for certain life stages (e.g., Alaska pollock, Blue whiting), as there is no age structure in the majority of these Ecopath models. More importantly, the ex-vessel

Figure 5.7a
Cross-ecosystem comparison of mean catch of forage fish (blue bars) and mean contribution of forage fish to other species' catch (orange bars) with standard error plotted.

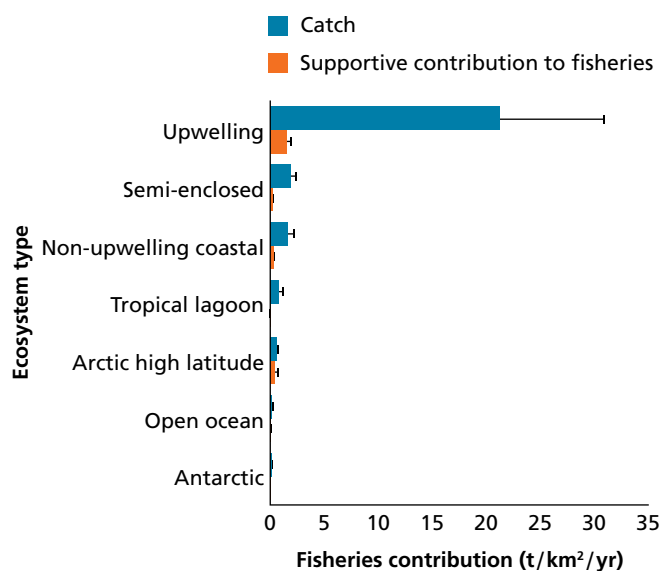


Figure 5.7b
Average forage fish contribution to (non-commercial) ecosystem predator production by ecosystem type with standard error plotted.

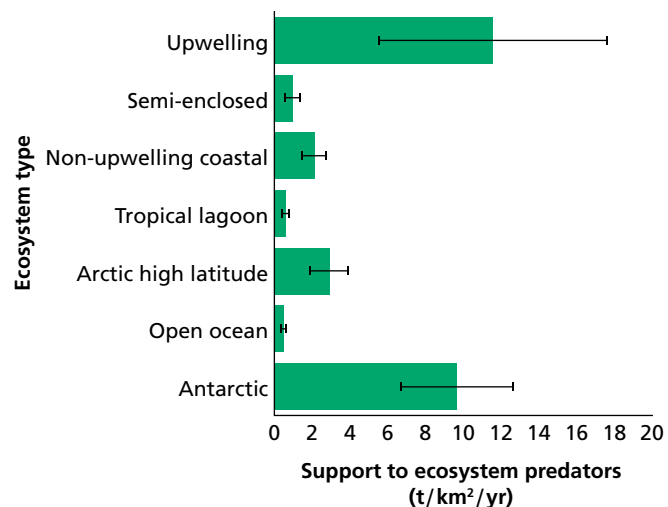


Figure 5.8

Economic importance of forage fish

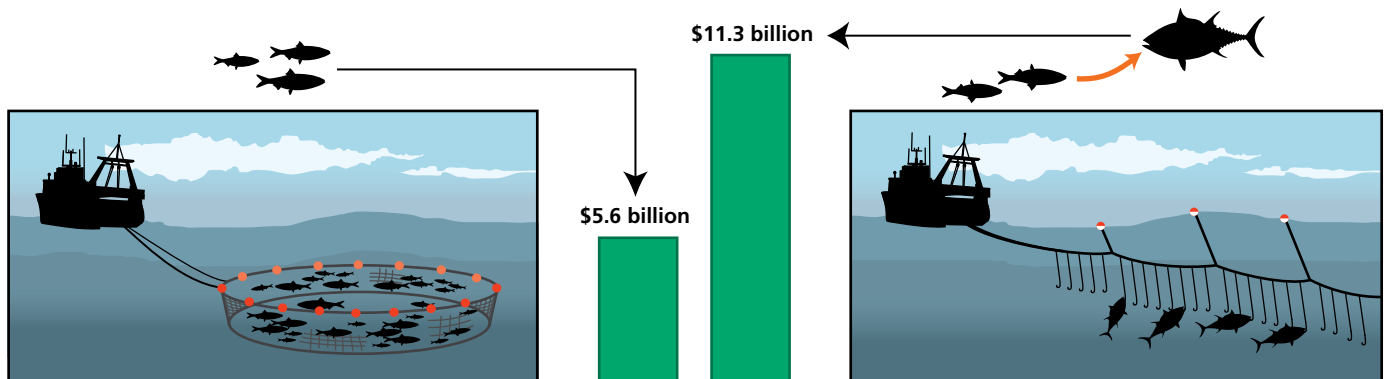
The total value of forage fish to global commercial fisheries was \$16.9 billion (2006 dollars). The value of fisheries supported by forage fish (e.g., cod, striped bass, salmon) was twice the direct value of forage fish.

FORAGE FISH DIRECT VALUE

The commercial catch of forage fish was \$5.6 billion.

FORAGE FISH SUPPORTIVE VALUE

Forage fish added \$11.3 billion in value to commercial catch of predators.



value of commercial fisheries is only one of many other indicators of the economic contributions of forage fish, and thus is clearly an underestimate of total economic worth. Significantly, we have not accounted for the potential economic value of forage fish to recreational fisheries, to ecotourism (e.g., the global potential for the whale-watching industry is estimated at \$2.5 billion 2009 USD annually (Cisneros-Montemayor *et al.* 2010), as bait for fisheries, and to the provision of other ecosystem services such as water filtration.

The supportive contribution of forage fish to all ecosystem consumers—We found that the amount of total predator production supported by forage fish varied greatly among the 72 models in this analysis (Appendix E, Figure 5.5).^{*} Forage fish contribute to the production of all ecosystem predators, whether or not they are commercially important in marine ecosystems. Total predator production supported by forage fish was largest for two upwelling ecosystems, the northern California Current and central Chile, where forage fish were estimated to contribute more than 52 t/km²/yr and 17 t/km²/yr to predator production, respectively. When the contribution of krill to production of other forage fish (e.g. sardines and anchovies) is removed in the northern California Current model, the support

service to predators drops to 32 t/km²/yr, which is still the largest of all ecosystems in this analysis. In terms of latitude groupings (with upwelling ecosystems excluded), we found that the greatest average supportive contributions of forage fish to predator production were found in high latitude regions (4.06 t/km²/yr ± 1.21 SE), followed by temperate latitudes (2.28 t/km²/yr ± 0.98 SE), and were lowest in tropical-subtropical latitudes (1.01 t/km² ± 0.16 SE; Appendix E, Figure 5.6).^{*} By a large margin, the greatest supportive contribution of forage fish to predator production was seen in upwelling and Antarctic ecosystems (Figure 5.7b). The supportive contributions to predator production in both these ecosystem types exceeded 9 t/km²/yr and were more than three times greater than values seen for Arctic ecosystems and non-upwelling coastal ecosystems, and more than an order of magnitude greater than open-ocean, tropical lagoon, and semi-enclosed ecosystems (Figure 5.7b).

Large differences were seen in the support service contribution of forage fish to total predator production compared with the two (direct and supportive) contributions of forage fish to commercial fisheries catch across latitude groups (Figure 5.9). Upwelling ecosystems exhibited the greatest forage fish contributions for

^{*} www.lenfestocean.org/foragefish

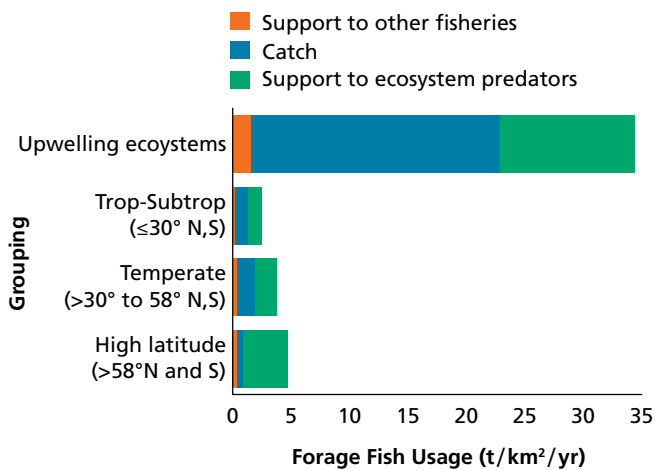


Some seabirds are “extremely dependent” on forage fish, relying on them for 75 percent or more of their diet needs. In fact, seabirds had the highest proportion of this dependency level out of all the predator types in our analysis.

Nesting colony of pelicans, Peru. Photo: © Tui De Roy/Minden Pictures

Figure 5.9

Forage fish usage across latitudes.



every category (direct catch, support service catch, and support to predator production). A poleward increase in the proportion of forage fish supporting total predator production (both commercially and non-commercially important predators) is evident from tropical-subtropical latitudes to high-latitude ecosystems (Figure 5.9). In the high-latitude grouping, the contribution of forage fish to predator production was 7.8 times greater than the direct catch of forage fish, while in lower latitudes these roles were of approximately equal importance.

Major Findings and Conclusions

Our analysis is the first to provide global estimates of the importance of forage fish as support for all predators in marine ecosystems. Additionally we provide the first estimate of the ex-vessel value and tonnage that forage fish contribute to non-forage fish fisheries worldwide. Quantification and comparison of the allocation of forage fish usage among direct catch, support to commercially targeted predators, and support to all other ecosystem predators (Figure 5.9) allows identification of potential trade-offs that may occur among uses.

Our results indicated that forage fish catch and value (both in terms of direct and supportive service) vary tremendously across the globe, with discernible patterns seen across latitude groupings and ecosystem types. In particular, we have found a decreasing poleward trend

in the economic value of direct forage fishery catch, with average economic values greatest in tropical-subtropical latitudes and decreasing with higher latitude. The opposite poleward trend was seen in the support of forage fish to other commercially important fisheries. Fisheries supported by forage fish were most valuable in high latitude ecosystems and value decreased towards lower latitudes. Upwelling ecosystems, particularly the Humboldt Current, stand apart from other ecosystem types in having the largest forage fish fisheries in terms of both volume and economic value. Forage fish also provide some of the greatest support to other fisheries and to predator production in upwelling ecosystems, in absolute terms. In proportional terms, the greatest contributions to ecosystem predator production are found in the high-latitude grouping and are lowest in the upwelling ecosystem group. Competition for the use of forage fish among competing ecological and economic interests and the resulting trade-offs can lead to conflicts in the management of forage fish and should be explicitly considered in the decision-making processes for management and conservation.

We described many types of forage fish predators, which were seen in all the geographic regions examined. Many predators have diets that are heavily dependent on forage fish, possibly making them more vulnerable to reductions or fluctuations in forage fish biomass. Extremely dependent predators included fish, seabirds, marine mammals, and one species of squid. These predators were most commonly found in upwelling and Antarctic ecosystems.

Our results are useful for understanding the tradeoffs that can occur between direct fisheries for forage fish, forage fish-dependent commercially important fisheries, and other forage fish predators in marine ecosystems. Our analysis provides a method for identifying dependent forage fish predators across marine ecosystems. We also provide information about ecosystem types where forage fish may play an especially important ecological role as prey for dependent forage fish predators. This work represents an important step towards a comprehensive quantification of the overall direct and supportive contributions forage fish make to marine ecosystems and to the global economy.

6

Comparison of Fisheries Management Strategies and Ecosystem Responses to the Depletion of Forage Fish

In this chapter, we report on the methods and results of our research using quantitative food web models to explore how ecosystems respond to forage fish management strategies. The results of the model effort appear robust, particularly because they appear to reflect real-world changes seen in ecosystems subjected to overfishing. Using a suite of published ecosystem models, we evaluated the effects of alternative harvest control rules, including constant fishing mortality and constant yield, on target forage fish species and their dependent predators. We compared how each of the harvest control rules performed in relation to several performance indicators, including avoiding forage fish population collapses, sustaining reasonably high catch levels of the target species, or minimizing the impacts of fishing on dependent species. We then identified those control rules that resulted in the best outcomes for the performance indicators.



Fishing at half of the traditional F_{MSY} rate results in low probability of collapse for forage species, and lower declines in dependent species.

Baltic herring in a net on a fishing boat, Sweden. Salted herring, background, © Shutterstock.

KEY POINTS

- We assessed the ecological impacts of forage fish fishing on whole ecosystems by examining the responses of organisms to variations in the harvest rate for forage species in 10 Ecopath with Ecosim models.
- Diet dependency plays a critical role in the effects of forage fish removals on top predators.
- We developed a predictive model, Predator Response to Exploitation of Prey (PREP), which indicates the expected decline in predators as forage fishes are depleted.
- Significant reductions in dependent predators can occur with forage fish removals of greater than 20 percent of the biomass predicted by the ecosystem model when there is no fishing.
- We found that harvesting at a constant rate based on Maximum Sustainable Yield led to the largest and most variable reductions in forage fish and predator biomass. Fishing with a conservative “cutoff” and gradual increase in harvest rate with forage fish biomass had much lower impacts on the ecosystem and a lower probability of stock collapse.

Methods

We assembled 10 independently published Ecopath with Ecosim models (Christensen and Walters 2004; hereafter referred to as EwE models), each representing an ecosystem in one of 10 regions of the world, ranging from coastal upwelling systems to semi-enclosed seas (Appendix E; Table 6.1).^{*18} These models were used without modifications from the published papers. We applied EwE version 6.0.7 with an additional module¹⁹ developed to enable consideration of observation error and to facilitate testing of multiple harvest control rule strategies (Christensen and Walters 2004). Both deterministic and stochastic models were employed to assess the effectiveness of harvest control rules on forage fish fisheries. The deterministic models were used to evaluate general properties of system responses to fishing. The more complex, stochastic models included

perturbations and realistic variability of the fishing mortality rate, and thus better reflect how the harvest control rules compared under more realistic settings. Following the specific example of South African sardines given by de Moor *et al.* (2008) and the broader outlines in Smith (1993) and Hilborn and Liermann (1998), we used a coefficient of variation (CV) of 30 percent on the fishing mortalities.

Although other multispecies trophic models exist (e.g., Osmose, Atlantis), we used EwE exclusively because we wanted to evaluate alternative harvest control rules across many ecosystems using a consistent model format and a significant number of models. EwE is the most widely used marine ecosystem modeling platform, is available to the public, and is particularly effective and capable of testing multiple harvest control rules (Fulton 2010).

* www.lenfestocean.org/foragefish

¹⁸. A description of each ecosystem and EwE model in this meta-analysis can be found in Appendix F.*

¹⁹. A more detailed description of the module developed for this analysis can be found in Appendix G.*

TABLE 6.1**Ecosystems and their forage fish species**

The forage fish species and species groups analyzed in our research, along with their respective ecosystems and the EWE models' authors.

Ecosystem	Forage fish species or group (as developed by modeler)	Model authors and reference
Aleutian Islands	<ul style="list-style-type: none"> • herring (<i>Clupea pallasii pallasii</i>) • sand lance (<i>Ammodytes hexapterus</i>) • small pelagics (<i>Mallotus villosus</i>, <i>Engraulis mordax</i>, <i>Scomber japonicus</i>, Osmeridae) 	Gu�nette et al. (2006)
Baltic Sea	<ul style="list-style-type: none"> • herring (<i>Clupea harengus</i>) • sprat (<i>Sprattus sprattus</i>) 	Hansson et al. (2007)
Barents Sea	<ul style="list-style-type: none"> • capelin (<i>Mallotus villosus</i>) • herring (<i>Clupea harengus</i>) • pelagic planktivorous fish (<i>Ammodytidae</i>, <i>Trisopterus esmarkii</i>, <i>Micromesistius poutassou</i>, <i>Argentine</i> spp., <i>Cyclopterus lumpus</i>, <i>Sprattus sprattus</i>, Osmeridae, Clupeidae) 	Blanchard et al. (2002)
Chesapeake Bay	<ul style="list-style-type: none"> • alewives & herring (<i>Alosa pseudoharengus</i> and <i>A. aestivalis</i>) • American shad (<i>Alosa sapidissima</i> and <i>A. mediocris</i>) • Atlantic menhaden (<i>Brevoortia tyrannus</i>) 	Christensen et al. (2009)
Gulf of Mexico	<ul style="list-style-type: none"> • bay anchovy (<i>Anchoa mitchilli</i>) • Gulf menhaden (<i>Brevoortia patronus</i>) • scaled sardine (<i>Harengula jaguana</i>) • threadfin herring (<i>Dorosoma petenense</i>) 	Walters et al. (2006)
Humboldt Current	<ul style="list-style-type: none"> • Peruvian anchoveta (<i>Engraulis ringens</i>) • sardine (<i>Sardinops sagax</i>) 	Taylor et al. (2008)
Northern California Current	<ul style="list-style-type: none"> • euphausiids (order Euphausiacea) • forage fish (<i>Engraulis mordax</i>, <i>Clupea harengus pallasii</i>, <i>Thaleichthys pacificus</i>, <i>Allosmerus elongates</i>) • sardine (<i>Sardinops sagax caerulea</i>) 	Field et al. (2006)
North Sea	<ul style="list-style-type: none"> • herring (<i>Clupea harengus</i>) • sand eel (<i>Ammodytes</i> spp.) • sprat (<i>Sprattus sprattus</i>) 	Mackinson and Daskalov (2007)
Southeast Alaska	<ul style="list-style-type: none"> • herring (<i>Clupea harengus</i>) • sand lance (<i>Ammodytes hexapterus</i>) • small pelagics (<i>Mallotus villosus</i>, <i>Engraulis mordax</i>, <i>Scomber japonicus</i>, Osmeridae) 	Gu�nette et al. (2006)
Western English Channel	<ul style="list-style-type: none"> • herring (<i>Clupea harengus</i>) • pilchard (<i>Sardina pilchardus</i>) • sand eel (<i>Ammodytes tobianus</i>) • sprat (<i>Sprattus sprattus</i>) 	Araujo et al. (2005)



Fishing nets, North Sea, © Shutterstock.

The harvest strategies, or harvest control rules, we examined included constant fishing mortality, constant yield, “step” functions, and “hockey stick” control rules.

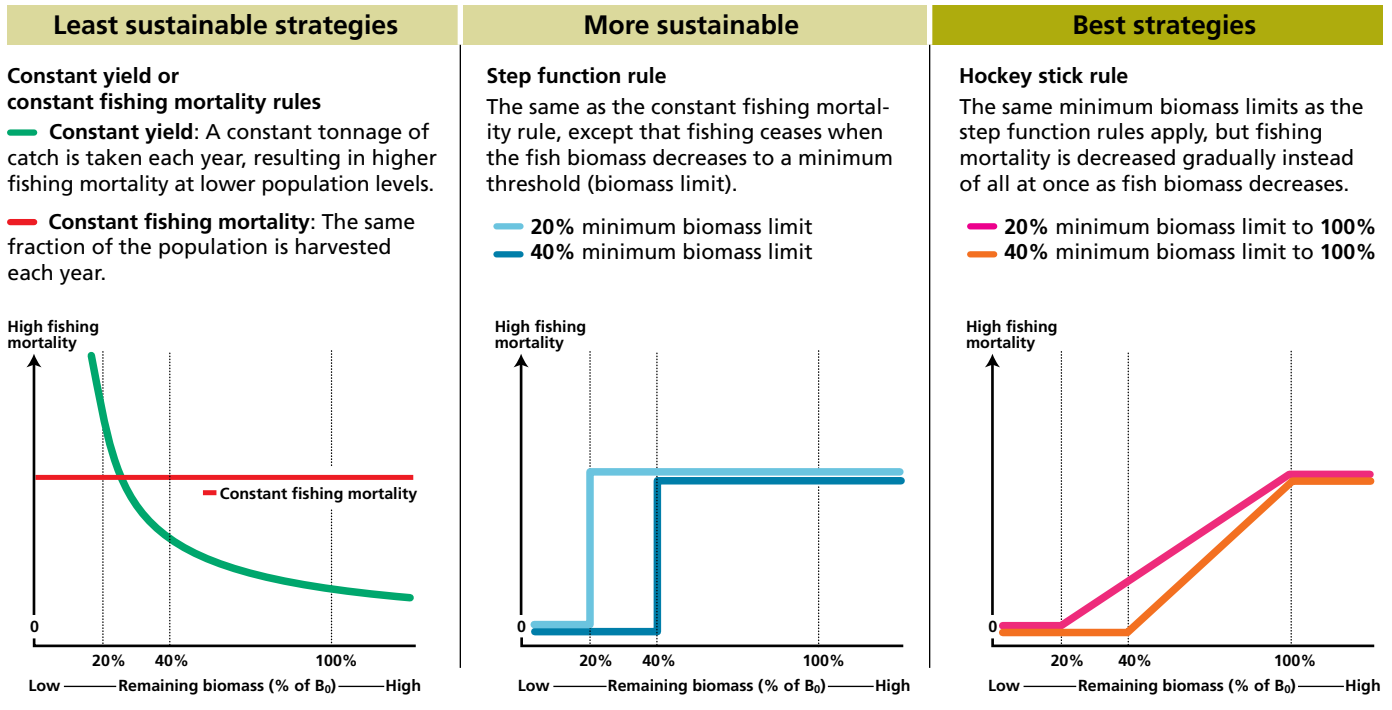
EwE models share many of the limitations described in Chapter 5 for Ecopath models. EwE models employ key parameters from Ecopath and build upon them using additional abundance, fishing effort, and mortality estimates. As with any large model, the reliability of the results depends on the accuracy of the input data and on the robustness of assumptions made about ecosystem dynamics. The base EwE models we compiled are deterministic models; they do not incorporate randomness and provide the same results for a set of initial conditions. Importantly, they always converge to an equilibrium state, whereby biomasses of each ecosystem component become constant. We added the ability to simulate stochasticity (via the module) so that we could explicitly examine the effects of unpredictability and uncertainty on model results. Another caveat is that the large geographic scale often represented in the models used may not portray important relationships that can occur on relatively small spatial scales. These drawbacks are minor when compared with the merits of being able to evaluate and compare the responses to various harvest control rules of 10 food web models constructed on an identical platform representing 10 different marine ecosystems.

Harvest control rules. The harvest strategies, or harvest control rules, we examined included constant fishing mortality (CF), constant yield (CY), “step” functions, and “hockey stick” (HS) control rules. We define a harvest control rule as a management approach that specifies how fishing intensity will vary (or not vary) depending on the state of the fishery. The harvest control rules are graphically illustrated in Figure 6.1 and described in the text that follows. The CF rule keeps mortality the same no matter the fish population biomass. Similarly, the CY rule keeps fish catch constant at all fish biomass levels. Step functions apply a fixed fishing rate (F) until the forage fish population biomass decreases to a minimum biomass threshold B_{LIM} , at or below which point there is no fishing. We denote the step strategies examined as $20 B_{LIM}$ and $40 B_{LIM}$, respectively, for minimum biomass thresholds of $0.2 B_0$ and $0.4 B_0$. We selected these thresholds because the smaller value has frequently been used when biomass thresholds are applied, and the larger value was selected to be substantially higher (i.e., twice as high) as the lower value and is close to the median values where impacts on vital rates of dependent predators have been found (see, for example, Cury *et al.* 2011 and other literature on empirical studies cited herein).

Figure 6.1

Comparison of harvest control rules

Strategies for setting the allowable catch rate (fishing mortality) based on the percentage of the unfished biomass (B_0) remaining in the fishery.



Population levels were calculated in terms of biomass (number x weight) and referenced to the biomass that the forage fish stock would be expected to reach if it were not fished (B_0), holding all other model parameters constant. HS control rules had the same minimum biomass limits as the step functions, but in addition, the fishing rate increased linearly for biomass between B_{LIM} and B_0 , and a CF rate was applied for biomass above B_0 . We denote the two HS control rules we investigated as 20/100 HS and 40/100 HS for B_{LIM} of 20 percent and 40 percent of unfished biomass, respectively.

We implemented the harvest control rules for each of the individual forage fish species separately in each EwE model for both deterministic and stochastic modeling approaches. The species-by-species harvest strategy approach we used may have resulted in conservative estimates of ecosystem responses to forage fish depletion because in our simulations, we did not deplete

multiple forage fish groups concurrently. Some models grouped individual forage fish species into one model category (e.g., alewives and herring were treated as one species group in the Chesapeake Bay EwE model). Hereafter, these model groups will be referred to as forage fish species or target species. Altogether, there were 30 forage fish “species” among the 10 EwE models analyzed (Table 6.1).

For the deterministic runs, we assessed and compared CF and CY control rules. To evaluate the constant fishing rate rule (CF), we ran the model numerous times with each run exploring a different fixed fishing rate (F). The sequence of runs examined a range of rates from a low of $F=0.0$, continuing upwards in fishing mortality rate increments of 0.01 from $F=0.0$ to $F=0.1$, and then in increments of 0.05 for higher F levels. The runs terminated once a level of fishing was reached that caused the forage fish population to experience extreme

collapse (i.e., the biomass fell below $0.01 B_0$). The number of runs conducted varied among species and ranged from 20 to 60.

Similarly, for the constant yield (CY) rule, a set amount of catch was taken every year for all years in a model run, with catch levels varying among runs. We tested CY harvest rules for all ecosystem models at seven yield levels, specifically: 1) $0.05 M B_0$, 2) $0.1 M B_0$, 3) $0.15 M B_0$, 4) $0.2 M B_0$, 5) $0.25 M B_0$, 6) $0.3 M B_0$, and 7) $0.5 M B_0$, where M is the equilibrium natural mortality rate when the population is unfished (i.e., $F=0$) and is predefined by the original EwE model. The deterministic models were run until Year 150 to ensure stabilization of the systems. Exploitation rates on all non-forage fish species were fixed at baseline levels (i.e., the levels provided by the fitted EwE model for that ecosystem) for all simulations.

For the stochastic runs, we assessed five harvest control rules: constant fishing mortality, the two step functions and the two hockey stick control rules. As explained in the results section, we chose not to pursue the constant yield rule for the stochastic runs because it proved to be an undesirable harvest strategy even under deterministic conditions. The CF rule we tested was similar to that used in the deterministic runs except that the mortality rate varied each year with a 30 percent CV. For the step function and HS control rules, as described above, a 30 percent CV was applied to fishing mortalities when forage fish biomass was greater than the lower biomass limit. Note that there is a mean-variance relationship: As fishing mortality increases, the associated variance also increases.

Parameters for stochastic runs. The results from the deterministic CF runs informed the parameter values used for the stochastic tests of the harvest control strategies. We conducted deterministic CF runs for each species and evaluated the effects of CF rates ranging from no fishing to complete extirpation. From these results, we calculated the model-specific, deterministic maximum sustainable yield (MSY, the maximum level of fishing that can be maintained), the corresponding forage fish biomass (B_{MSY}), the fishing mortality at which

MSY is achieved (F_{MSY}) and the unfished biomass (B_0) for the target species. The MSY was computed based on the fishing mortality rate that led to the largest median yield, with median computed from the last 10 percent of the years of the run. B_0 was calculated as the median terminal forage fish biomass, with the median calculated for the last 10 percent of the years for the zero fishing mortality run. These values from the deterministic runs were used to set the harvest control rule strategies for the stochastic runs as follows: B_0 was used to set the lower limits of the step and HS rules and were used in reporting the results; and F_{MSY} was used to set the maximum fishing levels for all rules.

To understand the ecosystem responses to forage fish depletion under variable conditions of forage fish biomass and fishing levels, we used the stochastic models to compare harvest control strategy performance for three nominal fishing mortality levels, 50 percent F_{MSY} , 75 percent F_{MSY} , and 100 percent F_{MSY} . The actual fishing mortality rate for a given species varied from year to year based on inclusion of the 30 percent CV.²⁰ For a given fishing mortality, we ran 100 simulations for each of the five stochastic control rules. Each simulation was run for 50 years to allow most species to complete three generations.

Presentation of the results. The results are presented in terms of percent depletion relative to B_0 and yield as a fraction of MSY to normalize the results across species. In general, we compared biomasses at Year 50 and compared average yields over the entire period from Years 1 to 50. We looked at average yields because of the high variability in yields between years and simulations. The results for non-forage fish species' responses are represented as percent changes from a conditional unfished biomass (CUB). The CUB for a given species is its biomass when there is no forage fish fishing mortality but all other species are fished at the rate given by the fitted EwE model. CUB values, similar to the way in which B_0 was calculated, were tallied as the median biomasses that the species attained when forage fish fishing mortality was set to zero, using the last 10 percent of the years of the deterministic CF runs.

* www.lenfestocean.org/foragefish

²⁰ Details on the implementation error can be found in Appendix G.*

We evaluated the results within and across models, for both the deterministic and stochastic models. Within-model effects (e.g., deterministic model for each ecosystem) showed which forage fish species were most important in each ecosystem, and which harvest control rules and respective implementation levels produced the highest forage fish yields while minimizing impacts on other ecosystem components. Cross-model comparisons aided us in developing basic rule-of-thumb recommendations for forage fisheries management that were effective across all the ecosystems examined.

Predator response prediction. Finally, we used cross-model deterministic EwE results to develop a general equation to predict predator responses to specific levels of forage fish depletion. We refer to this as the PREP (predator response to the exploitation of prey) equation. Across all ecosystems, the deterministic EwE results showed a strong, consistent pattern in the relationships between predator decline, predator diet dependency on the target forage fish species, and target species' depletion level. We used these EwE data to develop a statistical regression model that calculates the level of forage fish biomass relative to B_0 needed to avoid any specified decline in a predator's biomass as a function of predator dependence, where predator dependence is measured as the fraction of a predator's diet that consists of forage fish (Appendix H).^{*} Because the PREP equation enables prediction of predator response to forage fish depletion with relatively little information, it may be particularly useful when empirical data on the predator-prey dynamics and interaction strengths are lacking, or when one does not have the time, resources, or level of information needed to develop a quantitative food web model such as Ecopath.

Results

The results are separated into several sections. First we give the deterministic results for the constant yield (CY) and constant fishing mortality (CF) control rules. Next, we discuss how a meta-analysis of CF deterministic results produced the PREP equation. Finally, we present results from the stochastic constant fishing, step

functions, and hockey stick control rules. The findings from the five stochastic harvest control rules are described individually and then in tandem. For each control rule, we looked at five performance indicators: the median terminal biomass of the forage fish, the average yield of the forage fish, the probability of forage fish collapse, the response to the harvest control rule strategy for all predators combined, and seabird responses specifically. We highlighted seabirds because they tended to display the strongest responses to forage fish depletion relative to other predator taxonomic groups. The significance of differences between rules were tested using matched-pairs Wilcoxon tests, unless otherwise stated.

Deterministic model results using the constant yield control rule

All forage fish species modeled were able to sustain a CY level as high as $0.10 M B_0$, but as the attempted catch level increased, the percent of species that could sustain those catches decreased (Figure 6.2). A population was considered sustained if its biomass did not drop below $0.10 B_0$ during the run. Catches equal to $0.25 M B_0$ were sustainable by 57 percent of the populations modeled, while catches of $0.5 M B_0$ were sustainable by only 30 percent of the populations. Overall, these results indicate that implementation of a constant catch strategy for forage fish will generally require a very low level of catch so as to avoid a very high risk of target species collapse. We did not conduct additional analyses for the constant yield strategy because other harvest strategies examined were clearly superior from both yield and risk standpoints.

Deterministic model results using the constant fishing control rule

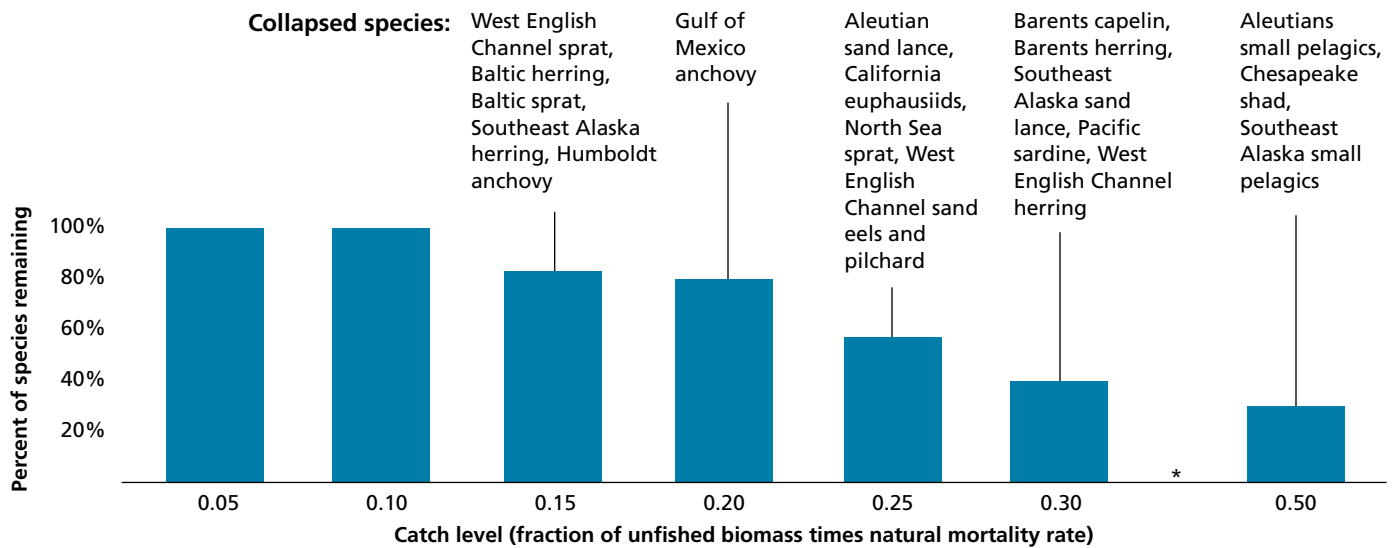
As expected, forage fish biomass was negatively correlated with increased fishing mortality throughout all model simulations; however the intensity of this relationship (the slope) varied across species and ecosystem models. Predator responses to forage fish fishery depletions tended to be strongest when the unfished biomass levels of forage fish were high (expressed as percentage

^{*} www.lenfestocean.org/foragefish

Figure 6.2

Forage species population collapses from constant yield strategies

Results of deterministic model simulations of the effect of a strategy of constant yield on the 30 forage fish species.



Note: Seven species did not collapse in any simulation.

*Model simulations were not run for levels 0.35, 0.40 and 0.45.

of total food web biomass). We measured the ratio of biomass at MSY (B_{MSY}) to B_0 for each forage fish species in each simulation model run. The median values taken across all forage fish species and ecosystems revealed that the median ratio of the B_{MSY} to B_0 was 43.8 percent, with the 5th and 95th percentiles being 24.4 and 60.3 percent, respectively. The lowest ratio, 22.4 percent, was found for Pacific herring in the Aleutian Islands, and the highest ratio, 71.1 percent, resulted for euphausiids in the Northern California Current. Differences among fish species in their biology (growth rate, reproduction rate, etc.) and differences among ecosystems (predator abundance, ecosystem productivity, food availability) probably account for the spread in the B_{MSY}/B_0 ratio. We also ran the deterministic models at other fishing mortality levels and compared the results with the $F=F_{MSY}$ results. At the $F=0.5 M$ fishing level, the median terminal (Year 50) forage fish biomass was 52.9 percent of B_0 , with the 5th and 95th percentiles at zero and 79.9 percent, respectively; five of the 30 fisheries collapsed. The median $B_{F=0.5 M}/B_0$ ratio (52.9 percent) was higher than the B_{MSY}/B_0 ratio (43.8 percent).

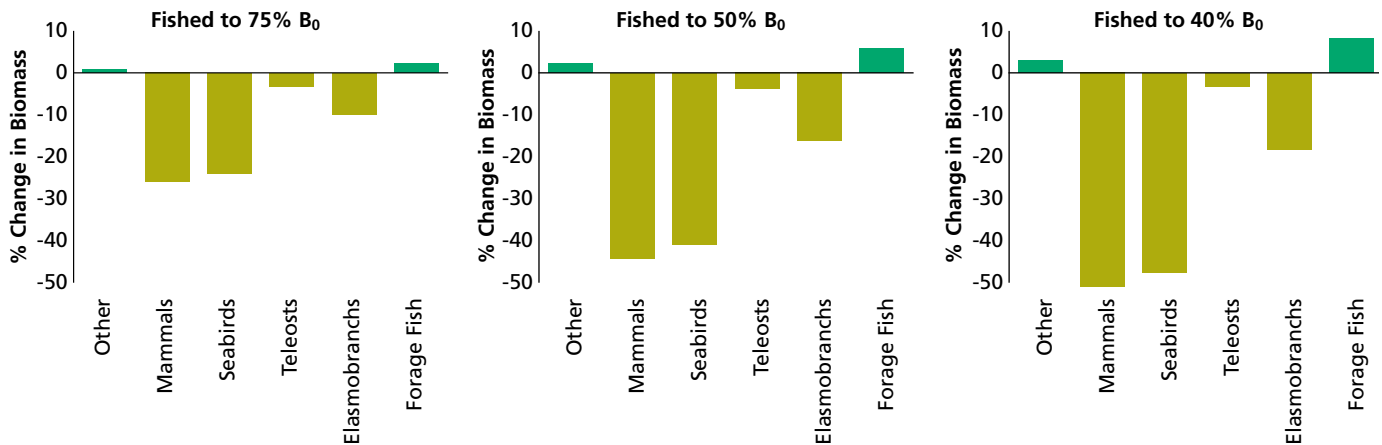
The effect of forage fish depletion among ecosystems, forage fish species, other species in the ecosystem, as well as the extent of target species depletion, all varied. However some consistent patterns were observed. In general, as fishing mortalities for forage fish increased, changes in abundances of all other species also tended to increase (Figures 6.3 and 6.4).

Qualitative and quantitative responses varied across taxonomic groups (Figure 6.3). Generally, the abundance of seabirds and marine mammals declined most strongly in response to decreased forage fish abundance. Elasmobranchs (sharks and rays) also exhibited consistent declines in abundance with decreased forage fish—though the magnitude of responses was generally smaller than those for seabirds and marine mammals. Other (nontarget) forage fish often exhibited a small increase in response to target forage fish exploitation, probably because they compete with the target forage fish species, while other teleosts (bony fish) tended to show a small decrease in abundance. On average, other taxonomic groups not mentioned above showed

Figure 6.3

Biomass changes in response to sand eel depletion

Plots of the percent change for each taxonomic group as a function of depletion of sand eels relative to unfished biomass levels. These results are from the deterministic CF runs for the North Sea EwE model. This model was chosen as a representative example of ecosystem response. In this example, forage fish other than sand eel biomass increased as the sand eels' biomass decreased as a compensatory response.



minimal change from baseline conditions. Perhaps the most striking pattern seen was that the extent of decline was strongly related to the extent of predator dependence on forage fish. Highly dependent predators, whose diet consisted of a large percentage of forage fish, showed the sharpest declines. Generally, for a given level of forage fish depletion (e.g., biomass at 0.5 B₀), the relationship between diet dependence and species decline was negative and linear (Figure 6.4). In addition, the slopes relating predator decline to dependency on forage fish became more negative as the forage fish biomass became further depleted (Figure 6.4).

We synthesized the results from all model runs via a meta-analysis to predict the level of predator depletion expected from various levels of forage fish depletion. Preliminary analyses suggested that either a linear or log-linear model would describe the response of predators across all systems reasonably adequately. From first principles, we expected that the decline would be near zero for species that do not consume the forage fish, and for all species whenever forage fish have not been subjected to fishing pressure. The equation (1) accounts for this and relates predator response, measured as

the biomass decline of the predator, to a given level of forage fish depletion and predator diet dependence D . R is the percentage decline from the predator's CUB value, and D is the fraction of the predator's diet that is composed of the target forage fish. Model simulations were used to fit the equation:

$$R = \rho D^{\alpha} \left(1 - \frac{B}{B_0}\right)^{\beta} \quad \text{Eq. (1)}$$

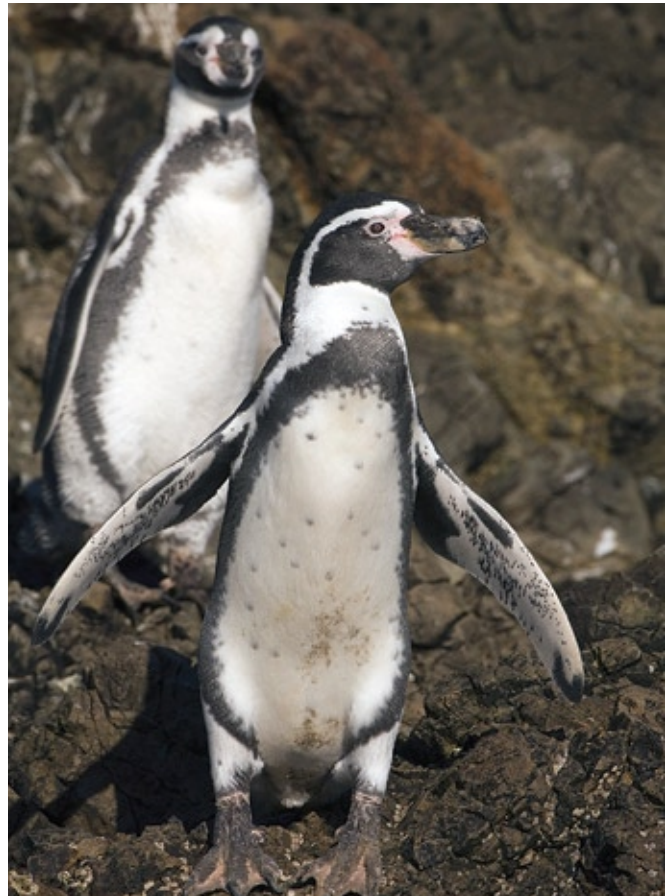
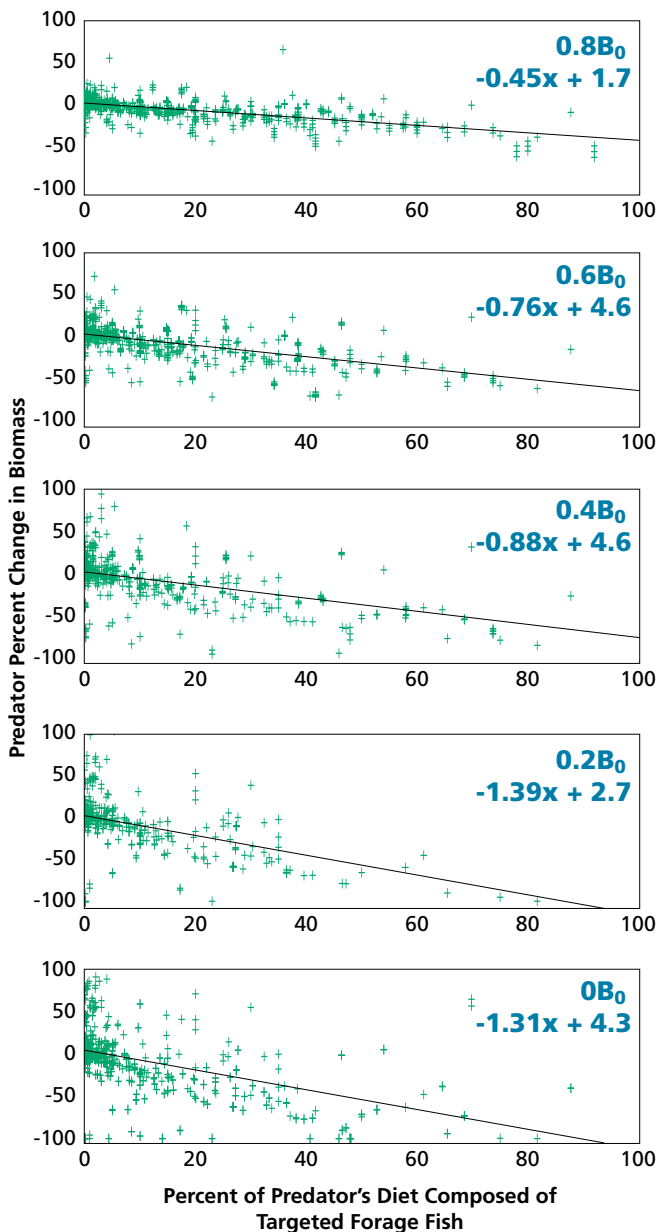
where ρ , α and β are estimated model parameters that control the shape of the function, and B/B_0 is the relative depletion level of forage fish. Some species will increase as B/B_0 declines, but these are generally competitors or predators that specialize on target species competitors, and Eq. (1) does not consider these types of responses.

We estimated general, system-specific and trophic-level-specific values of the parameters by taking logarithms of both sides of Eq. (1) and applying linear mixed effects model regression techniques. The data used to estimate the parameters involved multiple predators from each ecosystem and considered multiple depletion levels for each target forage fish. The resulting parameter estimates for the PREP equation are given in Table 6.2 for all

Figure 6.4

Predator responses to forage fish depletions

The results are from the deterministic, constant fishing (CF) mortality rule. Each point represents a particular predator species within one of the ecosystem models, and thus all species and ecosystems are included in each panel. Each panel represents a different level of forage fish depletion, which is noted in the upper right hand corner along with the linear regression equation. Fishing level increases as one moves downwards from the upper-most panel to the bottom lower right panel.



Humboldt Penguins, Chiloe Island, Chile, © Kevin Schafer/Minden Pictures.

species combined and for individual taxonomic groups. The parameter estimates varied considerably across taxonomic groups (Table 6.2).

Table 6.3 can be used to find the forage fish biomass level that will ensure avoidance of large declines in predator abundance. For example, if we wanted to be very certain (i.e., have a 95 percent chance of success) that a predator in the ecosystem whose diet

is composed of 75 percent of the targeted forage fish, would not decline by 50 percent or more, then forage fish should be maintained at 88 percent of B_0 or higher. We note that because these are combined results based on several ecosystem models, the results for any specific ecosystem may differ. In addition to providing a summary overview of the results, we see their major value as providing robust benchmarks for systems for which EwE or other food web models are not available.

Table 6.2

Group-specific parameter estimates for the PREP equation $R = \rho D^\alpha \left(1 - \frac{B}{B_0}\right)^\beta$

The numbers in parentheses are 1 standard error. The final row lists the percentage of variance explained (approximate R^2 values).

Par.	All	Teleosts	Birds	Mammals	Elasmobranchs	Invertebrates
α	0.62 (0.01)	0.58 (0.01)	0.74 (0.03)	0.68 (0.03)	0.76 (0.02)	0.99 (0.05)
β	0.91 (0.01)	0.83 (0.02)	0.88 (0.03)	0.85 (0.04)	0.91 (0.03)	0.99 (0.06)
$\ln(\rho)$	4.49 (0.04)	4.30 (0.05)	4.92 (0.08)	4.44 (0.10)	4.93 (0.09)	5.32 (0.22)
R^2	0.62	0.60	0.85	0.58	0.81	0.75

Table 6.3

Critical forage fish biomass levels

Critical forage fish biomasses needed (as percentages of B_0) to avoid a 50 percent decline in all dependent predators, and specifically for seabirds, derived from the PREP equation. The relationship between forage fish biomass levels and dependent predators is broken into four levels: predators whose diet dependency is 0–25 percent forage fish, 25–50 percent forage fish, 50–75 percent forage fish, and 75–95 percent forage fish. Ninety-five percent was the highest diet composition of target forage fish species observed in the EwE models.

Diet Dependency	95% Confidence of success		75% Confidence of success	
	All groups	Seabirds	All groups	Seabirds
25%	0.79	0.74	0.42	0.45
50%	0.85	0.88	0.57	0.74
75%	0.88	0.90	0.66	0.78
Max	0.90	0.91	0.73	0.81

Stochastic constant fishing control rules

The differences in forage fish terminal (Year 50) biomasses were statistically significant, both between the $F=50$ percent F_{MSY} and 75 percent F_{MSY} runs ($p<0.001$) and between the 75 percent F_{MSY} and 100 percent F_{MSY} strategies ($p<0.001$) (Figure 6.5).

For most forage fish, yields increased as fishing mortality increased, although at the highest fishing levels (100 percent F_{MSY}), some forage fish populations collapsed, thus resulting in no yield. As a reminder, we considered a forage fish population collapsed if its biomass fell below $0.10 B_0$ in a simulation. Because of the lower occurrence of collapses at the 75 percent F_{MSY} levels, there is a higher average yield than for the 100 percent F_{MSY} simulations when taken across all forage fish species (left part of Figure 6.6a). However, differences in yields were not significantly different (nonparametric Kruskal-Wallis test, $p=0.18$) between 75 percent F_{MSY}

and 100 percent F_{MSY} . Because predator response to forage fish depletion depends on diet dependency, our results on predator response focus on predators whose diet dependency is greater than 10 percent. For these species, there was a median 14 percent decline for 50 percent F_{MSY} fishing, 24 percent decline for 75 percent F_{MSY} , and 27 percent for 100 percent F_{MSY} (Figure 6.6b). Among taxonomic groups, seabirds exhibited the largest declines, 25, 39, and 54 percent, respectively (left data points in Figure 6.6c). All differences were significant (at $p<0.01$ levels; comparisons made with paired t-tests).

When looking at how these same strategies impacted forage fish populations rather than predators, the CF control rule with $F=100$ percent F_{MSY} was safe for some forage fish species but catastrophic for others. The mean probability of collapse across all species groups was 6 percent for $F=50$ percent F_{MSY} , 24 percent for $F=75$ percent F_{MSY} , and 42 percent for $F=100$ percent F_{MSY} (left data points in Figure 6.6d). Therefore, on average,

Figure 6.5

Median forage fish biomasses for the stochastic runs at Year 50 under all five harvest control rules, across all species and ecosystems.

From left, the harvest control rules are constant fishing, 20 percent B_{LIM} step function, 40 percent B_{LIM} step function, 20/100 hockey stick and 40/100 hockey stick. The bottom edge of each boxplot represents the 25 percent quartile, and the top edge represents the 75 percent quartile for each strategy.

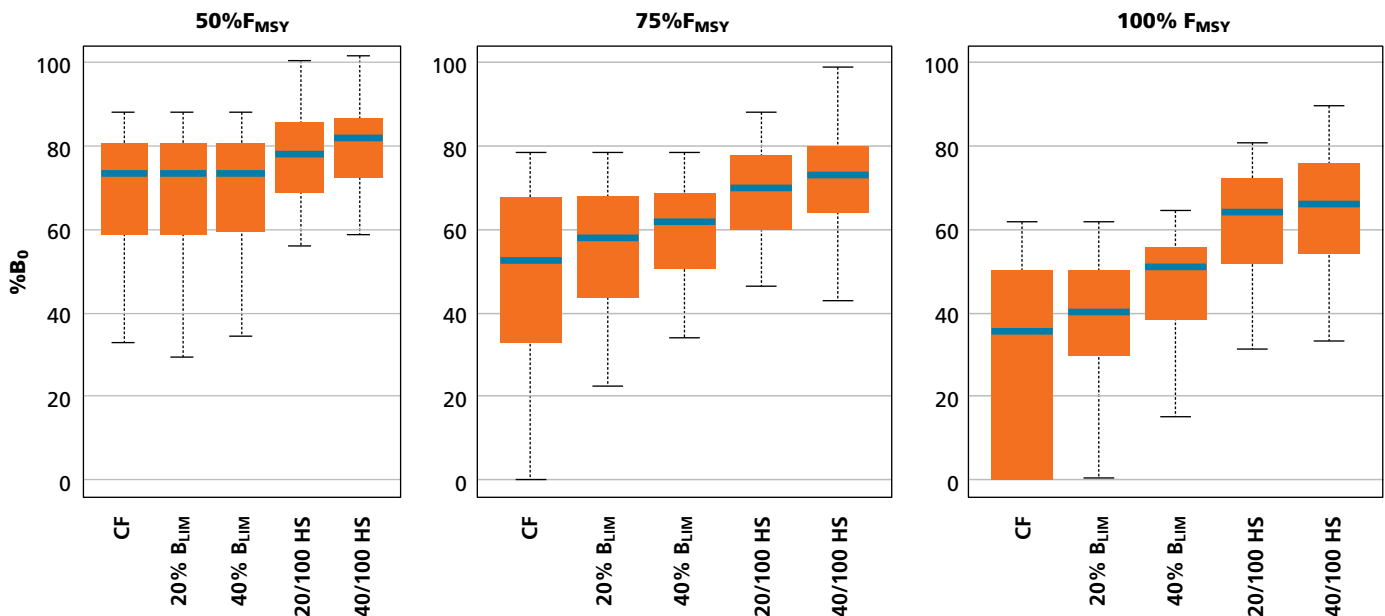
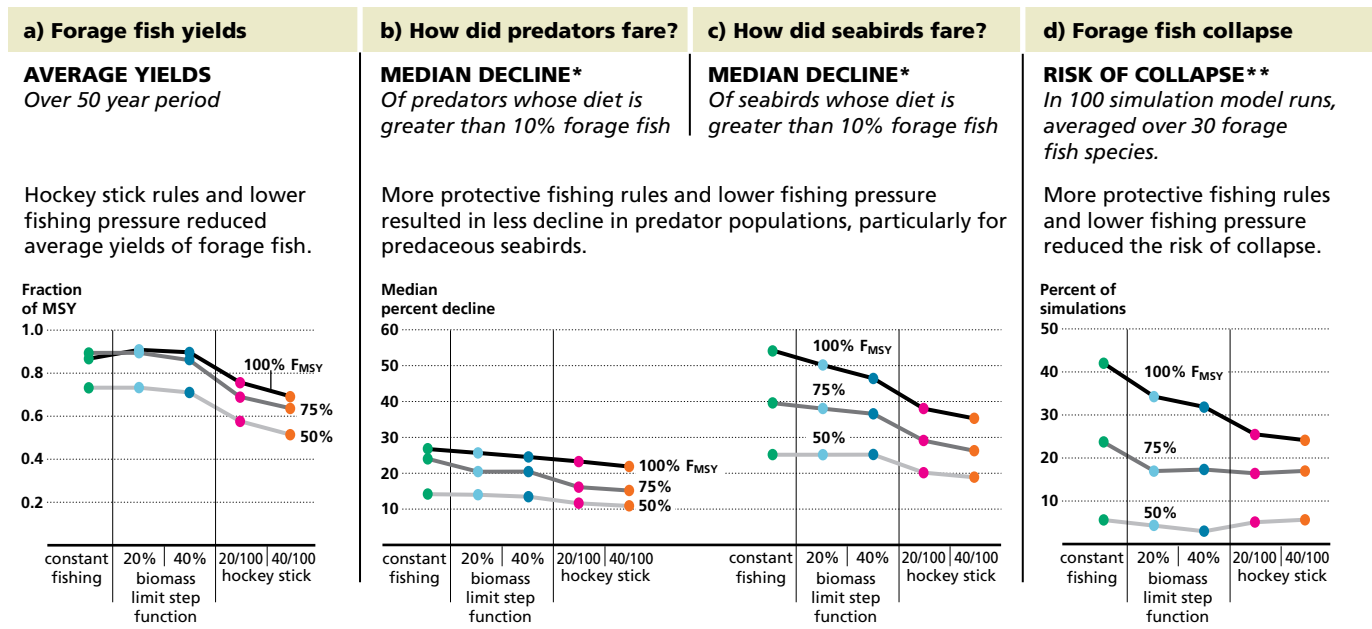


Figure 6.6

Results of testing of harvest control rules

The impacts of the harvest control rules from Figure 6.1 (except for the constant yield rule) were tested using stochastic ecosystem models (Ecopath with Ecosim) at three different levels of fishing pressure. More protective rules reduced yields, but were much better at protecting predators and maintaining forage fish.



* Median is for 100 simulations at the end of 50 years. Decline is relative to predator biomass in the model with no fishing of forage fish.
 ** A species is considered collapsed if it falls below 10 percent of estimated unfished biomass during 50 years of simulation.

the forage fish population collapsed in 45 of the 100 simulations at the $F=100$ percent F_{MSY} level. For the $F=50$ percent F_{MSY} runs, all forage fish species remained viable for a majority of the simulations. For the $F=75$ percent F_{MSY} runs, 3 of the 30 forage fish populations collapsed in 90 percent or more of the simulations. At $F=100$ percent F_{MSY} , 10 of the 30 forage fish populations collapsed in 90 percent or more of the simulations. Our results clearly show that constant fishing at $F=F_{MSY}$ is a risky strategy for both forage fish populations and their dependent predators.

Stochastic step function rules

At 50 percent F_{MSY} , the step functions 20 percent B_{LIM} and 40 percent B_{LIM} performed essentially the same as the CF runs for all metrics described above (Figures 6.5 and 6.6); the lower biomass limits were not approached

often enough for them to have an effect on the terminal median biomasses, average yields, or predator responses.

At 75 percent F_{MSY} , both step functions showed improved results over the CF rule, and the 40 percent B_{LIM} showed small but significant ($p<0.001$) improvements over the 20 percent B_{LIM} in terms of terminal forage fish biomass (Figure 6.5). The CF strategy led to slightly higher yields ($p=0.09$) than the 20 percent B_{LIM} yields and significantly higher yields compared to the 40 percent B_{LIM} yields ($p<0.001$) (Figure 6.6a). However, for the step functions, the probability of target species collapse was significantly smaller (Figure 6.6d) and forage fish consumers exhibited a significantly smaller decline (Figures 6.6b and 6.6c). These patterns were amplified when fishing mortality was increased to $F=100$ percent F_{MSY} . Step functions, which include a hard biomass threshold, were thus seen to substantially reduce the

risk of collapse for target forage fish species, and the depletion of dependent consumers, and are of particular importance at high fishing mortality levels.

Stochastic hockey stick control rule

The HS rules led to higher forage fish biomasses and lower predator declines for all fishing levels, with the 40/100 HS rule consistently performing better in terms of maintaining target species biomass at reasonably high levels, and avoiding large declines in dependent predators, than the 20/100 rule. The differences between ecosystems were greater than the differences within an ecosystem. Therefore, the overall summary plots (Figures 6.5 and 6.6) may not suggest significant differences between rules, but non-parametric paired tests showed the significant differences between biomasses ($p=0.001$) and predator declines ($p<0.001$). The yields from the 20/100 rule were similarly consistently higher than the yields from the 40/100 rule ($p<0.001$) (Figure 6.6a), indicating that there is a trade-off between achieving high yields and conserving dependent predators. The time series from specific simulations demonstrate the consistent differences between rules that were maintained during the course of the simulations (Figure 6.7).

For the 50 and 75 percent F_{MSY} levels, median predator decline was below 20 percent, and it was below 25 percent for the 100 percent F_{MSY} level (Figure 6.6b). There was a large difference in seabird declines between the step functions and the HS rule, at both the 75 and 100 percent F_{MSY} fishing mortalities (Figure 6.6c). The 100 percent F_{MSY} HS rules led to predator declines most similar to the 50 percent F_{MSY} levels of the other strategies.

The probability of forage fish collapse was similar for both the 20/100 and 40/100 HS rules examined but there were differences observed among fishing levels (Figure 6.6d). When the maximum fishing level was 50 percent F_{MSY} , none of the forage fish populations collapsed in a majority of their simulations. However, when the maximum fishing level was 100 percent F_{MSY} , three forage fish—Gulf of Mexico anchovy, Gulf of Mexico herring, and Northern California euphausiids—collapsed in 90 percent or more of the simulations.



Guanay cormorant nesting colony, Argentina, © Doug Allan/Minden Pictures.

Comparison of control rules using deterministic and stochastic models

The only harvest control rule examined for both deterministic and stochastic simulations was the CF policy. For the CF rule and deterministic runs, the MSY was obtained at $F=F_{MSY}$, and only at higher fishing rates did the population collapse. For the stochastic runs, F set equal to the deterministic F_{MSY} led to collapsed forage fish populations in 33 percent of the runs. For most (22 of the 30) forage fish, the population collapsed (fell below 10 percent B_0) in at least one simulation at this level of F . Thus, our results show that advice generated by deterministic models may result in fishing mortality rates that are too high to sustain forage fish populations if F is set at F_{MSY} .

Comparison of control rules with stochastic models

When testing the five control rules, we looked at how they performed in three key respects: sustaining forage fish populations, limiting predator declines, and producing target species yields. The CF strategies

Figure 6.7

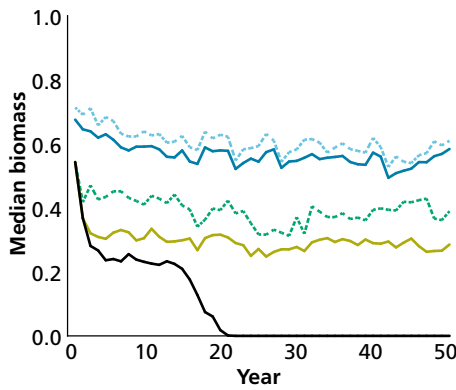
Time series of stochastic model runs

Examples of stochastic model results to compare the impacts of the five stochastic harvest control rules. All lines represent the median responses (medians taken across 100 simulations) for the specified forage fish.

— CF — 20% B_{LIM} - - - 40% B_{LIM} — 20/100 HS - - - 40/100 HS

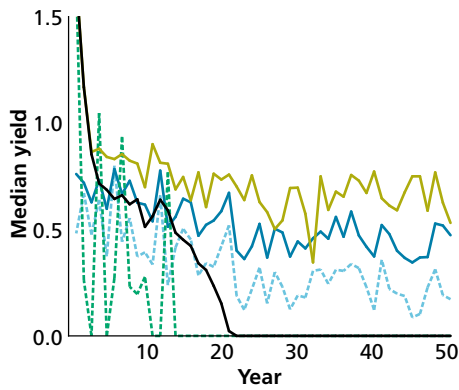
Biomass

Southeast Alaska sand lance



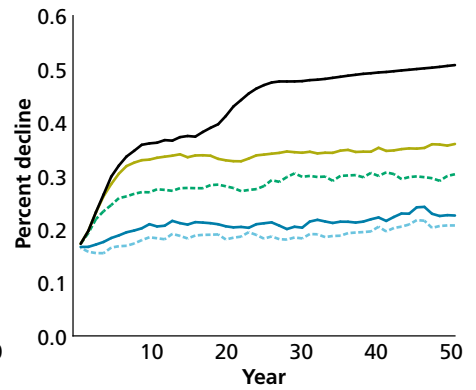
Yield

Southeast Alaska sand lance

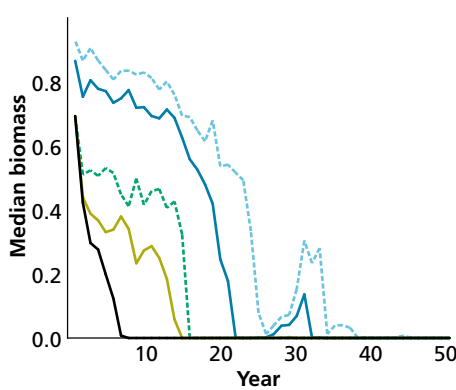


Seabird Decline

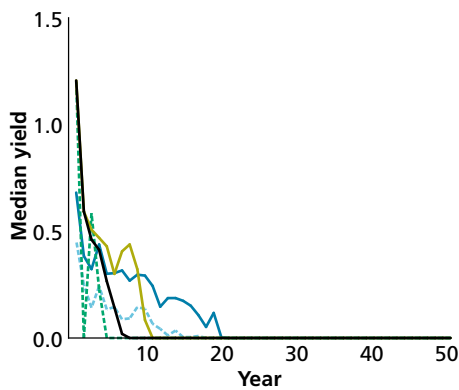
Southeast Alaska sand lance



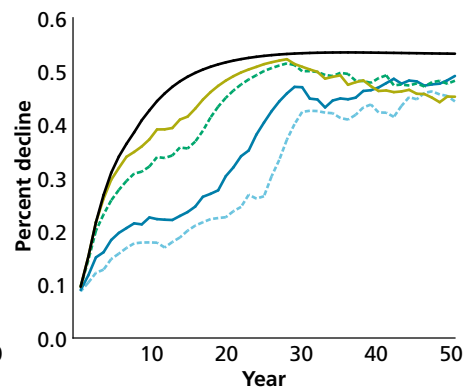
North Sea sand eels



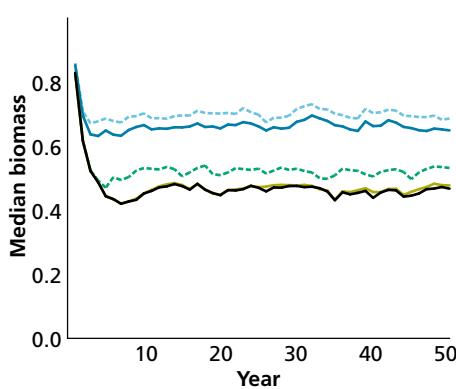
North Sea sand eels



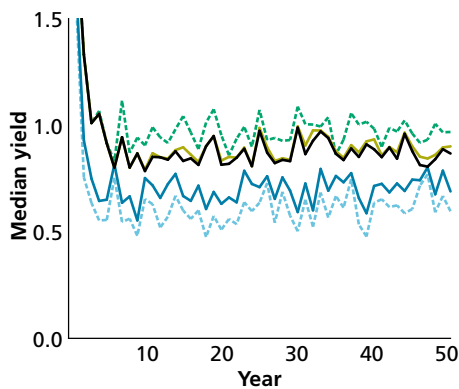
North Sea sand eels



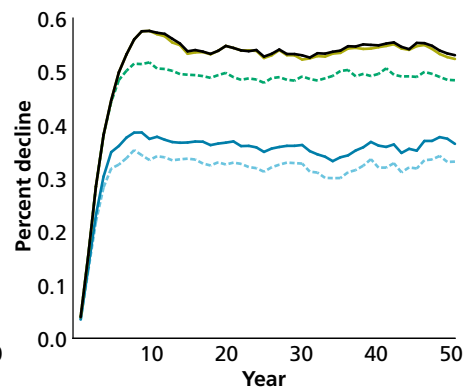
Barents pelagic planktivores



Barents pelagic planktivores



Barents pelagic planktivores



were inferior to all others examined (all of which included a hard biomass lower limit) for all three of the performance indicators.

Generally, the HS control rules outperformed the other control rules for two of the performance indicators (sustaining forage fish populations and limiting declines of forage fish predators) (Figures 6.6d and 6.6b, respectively). There was a consistent pattern among the five strategies examined for these output variables, with the 40/100 rule performing best (from best to worst: 40/100 HS rule, 20/100 HS rule, 40 percent B_{LIM} step, 20 percent B_{LIM} step, and the CF rule). The 20 percent B_{LIM} step rule was often just as risky as the constant fishing strategy (Figure 6.7). Predictably, the lowest fishing mortality ($F=50$ percent F_{MSY}) resulted in higher median biomass across all species and systems (Figure 6.5).

The superior performance of both step function and HS strategies over the CF strategy stemmed from the presence in both harvest control rules of hard lower biomass limits—below which fishing mortality ceased. It is clear that the HS strategy's superior performance over the step functions is because in addition to a lower biomass limit, the former strategy adjusts fishing mortality rate over a broad biomass range, reducing fishing mortality as target species' biomass decreases.

There was an interaction between harvest control rules and maximum fishing mortality rates. The choice of harvest control rule mattered much more for the high fishing mortality scenarios. To achieve a median forage fish biomass close to 80 percent B_0 (a value suggested from the PREP equation as a reasonably safe level for forage fish-dependent predators), the maximum fishing needs to be 50 percent F_{MSY} . The strategy that most closely achieved that goal was the 40/100 HS rule, with maximum fishing of 50 percent F_{MSY} . At the $F=50$ percent F_{MSY} levels, the probability of forage fish collapse was low for all harvest control rules, and the level of predator decline was smallest compared with other fishing levels (Figures 6.6d and 6.6b).



When testing the five control rules, we looked at how they performed in three key respects: sustaining forage fish populations, limiting predator declines, and producing target species yields.

Sprats in a market stall, © Shutterstock.

When the maximum fishing was at higher levels (i.e., 75 percent or 100 percent F_{MSY}), the strategies were further differentiated. At the highest fishing mortality rate, 100 percent F_{MSY} , the number of forage fish species that collapsed in virtually all simulations dropped from nine to three by using the HS control rule compared with the CF control rule. HS strategies performed best at protecting dependent predators, resulting in the lowest predator declines across all species (Figure 6.5b). For seabirds with diet > 10 percent forage fish, median declines in abundance were substantial for all harvest policies and generally were high (>30 percent) when fishing was greater than 50 percent F_{MSY} . Regardless of the control rule used, a maximum fishing of 100 percent F_{MSY} could not be tolerated by some forage fish species, and the probability of collapse was much lower for fishing mortality rates at half this level (maximum $F=50$ percent F_{MSY}).



Even under the more cautionary hockey stick rule, some forage fish populations collapsed when maximum fishing was 100 percent F_{MSY} , exemplifying that no strategy can prevent extinction when high levels of fishing are permitted.

California sea lions feeding on Pacific sardines, © Brandon Cole.

HS control rules resulted in the lowest median yields. These yields were low in part because fishing must decrease as the target species' biomass declines and must stop when biomass reaches a lower limit, leading to years when yields were zero. The harvest control rule producing the highest yields varied across forage fish species, but in several cases, the step rules produced the highest sustainable yields.

Major Findings and Conclusions

The degree of ecological impact of forage fish fishing varied among species and ecosystems, yet consistent patterns were found that allowed us to predict impact based on diet dependency, predator type, and the intensity of fishing effort. We developed a quantitative predictive model, which we termed the PREP equation, to summarize our deterministic model results. The PREP equation has relatively simple data requirements, and thus may be especially useful in data-poor situations and where detailed food web models are not available. Application of the PREP equation requires diet composition information, which is often available for species of major concern. In instances where diet information is lacking, it can often be obtained relatively easily.

It is important that an implementation of a control rule does not result in the loss or significant decline²¹ of another, dependent species. The PREP equation

quantifies these impacts, and its application suggests that forage fish biomass be near 80 percent B_0 to prevent these declines. In our stochastic model runs, this result was achieved only when the maximum fishing mortality was 50 percent F_{MSY} . At higher fishing levels, these biomasses were only approached using a hockey stick control rule.

Fishing at F_{MSY} led to highly significant effects for many dependent predators in many ecosystems and led to a high risk of collapse of the forage fish population. For the constant fishing strategy with the maximum fishing set to 100 percent F_{MSY} , a full 30 percent of the forage fish populations collapsed in almost every simulation run. Even under the more cautionary hockey stick rule, some forage fish populations collapsed when maximum fishing was 100 percent F_{MSY} , exemplifying that no strategy can prevent extinction when high levels of fishing are permitted. When stock size is uncertain, the hockey stick control rule appears to be the best management strategy. Its decreased fishing mortality at lower forage fish biomasses eases the impact of not knowing what the exact value of the lower limit should be. This precautionary approach combined with an appropriate maximum fishing level will minimize potentially irreversible ecosystem depletions. We elaborate on how to operationalize these rules and strategies in the recommendations that follow in the next chapter.

²¹ We elaborate on standards for impacts to dependent species in our recommendations (Chapter 7). Specifically, we deem fishing levels that result in any predator falling into the "Vulnerable" or more threatened category, according to IUCN criteria, as unacceptably high.

7

Key Findings and Recommendations

Key Findings

Based on our review of the literature, case studies, original research results, and task force member deliberations, we highlight our key findings about the biological and ecological characteristics of forage fish, their economic and ecological value, and implications for their management:

1. Forage fish abundance is highly variable and often unpredictable.

Major fluctuations in forage fish abundance have been observed and recorded for centuries (Chapter

1). Forage fish can respond dramatically to shifts in oceanic conditions and may exhibit strong decadal-scale variability. Forage fish may be capable of responding quickly to favorable environmental conditions, but their populations cannot be expected to maintain a steady state and can plummet when conditions become unfavorable (Chapter 1).

2. Forage fish are easily caught, even when their abundance decreases.

Forage fish have a propensity to form large shoals, or groups. This behavior is believed to have evolved as a defense against natural predators, but it makes these fish



Overall, our results support setting much more conservative targets and limits for forage fishery management than have been commonly recommended and applied in the past.

Chinook salmon, Rogue River, Oregon, © Mark Conlin/SeaPics.com. Antarctic krill, background, © Flip Nicklin/Minden Pictures.

easily detectable and catchable by modern fish spotting and catching technologies (Chapter 1). Catchability, defined as the level of fishing mortality attributable to a unit of fishing effort, is not generally constant for forage fish; rather, it usually increases when abundance declines (Chapter 2). Similarly, declines in forage fish abundance may be accompanied by stable or even increasing catch per unit of fishing effort because these fish are still easy to catch in their shoals. Thus declines in forage fish abundance are particularly difficult to detect, especially in cases where only fishery-dependent data are available.

3. Forage fish populations are vulnerable to overfishing and collapse and do not always recover readily from depletion.

Evidence has grown that earlier beliefs about the resiliency of forage fish populations—that they are resistant to collapse because of their great abundance, high fecundity and rebound potential, and other life history traits—are not well founded. Fishing has caused or exacerbated the collapse of several forage fish populations during the past century (Chapter 1), and some collapsed populations have not recovered (e.g., Northern Benguela case study, Chapter 4). Although forage fish can generally withstand greater fishing pressure compared with slower-growing species, they are just as vulnerable to collapse when fished beyond sustainable levels (e.g., Pinsky *et al.* 2011). Further, our modeling results (Chapter 6) indicated that for many forage fish species, there is a high probability of population collapse when a constant fishing mortality rate of F_{MSY} (a level often used as a standard or ideal in fisheries management) is applied.

4. Globally, the economic value of forage fish as prey for other commercial fisheries is twice the value of forage fish as catch.

The relative importance of forage fish in directed fisheries (in which the forage fish is the fishery target) and in ecological support of production of other commercially important fishery target species varied across the 72 ecosystems whose food web models we evaluated. Overall, we estimated that forage fish contribute about \$16.9 billion (2006 USD) to global fisheries annually

(ex-vessel value). The amount attributable to support of other commercial fisheries was \$11.3 billion (67 percent of the total value), which was twice the \$5.6 billion (33 percent) of direct catches of forage fish. Quantifying the supportive value of forage fish helps to identify economic trade-offs that may exist between harvesting forage fish and allowing them to remain in the ocean, where they can provide support for other commercially important species.

5. Predators highly dependent on forage fish (for 50 percent or more of their diet) are common, occurring in three-fourths of marine ecosystems we examined.

Our results clearly show that predators highly dependent on forage fish are common across marine ecosystems. Using an analysis of food web models (Chapter 5), we found that nearly 30 percent of the ecosystems we considered had at least one predator for which forage fish made up 75 percent or more of its diet. We found that 75 percent of the ecosystems contained one or more predators with a forage fish dependency of 50 percent or greater.

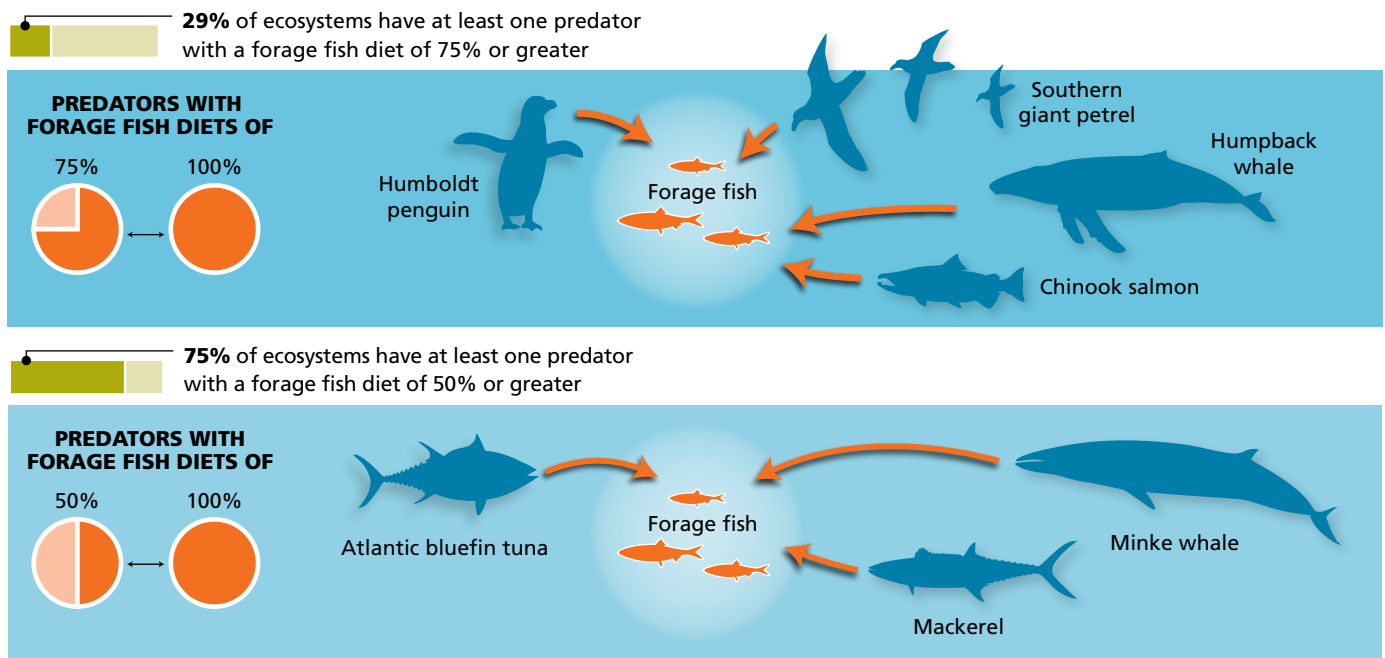
6. Predators dependent on forage fish in their diet are more sensitive to changes in forage fish abundance than are less-dependent species.

Forage fisheries act as a new predator in an ecosystem. When one species of forage fish is depleted, the availability of food for predators dependent on that forage fish will probably be lowered, with consequent impacts. Empirical evidence detailed in this report demonstrates the significant impact that changes in forage fish abundance can have on the vital rates of predators, such as reproductive success (Chapters 1, 3; Box 3.1; Boyd and Murray 2001; Boersma and Rebstock 2009; Cury *et al.* 2011). We found that the severity of the response of a predator to forage fish exploitation increased along with its diet dependency and the extent of forage fish depletion (Chapter 6). We were able to quantify and predict this response with a quantitative model we developed called the PREP (Predator Response to the Exploitation of Prey) equation (Tables 6.2 and 6.3).

Figure 7.1

Ecological importance of forage species

Numerous marine predators depend on forage fish, and the Task Force found that three-fourths of the ecosystems studied have at least one highly and/or extremely dependent predator.



7. Conventional fisheries management targets and limits are not conservative enough to protect forage fish populations from collapse or to prevent impacts on other species.

Our analyses demonstrated that conventional fishery management approaches do not adequately account for the population dynamics of forage fish and their role in the ecosystem. Traditionally, fisheries management strives to maintain a stock at a constant biomass at which maximum sustainable yield (MSY) can be taken. In the absence of information to assess MSY for a stock, rules of thumb may be used to set management targets for forage fish, including striving to maintain population biomass at half the unfished level, using a cutoff of 20 percent of unfished biomass below which fishing must stop, or setting fishing mortality to be equal to natural mortality.

However, our analysis and synthesis have demonstrated that such rules are not adequate to prevent the collapse

of forage fish populations and also pose a substantial risk to the persistence of other species within marine ecosystems. For example, our food web modeling results revealed that fishing at a typical rate, F_{MSY} , often led to collapses of forage fish populations (Figures 6.6d and 6.7) and large decreases in the abundance of dependent predators (Figure 6.6b, c). In general, our results show that relative to traditional measures, higher levels of forage fish biomass and lower rates of forage fish fishing are required.

8. Model simulations showed that forage fish populations and their dependent predators were reliably sustained when fishing pressure was half as high and forage fish biomass in the ocean was twice as large as traditionally practiced.

In our model simulations, hockey stick harvest control rules that employ a variable fishing mortality, which decreases as forage fish biomass decreases, as well as a

hard lower biomass limit below which fishing is prohibited, performed much better at maintaining forage fish biomass and preventing impacts to dependent species than did constant fishing mortality (F) policies, especially at fishing mortality rates exceeding $0.5 F_{MSY}$ (Chapter 6).

Our model results also indicate that, in general, fishing mortality should not exceed half of the rate that would be commonly recommended for forage fish (i.e., $F=0.5 F_{MSY}$ or about half the species' natural mortality rate $F=0.5 M$), to ensure with high probability (75 to 95 percent) that forage fishing will not place dependent predators at jeopardy of extinction (according to international standards). Overall, our results support setting much more conservative targets and limits for forage fishery management than have been commonly recommended and applied in the past.

9. Temporal and spatial management will often be useful, and at times crucial, for managing the impact of forage fisheries on dependent predators.

As part of a comprehensive management package, temporal and spatial measures can ensure sufficient prey, improve predator reproductive success, and reduce and prevent bycatch of forage fish consumers (Chapter 4). Such measures can also prevent localized depletions of forage fish (Chapter 2) that can occur even when a forage fish stock is abundant. Area closures have often been used near predator colonies or forage fish spawning areas (Chapter 4). Significant study, perhaps including large-scale experiments, may be required to determine the most effective location, size, and timing of closures and monitor their impact.

The following pages detail the recommendations of this report, which are summarized in Box 7.1.

Box 7.1

Recommendations at a Glance

- Forage fisheries should be managed to sustain both forage fish and predators. Managers should set catch levels that protect forage populations from collapse and, with high probability, do not make predator species vulnerable to extinction.
- Managers should use greater caution when there is less information on forage fish and their interactions with predators and the environment. The Task Force proposes “information tiers” to aid in this.
- The Task Force expects that most forage fisheries now considered as well-managed will fall into the “intermediate” information tier. For these fisheries, fishing mortality should be at most half the conventional rate (half of F_{MSY}) and the amount of fish left in the ocean should be at least twice as large (40 percent of B_0).
- For the “low” information tier, no new forage fisheries should be initiated, and existing fisheries should be severely restricted so that forage fish biomass will not fall below 80 percent of B_0 .
- When the “high” information tier is achieved, the Task Force recommends setting conservative fishing limits to account for uncertainty. In no case should fishing mortality exceed 75 percent of conventional levels, or leave less than 30 percent of unfished forage biomass in the ocean.
- Closing areas to fishing—such as those near seabird breeding colonies—will often be helpful to sustain forage fish and dependent predators, as will closing fishing during critical seasons, such as spawning.

Recommendations

Apply a risk-based assessment to foster an ecosystem approach to forage fisheries management.

A primary challenge for fisheries managers and policy-makers is to determine a level of catch that accounts for the important ecological role that forage fish play in the larger marine environment. We conducted our research and devised our recommendations with this objective in mind. The inherent unpredictability of marine ecosystems, and forage fish populations in particular, combined with our inability to fully understand their population dynamics underscores the need for precaution when determining catch levels for forage fish (see Table 7.1). Below we propose a series of recommendations to address these challenges. We designed a precautionary, risk-averse approach for forage fishery management that explicitly takes into account predator needs and considers the amount of information available for a particular fishery and ecosystem.

We propose a three-tiered management framework based on knowledge of forage fish and the ecosystem, in which more precautionary policies are implemented when there is greater uncertainty about fisheries effects on forage fish and food webs. We identify three tiers of information—low, intermediate, and high—based on the degree of knowledge regarding forage fish stock dynamics and the status and the effects of forage fisheries on dependent predators. The goal of the specified management strategy in each tier is to regulate fishing intensity so that there is a low risk of significantly affecting dependent predators.

Above all, and irrespective of the information available, management of a forage fishery should be expected to meet the following **Dependent Predator Performance Criterion**:

Adopt harvest strategies and management measures so that there is a greater than 95 percent chance that fishing on forage fish will not deplete any dependent predator population to levels that would meet the IUCN “vulnerable” criteria.²²

The current status of dependent predators relative to pristine abundance levels should be taken into account in evaluating the performance criterion.

Dependent predators are those species whose productivity (growth, reproduction, and survival) is strongly linked to the availability of forage fish prey. This determination may be based on direct empirical evidence linking demographic rates to forage fish availability or based on predicted impacts from predator behavior, life history, or ecology (e.g., from diet contribution or the PREP equation). Our summary of PREP equation results suggests that forage fish biomass requirements are near 80 percent of unfished biomass to prevent declines consistent with the Dependent Predator Performance Criterion for at least some dependent species across the ecosystems examined.

For stochastic model runs with a constant fishing mortality rate strategy, this criterion was achieved only when the maximum fishing mortality was set at the lowest level examined (50 percent of F_{MSY}). Across all fishing levels, the strategy that yielded the highest probability of meeting the Performance Criterion was the hockey stick control rule, with B_{LIM} set at 0.4 B_0 (no fishing is allowed at biomass levels below 40 percent of unfished biomass). Achieving the Performance Criterion must be demonstrated by quantitative analysis that consists of statistical or empirical testing of the harvest strategy, along with ongoing monitoring, evaluation, and modification of the harvest strategy in an adaptive framework. For the lower information tiers, decreased understanding of population and ecosystem processes must be compensated for by greater precaution in the harvest strategy and management measures, such that there is a coherent basis for evaluating whether the Performance Criterion is likely to

²² A population is classified as vulnerable to extinction under IUCN criteria if it declined by 50 percent or more in the previous 10 years or three generations, whichever is longer, and where the causes of the reduction are clearly reversible and understood. However, a population may qualify as vulnerable if it declines by 30 percent or more in the same period if the causes of reduction have not ceased or are not understood or reversible. Classification as vulnerable can also be triggered by other means, including geographic characteristics, number of individuals left in the population, or the estimated risk of extinction. More information on IUCN criteria can be found at www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria.

be met. For the intermediate and low information tiers, increasingly precautionary default approaches to achieve the Performance Criterion are provided based on our analysis of many ecosystems and dependent predators.

In all cases, harvest strategies should include buffers to account for scientific uncertainty, to consider limits on ability to control fishing, and to allow for the possibility of unanticipated changes in fleet behaviors that accompany policy changes.

Because forage fish experience high variability in abundance and distribution, detailed monitoring and adaptive management are important components of any harvest strategy. Models used to evaluate criteria should be updated regularly with new information from the fishery as well as independent sampling of the target species and dependent predators.

Information tiers and corresponding management actions

The criteria defining the three tiers are based on information needed to project the impact of fisheries on forage fish and on the predators that feed on them. Classification into one of these three tiers implies that criteria for both forage fish production dynamics and dependent predators are met. Currently, few, if any, fisheries meet all the specified requirements for the high information tier. However, by identifying information needs from this list, fisheries that are classified as intermediate can establish a framework for research and monitoring that can promote them to the high tier in the future. In addition, even in high information systems, it is important to continue to increase knowledge and predictive powers because of unexpected consequences.

For each information tier, we recommend appropriate management actions designed to ensure, with high probability, that the Dependent Predator Performance Criterion is met. For all tiers, we recommend that the harvest strategy include an upper limit to fishing mortality ($MAX F$), a lower limit to forage fish abundance below which targeted fishing ceases (B_{LIM}), and that fishing mortality be reduced as the lower abundance limit is



Anchovies at a Tel Aviv market.

approached. The recommended values of $MAX F$ and B_{LIM} differ across information tiers, with information-rich situations allowing for greater forage fishing rates and yields than information-poor circumstances. Further, we recommend that fishing mortality should only be set at the $MAX F$ level during periods of high forage fish abundance and productivity. In addition, the harvest strategy must include precautionary buffers that account for limits on the ability to predict fisheries and food web dynamics.

For the high information tier, biomass and fishing mortality limits combined with the pattern of reduction in fishing mortality with decreased abundance must be shown by testing of the harvest strategy to (a) achieve the Dependent Predator Performance Criterion, (b) protect the forage fish stock from depletion caused by the fishery that impairs reproduction or population productivity, and (c) allow for recovery of the forage fish population through periods of natural fluctuation in population productivity. Testing of the harvest strategy with respect to achieving these criteria must be by quantitative analysis and modeling that is independently reviewed by scientists, and it must include realistic recognition and representation of environmental forcing of forage fish production dynamics, management implementation, and enforcement error.

Because estimating uncertainty and risk is difficult and often biased even in forage fisheries with high

Table 7.1

A three-tiered precautionary approach to the management of forage fish developed by the Lenfest Forage Fish Task Force

Information Tier	Forage fish stock dynamics and fisheries	Knowledge of status, trends, and dependencies of predators	Recommended management action
Low	<ol style="list-style-type: none"> Information is limited on population abundance, status, and trends so that there is little certainty that a determined stock status is reliable, and in particular there is little certainty that the stock is above minimum biomass levels. Environmental drivers have not been examined sufficiently to enable precise predictions of forage fish production dynamics. Fishery monitoring and enforcement are not sufficient to ascertain whether catches are within specified limits. 	<ol style="list-style-type: none"> Dependent predators have not been identified on the basis of empirical evidence from the relevant ecosystem. Evidence is insufficient to judge the status and trends of predators either known or likely to be dependent upon forage fish. Spatial patterns of foraging are not known. 	<ol style="list-style-type: none"> No new forage fisheries should be allowed to operate. Existing forage fisheries should be severely restricted so that depletion from fisheries is no more than 20% of unfished population.²³ Precautionary spatial closures should be implemented to protect against localized depletion of forage fish and to protect potential foraging areas of land-based predators. Data should be gathered that is sufficient to reach at least the intermediate tier.
Intermediate	<ol style="list-style-type: none"> Population abundance, status, and trends are monitored so that catch control rules are likely to result in population levels within specified biological limits. Putative environmental drivers of forage fish productivity are identified, providing some ability to predict production dynamics and account for them in the harvest control rule. There is some monitoring and enforcement of fisheries so that catches are likely to be within specified limits. 	<ol style="list-style-type: none"> Dependent predators have been identified so that effects of forage fish on their abundance can be predicted on the basis of food web models or the PREP equation. Population status and trends of dependent predators are monitored but with considerable uncertainty. Spatial patterns of foraging are known and sufficient to support predictions about the effects of localized depletion. 	<ol style="list-style-type: none"> Apply the PREP equation, or use data or models specific to the ecosystem, to assess the impacts of forage fish depletion on dependent species (using the upper 95% confidence interval). Apply a hockey stick harvest control rule with $B_{LIM} \geq 0.4B_0$ and $F \leq$ the lesser of 0.5M and $0.5F_{MSY}$. Increase B_{LIM} and decrease F when the ecosystem contains highly dependent predators or when precision of diet dependencies is low. Use spatial management to protect predators likely to be adversely affected by localized depletion.

²³ That is, with a high probability that forage fish biomass will equal or exceed 80 percent B_0 . The recommended level is based on the upper 95 percent confidence interval of the PREP equation, protecting with high probability all but the highest quartile of diet dependencies (Table 6.4).

Information Tier	Forage fish stock dynamics and fisheries	Knowledge of status, trends, and dependencies of predators	Recommended management action
High	<ol style="list-style-type: none"> 1. Population abundance, status, and trends are known with sufficient precision and lead time to adjust fishing levels according to a harvest control rule, resulting in a high likelihood of achieving management goals. 2. Environmental drivers of forage fish productivity are well known and are accounted for in the harvest control rule. 3. High ability to monitor and enforce fisheries regulations (at sea and/or with dockside observers) so that catches are highly likely to be within specified limits. 	<ol style="list-style-type: none"> 1. The functional responses of dependent predators to forage fish abundance are well defined based on empirical evidence from the relevant ecosystem so that effects of fishing can be determined with a high degree of certainty. Models reflect what is known from the field and continue to be tested and modified as new information is available. 2. The population status and trends of dependent predators are measured with high certainty and at frequent intervals. 3. Localized forage fish requirements of dependent predators can be estimated with high precision so that effects of localized depletion on dependent predators are well described. 	<ol style="list-style-type: none"> 1. The harvest strategy must include an upper limit to F, a lower limit below which targeted fishing ceases (B_{LIM}), and F should be reduced as B_{LIM} is approached. 2. The harvest strategy must include precautionary buffers that account for limits on the ability to predict fisheries and food web dynamics. 3. In any case, lower biomass limits should not be less than $0.3 B_0$, and MAX F should not exceed $0.75 F_{MSY}$ or $0.75M$. 4. The harvest strategy must—by independent, realistic, quantitative testing—be shown to achieve the Dependent Predator Performance Criterion, protect the forage fish stock from impaired reproduction, and allow it to recover through periods of natural fluctuation in productivity. 5. Apply spatial management to account for localized depletion effects on spatially constrained predators.

information, we have placed additional constraints on the minimum lower biomass limit and upper fishing mortality for information-rich circumstances. Specifically, the minimum biomass level should be set at the greater of the value demonstrated to meet the Dependent Predator Performance Criterion and $0.3 B_0$, and MAX F should be set as the smaller of the value that meets the Performance Criterion and $0.75 F_{MSY}$ for information-rich circumstances. Based on our empirical and modeling results, we expect that for most ecosystems, the lower biomass limit will need to be substantially higher than $0.3 B_0$, and the maximum F will be substantially lower than $0.75 F_{MSY}$ in order to achieve conservation and management goals.

In many cases, spatial management will be needed to avoid effects of fishery-induced localized depletion of forage fish, especially on spatially constrained predators. Although spatial management is expected to be applied for all information tiers, increased extent and size of spatial/temporal closures for low and intermediate information tiers will help provide the extra precautionary buffer needed in these circumstances.

Concluding Remarks

We have presented a comprehensive account of the vulnerability of forage fish to overfishing and collapse, of their ecological and economic importance in specific locales and globally, and of the measured and predictable responses of forage fish consumers to the exploitation of these fish. It is clear from this compilation and synthesis that the management of forage fish needs to be much more cautious than standard past management guidance and practice, given the tremendous implications of forage fishing for the integrity of marine ecosystems.

Our recommendations are, in broad terms, consistent with other contemporary suggestions about forage fish management. However, we have gone several steps beyond general principles to produce recommendations that are both specific and practical to implement. We are explicit in our advice that fisheries should be constrained such that there is a high probability that fishing not jeopardize the persistence of other species in the ecosystem.

We refer to internationally agreed criteria for evaluating the vulnerability of a species to extinction. We provide unambiguous methods for determining the values of fisheries reference points that will satisfy this criterion, and default values to be used in circumstances where available system-specific values cannot be estimated. Our recommended defaults are, in turn, derived from thorough synthesis of existing empirical information and comprehensive quantitative analysis of food web models.

For the intermediate knowledge tier, where perhaps most fisheries now thought to be well managed from a single-species perspective may fall, we recommend that fishing intensity be about half as high, and the biomass of forage fish that remain in the ocean should be twice as large as current benchmarks for fisheries management. For less-understood ecosystems, we recommend that no new forage fisheries be initiated unless adequate information is obtained.

We recognize that adoption and implementation of our recommendations would constitute a major break from tradition and could significantly reduce allowable harvest levels for some ongoing forage fisheries. However, when considering the range of possibilities for criteria to ground ecosystem-based reference points, the Task Force felt strongly that avoiding pushing species toward extinction is a requirement for upholding ecosystem integrity. The benefits of implementing our recommended approach include a greater chance of maintaining fully functioning ecosystems and the ecological roles and support services provided by forage fish. A further benefit will be increased catches of dependent commercially valuable predators, which should more than compensate for economic losses due to lower forage fish catches.

The Task Force agreed that the recommendations herein constitute the next logical step for rational management of forage fish fisheries. It is the minimum required to ensure with reasonably high probability that the full complement of ocean life is maintained in marine ecosystems subject to forage fish fishing. We hope this concept will be considered as one of the essential pillars for ecosystem-based fisheries management, and of a holistic approach to fisheries management more generally.

Glossary

Allee effect—Populations at low numbers are affected by a positive relationship between per capita population growth rate and density, which increases their likelihood of population collapse.

B_0 , B_{zero} —Virgin or unfished biomass. Using mathematical models, it is calculated as the long-term average biomass value expected in the absence of fishing mortality. In production models, B_0 is also known as carrying capacity. It is often used as a biological reference point in fisheries management.

B_{LIM} —Minimum biomass threshold below which there is an unacceptable risk to a stock (or population).

B_{MEY} —Biomass required to produce maximum economic yield.

B_{MSY} —Biomass at maximum sustainable yield derived from a production model or from an age-based analysis using a stock recruitment model. Often used as a biological reference point in fisheries management, it is the calculated long-term average biomass value expected if fishing is at F_{MSY} .

B_{TARGET} —Target biomass representing the desired stock level.

B_{TH} —Minimum threshold of biomass, also known as biomass threshold.

Biomass—The total weight of a group (or stock) of living organisms (e.g., fish, plankton) or of some defined fraction of it (e.g., spawners), in a specific area at a particular time.

Bycatch—Part of a catch of a fishing unit taken incidentally in addition to the target species towards which fishing effort is directed. Some or all of it may be returned to the sea as discards, usually dead or dying.

Carrying capacity—The maximum population of a species that a specific ecosystem can support indefinitely without deterioration of the character and quality of the resource. It represents the point of balance between reproduction potential and environmental constraints.

Catchability—The extent to which a stock is susceptible to fishing. Catchability often increases with developments in fishing technology, and can depend on the abundance of fish.

Catch per unit effort (CPUE)—The quantity of fish caught (in number or in weight) with one standard unit of fishing effort; e.g., number of fish taken per 1,000 hooks per day or weight of fish, in tons, taken per hour of trawling. CPUE is often considered an index of fish biomass (or abundance).

Condition Factor (K)—A mathematical measurement of the degree of ‘plumpness’ or the general health of a fish or group of fishes.

Conditional unfished biomass (CUB)—Biomass when there is no forage fish fishing mortality but all other species are fished at the rate given by the fitted EwE model.

Constant fishing mortality (Constant F or CF)—Setting the catch equal to a fixed proportion of the estimate of the current population size.

Constant yield strategy—An approach wherein fisheries can be harvested up to MSY without compromising future fishing.

Control rules—Describes a plan for pre-agreed management actions as a function of variables related to the status of the stock in question. For example, a control rule can specify how fishing mortality or yield should vary with levels of estimated biomass.

Density-dependence—The dependence of a factor influencing population dynamics (such as survival rate or reproductive success) on population density. The effect is usually in the direction that contributes to the regulative capacity of a stock.

Deterministic model—A model whose behavior is fully specified by its form and parameters, unlike a stochastic model.

Discard—To release or return fish to the sea, dead or alive, whether or not such fish are brought fully on board a fishing vessel.

Ecosystem-based fisheries management—Approach that takes major ecosystem components and services—both structural and functional—into account in managing fisheries.

Ecosystem overfishing—Occurs when the historical species balance (composition and dominance) is significantly modified by fishing.

Ecopath model—Model that produces a static, mass-balanced snapshot of an ecosystem.

Ecopath with Ecosim (EwE) model—Modelling software with a time-dynamic simulation module for policy exploration.

Ecopath Value Ratio (EVR)—Ratio of the predator catch value supported by forage fish to the total fishery catch value, which includes both predators and non-predators of forage fish.

Exploitation rate—The proportion of a population at the beginning of a given time period that is caught during that time period (usually expressed on a yearly basis).

F—The part of the total mortality rate applying to a fish population that is caused by fishing.

F_{LIM}—Maximum fishing mortality rate above which removals from the population are considered too high.

F_{MSY}—Fishing mortality rate that, if applied constantly, would result in maximum sustainable yield.

F_{TARGET}—The fishing mortality rate corresponding to **B_{TARGET}** (defined above).

Fecundity—The potential reproductive capacity of an organism or population expressed in the number of eggs (or offspring) produced during each reproductive cycle. Fecundity usually increases with age and size. The information is used to compute stock or population spawning potential.

Fishing effort—The amount of fishing gear of a specific type used on the fishing grounds over a given unit of time; for example, hours trawled per day, number of hooks set per day, or number of hauls of a purse seine per day.

Fishmeal—Protein-rich meal derived from processing whole fish (usually small pelagic fish and by-catch) as well as residues and by-products from fish processing plants (fish offal). Used mainly as agriculture feed for poultry, pigs, and aquaculture feed for carnivorous aquatic species.

Forage fish/Foundation prey—Fish that provide the main pathway for energy to flow from very low trophic levels (plankton) to higher trophic levels (predatory fish, birds, and mammals). See Box 1.1 for a full definition of forage fish.

Harvest control rules—A set of well-defined rules used for determining a management action in the form of a total allowable catch (TAC) or allowable fishing effort.

High grading—The practice of discarding a portion of a vessel's legal catch that could have been sold, so that a higher or larger grade of fish can be subsequently caught that brings higher prices. This may occur in any fishery, but the incentive to do so is particularly great with catch limitations such as individual catch quotas.

“Hockey stick” control rules—These rules set a minimum fish biomass level below which there is no fishing. They also stipulate that the fishing mortality (catch) rate should increase linearly as the fish biomass increases from the “no fishing” level to some target level ($B_{\text{target}} \leq B_0$) and then is held constant until reaching a level that would be expected if the population were not fished.

Landings—Mass of fish unloaded at the dock. May be different from the catch (which includes discards).

Limit reference point (LRP)—Indicates the limit beyond which the state of a fishery is not considered viable. Fishery catches should be reduced or stopped before reaching it. If a LRP is inadvertently reached, management action should severely curtail or stop fishing, as appropriate, and corrective action should be taken.

Localized depletion—Occurs when localized catches take more fish in a specified period than can be replaced either locally or through fish migrating into the catch area. Local depletion can occur independent of the status of the overall stock, and can be greater than decreases in the entire stock.

Management Strategy Evaluation (MSE)—The process of testing alternative management strategies by simulation, in particular for robust performance in the presence of uncertainty.

Maximum Sustainable Yield (MSY)—The largest average catch or yield that can continuously be taken from a stock under existing environmental conditions. For species with fluctuating recruitment, the maximum might be obtained by taking fewer fish in some years than in others.

Meta-population—A set of populations that can effectively be separate, weakly coupled, or globally interacting, through strongly coupled patches.

Natural mortality—That part of total mortality applying to a fish population that is caused by factors other than fishing.

Obligate predator—A predator restricted to eating a single species of prey.

Pelagic—Inhabiting the water column as opposed to being associated with the sea floor; generally occurring anywhere from the surface to 1,000 meters.

Pelagic fish—Fish that spend most of their life swimming in the water column maintaining little contact with or dependency on the bottom of the ocean. Usually refers to the adult stage of a species.

Phytoplankton—Small, usually microscopic plants drifting in the upper layers of the ocean, consuming nutrients and light energy to produce biomass. In particularly nutrient-rich conditions (including eutrophication) phytoplankton blooms may occur and could be toxic.

Plankton—Floating organisms whose movements are largely dependent on currents. While some zooplankton exhibit active swimming movements that aid in maintaining vertical position, plankton as a whole is unable to move against appreciable currents.

Potential Biological Removal (PBR)—The maximum number of individuals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population.

Purse seine—Nets characterized by the use of a purse line at the bottom of the net. The purse line enables the net to be closed like a purse and thus retain all the fish caught. Purse seines, which may be very large, are operated by one or two boats.

Recruitment (R)—The number of fish added to the exploitable stock in the fishing area each year, through a process of growth (i.e., the fish grows to a size where it becomes catchable) or migration (i.e., the fish moves into the fishing area).

Reference point—A reference point indicates a particular state (value) of a fishery corresponding to a situation considered as desirable (target reference point, TRP), dangerous (threshold reference point) or undesirable (limit reference point, LRP). Both threshold and limit reference points require immediate action, and differ in the degree of urgency.

Relative species abundance—How common or rare a species is relative to other species in a defined location or community.

Serial spawning—Spawning in bursts or pulses more than once in a spawning season in response to an environmental stimulus.

Spatial TAC—Allocating the total allowable catch according to specific spatial zones.

Spawning Stock Biomass (SSB)—The total mass of all fish (both males and females) in the population which contribute to reproduction. Often conventionally defined as the biomass of all individuals beyond “age at first maturity” or “size at first maturity,” i.e., beyond the age or size class in which 50 percent of the individuals are mature.

Stochastic—A model that has components affected by random variability.

Stock—A group of individuals in a species occupying a well defined spatial range independent of other stocks of the same species. Such a group can be regarded as an entity for management or assessment purposes. Some species form a single stock while others are composed of several stocks. The impact of fishing on a species cannot be determined without knowledge of this stock structure.

Stock assessment—The process of collecting and analyzing biological and statistical information to determine the changes in the abundance of a fishery stock in response to fishing, and, to the extent possible, to predict future trends in stock abundance. Stock assessments are used as a basis to assess and specify the present and probable future condition of a fishery.

Stock/recruitment relationship (SRR)—The relationship between the level of parental biomass (e.g., spawning stock size) and subsequent recruitment level. Determination of this relationship is useful to analyze the sustainability of alternative harvesting regimes and the level of fishing beyond which stock collapse is likely. The relation is usually blurred by environmental variability and difficult to determine with any accuracy.

Total Allowable Catch (TAC)—The total catch allowed to be taken from a resource in a specified period (usually a year), as defined in the management plan. The TAC may be allocated to the stakeholders in the form of quotas, as specific quantities, or proportions.

Trophic cascade—Reciprocal predator-prey effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web.

Trophic level—Classification of natural communities or organisms according to their place in the food chain.

Upwelling—Upward movement of cool and nutrient-rich sub-surface waters towards the surface often leading to exceptionally productive areas. There exist various types of upwelling. For fisheries, the most important type is the wind-induced coastal upwelling where the upward movement is a consequence of wind stress (along shore) and Eckman transport (offshore).

Yield per recruit (YPR)—A model that estimates yield in terms of weight, but more often as a percentage of the maximum yield, for various combinations of natural mortality, fishing mortality, and time exposed to the fishery.

Zooplankton—Non-photosynthetic, heterotrophic planktonic organisms, including protists, small animals, and larvae, which exist within the water column.

List of Acronyms

ASMFC—Atlantic States Marine Fisheries Commission

CCAMLR—Commission for the Conservation of Antarctic Marine Living Resources

CF—Constant Fishing Mortality

CPUE—Catch Per Unit Effort

C_u —Conservation Factor

CUB—Conditional Unfished Biomass

CV—Coefficient of Variation

CY—Constant Yield

EVR—Ecopath Value Ratio

EwE—Ecopath with Ecosim

F —Fishing Mortality Rate

FMP—Fisheries Management Plan

HSA—High Seas Area

LME—Large Marine Ecosystem

LRP—Limit Reference Point

M —Natural Mortality Rate [also defined as “Variable Predation Mortality” in Chapt. 2]

MSE—Management Strategy Evaluation

MSY—Maximum Sustainable Yield

NMFS—National Marine Fisheries Service

NOAA—National Oceanic and Atmospheric Administration

P —Spawning Population Size

PREP—Predator Response to the Exploitation of Prey

R —Recruitment

SRR—Stock-Recruitment Relationship

SSB—Spawning Stock Biomass

TAC—Total Allowable Catch

TAB—Total Allowable Bycatch

TRP—Target Reference Point

Z —Total Mortality

Literature Cited

- Able, K. W., and Fahay, M. P. (2010). *Ecology of Estuarine Fishes: Temperate waters of the North Atlantic*. Baltimore, MD: The Johns Hopkins University Press.
- AFMA, Australian Fisheries Management Authority. (2007). *Commonwealth Fisheries Harvest Strategy: Policy and Guidelines*. Department of Agriculture, Fisheries, and Forestry.
- Ainsworth, C. H. et al. (2002). Ecosystem Models of Northern British Columbia for the Time Periods 2000, 1950, 1900, and 1750. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2002*, 10(4), 41 pp.
- Alaska Sea Grant. (1997). *Forage Fishes in Marine Ecosystems*. Proceedings of the international symposium on the role of forage fish in marine ecosystems. Alaska Sea Grant Report No. 97-01. Fairbanks, A.K.: University of Alaska.
- Alder, J., et al. (2008). Forage fish: from ecosystems to markets. *Annual Review of Environment and Resources*, 33, 153–166.
- Alder, J., and Pauly, D. (2006). On the multiple uses of forage fish: From Ecosystems to Markets. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2006*, 14(3), 120 pp.
- Alheit, J., and Niquen, M. (2004). Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography*, 60(2-4), 201–222.
- Alheit, J., et al. (2009). Decadal-scale variability in populations. In D. M., et al. (Eds.), *Climate Change and Small Pelagic Fish*. (pp. 64–87). Cambridge, U.K.: Cambridge University Press.
- Alonzo, S. H., et al. (2008). The importance of incorporating protogynous sex change into stock assessments. *Bulletin of Marine Science*, 83(1), 163–179.
- Amorim, P., et al. (2004). Preliminary Ecopath Model of the Guinea-Bissau Continental Shelf Ecosystem (NW Africa). In M.L.D. Palomares and D. Pauly (Eds.), *West African Marine Ecosystems: models and fisheries impacts*. (pp. 95–112). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(7), 221 pp.
- Araújo, J. (2005). *An Ecopath model of the western English Channel ecosystem with an exploration of its dynamic properties*: Centre for Environment, Fisheries and Aquaculture Science. Report Number 125.
- Arbach Leloup, F., et al. (2008). Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France). *Estuarine, Coastal and Shelf Science*, 76(1), 111–120.
- Arnott, S. A., and Ruxton, G. D. (2002). Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. *Marine Ecology Progress Series*, 238, 199–210.
- Arreguín-Sánchez, F., et al. (2002). Flows of biomass and structure in an exploited benthic ecosystem in the Gulf of California, Mexico. *Ecological Modelling*, 156(2-3), 167–183.
- Atlantic States Marine Fisheries Commission (ASMFC) (2006). *2006 Stock Assessment Report for Atlantic Menhaden*: Atlantic Menhaden Technical Committee. Report Number 10-02.
- ASMFC (2010). *Atlantic menhaden stock assessment and review panel reports*. Washington, D.C.
- ASMFC (2011a). *ASMFC Atlantic Menhaden Board Initiates Addendum to Increase Abundance and Spawning Stock Biomass*. News Release. Arlington, VA.
- ASMFC (2011b). *Draft addendum to Amendment 1 to the Atlantic menhaden fishery management plan for public comment. Alternative reference points and fishery management tools*. Washington, D.C.
- ASMFC (2011c). *ASMFC Atlantic Menhaden Board approves Draft Addendum V. Addendum establishes new fishing mortality reference points to increase spawning stock biomass*. News Release. Washington, D.C.
- Aydin, K.Y., et al. (2002). *A comparison of the eastern Bering and western Bering Sea shelf and slope ecosystems through the use of mass-balance food web models*. US Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center. Report Number 130.
- Bakun, A. (1990). Global climate change and intensification of coastal ocean upwelling. *Science*, 247(4939), 198–201.
- Bakun, A. (1993). The California Current, Benguela Current, and southwestern Atlantic shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. In K. Sherman, L. M. Alexander, and B. Gold (Eds.), *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. (pp. 199–224). American Association for the Advancement of Science.
- Bakun, A., and Weeks, S. J. (2006). Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish and Fisheries*, 7(4), 316–333.
- Barange, M., et al. (2009). Current trends in the assessment and management of small pelagic fish stocks. In D.M Checkley, C. Roy, J. Alheit, and Y. Oozeki (Eds.), *Climate Change and Small Pelagic Fish*. (pp. 191–256). Cambridge, UK: Cambridge University Press.
- Barth, J. A., et al. (2007). Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proceedings of the National Academy of Sciences*, 104(10), 3719–3724.
- Baum, J. K., and Myers, R. A. (2004). Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, 7(2): 135–145.
- Baumgartner, T., et al. (1992). Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *CalCOFI Report*, 33, 24–40.
- Becker, B. H., and Beissinger, S. R. (2006). Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology*, 20(2), 470–479.
- Becker, B. H., et al. (2007). Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series*, 329, 267–279.
- Belkin, I. M., et al. (2009). Fronts in large marine ecosystems. *Progress in Oceanography*, 81(1-4), 223–236.

- Bertrand, A., et al. (Eds.) (2008). The Northern Humboldt Current System: Ocean dynamics, Ecosystem processes, and Fisheries. *Progress in Oceanography*, 79(2-4), 95–412.
- Bertrand, S., et al. (2010). Pescadores y aves marinas compitiendo por el mismo recurso: Estrategias de forrajeo, interacciones y consecuencias. *Proceedings of the Ve International panel of experts on Peruvian anchovy. Boletín del Instituto del Mar del Perú*, 25(1), 39–44.
- Beverton, R., and Holt, S. (1957). On the dynamics of exploited fish populations. Fisheries Investigation Series II (Vol. 19). London: Ministry of Agriculture, Fisheries and Food.
- Beverton, R. (1990). Small marine pelagic fish and the threat of fishing; are they endangered? *Journal of Fish Biology*, 37 (Suppl. A), 5–16.
- Bigelow, H. B., and Schroeder, W. C. (1953). *Fishes of the Gulf of Maine* (2 ed.). Washington, DC: U.S. Department of the Interior.
- Blanchard, J., et al. (2002). Exploring marine mammal-fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea ecosystem. *Sci. Ser. Tech Rep*, 117, 52pp.
- Boeing, W. J., and Duffy-Anderson, J.T. (2008). Ichthyoplankton dynamics and biodiversity in the Gulf of Alaska: responses to environmental change. *Ecological Indicators*, 8(3), 292–302.
- Boersma, P. D. (1978). Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. *Science*, 200(4349), 1481–1483.
- Boersma, P. D. (2008). Penguins as marine sentinels. *BioScience*, 58(7), 597–607.
- Boersma, P. D., and Rebstock, G. A. (2009). Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series*, 375, 263–275.
- Boersma, P. D., et al. (2009). Following the fish: penguins and productivity in the South Atlantic. *Ecological Monographs*, 79(1), 59–76.
- Bograd, S. J., et al. (2009). Phenology of coastal upwelling in the California Current. *Geophys Res Lett*, 36(L01602), 5 pp.
- Bogstad, B., et al. (1997). MULTSPEC—a multi-species model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, 22, 317–341.
- Botsford, L. W., et al. (2003). Principles for the design of marine reserves. *Ecological Applications*, 13(1), 25–31.
- Bowen, W., and Harrison, G. (1996). Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology*, 74(1), 125–135.
- Boyd, I., et al. (1995). Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, 64(4), 505–518.
- Boyd, I. (1999). Foraging and provisioning in Antarctic fur seals. *Behavioral Ecology*, 10(2), 198–208.
- Boyd, I., and Murray, A. (2001). Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology*, 70(5), 747–760.
- Boyd, I. L. (2010). Assessing the effectiveness of conservation measures: Resolving the “wicked” problem of the Steller sea lion. *Biological Conservation*, 143(7), 1664–1674.
- Boyer, D., et al. (2001). Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment. *South African Journal of Marine Science*, 23(1), 67–84.
- Boyer, D., and Hampton, I. (2001). An overview of the living marine resources of Namibia. *South African Journal of Marine Science*, 23(1), 5–35.
- Brando, V. E., et al. (2004). Assessment of environmental management effects in a shallow water basin using mass-balance models. *Ecological Modelling*, 172(2-4), 213–232.
- Bredesen, E.L. (2004). *Krill and the Antarctic: Finding the Balance*. M.S. Thesis. University of British Columbia. p. 91.
- Buchary, E.A., et al. (2002). New Ecopath Model in Hong Kong marine ecosystem. In T.J. Pitcher, E. Buchary, and P. Trujillo (Eds.), Spatial simulations of Hong Kong's marine ecosystem: ecological and economic forecasting of marine protected areas with human-made reefs. (pp. 6–14). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2002*, 10(3), 170 pp.
- Butler, M., et al. (2006). The ecology of juvenile and adult lobsters. In R. Phillips (Ed.), *Lobsters: the biology, management aquaculture and fisheries*. (pp. 263–309). Oxford, UK: Blackwell Publishing Ltd.
- Butterworth, D. (1980). A critique of “The control of a pelagic fish resource” with a postscript “The assessment of the SWA pilchard stocks.” *South African Journal of Marine Science*, 76, 460–464.
- Butterworth, D., et al. (2011). Claim by Pichegru et al. that marine no-take zone benefits penguins remains premature. *Biology Letters*, eLetter in response to 6(4), 498–501.
- Cairns, D. (1987). Seabirds as indicators of marine food supplies. *Biological Oceanography*, 5(26), 1–267.
- Carlisle, D. W. (1998). *Estimation and evaluation of a harvest threshold for management of the Sitka herring sac roe fishery base on a percentage of average unfished biomass*. Alaska Department of Fish and Game, Department of Commercial Fisheries. Report No. 1J98-18.
- Casini, M., et al. (2008). Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, 275(1644), 1793–1801.
- Castillo, S., and Mendo, J. (1987). Estimation of unregistered Peruvian anchoveta (*Engraulis ringens*) in official catch statistics, 1951 to 1982. In D. Pauly and I. Tsukayama (Eds.), *The Peruvian anchoveta and its upwelling ecosystem: three decades of changes*. (pp. 109–116). ICLARM Studies and Reviews, 15, 351 pp.
- CBFEAP. (2006). Fisheries ecosystem planning for Chesapeake Bay. The Chesapeake Fisheries Ecosystem Plan Technical Advisory Panel, *American Fisheries Society*, Report Number 3.
- Chapman, E. W., et al. (2010). The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie penguin (*Pygoscelis adeliae*) chick growth: A modeling study. *Deep Sea Research Part II: Topical Studies in Oceanography*, 57(7-8), 543–558.
- Chavez, F. P., et al. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, 299(5604), 217–221.
- Chavez, F. P., et al. (2008). The northern Humboldt Current system: brief history, present status and a view towards the future. *Progress in Oceanography*, 79(2-4): 95–105.
- Checkley, D. M., and Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, 83(1-4), 49–64.

- Cheung, W. W. L., and Pitcher, T. J. (2005). A mass-balance model of the marine ecosystem and fisheries of the Falkland Islands. In M.L.D. Palomares, P. Pruvost, T.J. Pitcher and D. Pauly (Eds.), *Modeling Antarctic Marine Ecosystems*. (pp. 65–85). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2005*, 13(7), 98 pp.
- Cheung, W. W. L., et al. (2010). Large scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, 16(1), 24–35.
- Christensen, V., and Pauly, D. (1992). ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, 61(3-4), 169–185.
- Christensen, V. (1995). A model of trophic interactions in the North Sea in 1981, the year of the stomach. *Dana*, 11(1), 1–28.
- Christensen, V. and Walters, C.J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172(2-4), 109–139.
- Christensen, V., et al. (2005). *Ecopath with Ecosim: a user's guide*. The Fisheries Centre, University of British Columbia. November 2005 edition, 154 p. (available online at www.ecopath.org).
- Christensen, V., et al. (2009). *Fisheries ecosystem model of the Chesapeake Bay: Methodology, parameterization, and model exploration*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Tech. Memo. NMFS-F/SPO-106, 146 pp.
- Cisneros-Montemayor, A., et al. (2010). *The global potential for whale watching*. *Marine Policy*, 34(6), 1273–1278.
- Clark, C. W. (2006). *The worldwide crisis in fisheries: economic models and human behavior*. Cambridge, U.K.: Cambridge Univ Press. 270 pp.
- Clark, W. G. (1991). Groundfish exploitation rates based on life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(5), 734–750.
- Clarke, A., et al. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1477), 149–166.
- Coetzee, J. C., et al. (2008). Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science*, 65(9), 1676–1688.
- Coetzee, J. C. (2010). Claim by Pichegru et al. that marine no-take zone benefits penguins is premature. *Biology Letters*, eLetter in response to 6(4), 498–501.
- Coll, M., et al. (2006). Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwelling systems by means of standardized models and indicators. *Ecological Modelling*, 198(1-2), 53–70.
- Coll, M., et al. (2007). An ecological model of the northern and central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. *Journal of Marine Systems*, 67(1-2), 119–154.
- Coll, M., et al. (2008). Ecosystem overfishing in the ocean. *PLoS One*, 3(12), e3881.
- Collette, B. B., and Klein-Macphee, G. (2002). *Bigelow and Schroeder's Fishes of the Gulf of Maine*. Washington, D.C.: Smithsonian Institution Press.
- Collie, J. S., and Gislason, H. (2001). Biological reference points for fish stocks in a multispecies context. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(11), 2167–2176.
- Conover, D. O., et al. (2005). Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(4), 730–737.
- Constable, A. J., et al. (2000). Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal of Marine Science*, 57(3), 778–791.
- Constable, A. J. (2004). Managing fisheries effects on marine food webs in Antarctica: trade-offs among harvest strategies, monitoring, and assessment in achieving conservation objectives. *Bulletin of Marine Science*, 74(3), 583–605.
- Cox, S. P., et al. (2002). Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(11), 1736–1747.
- Crawford, R. J. M., and Dyer, B. M. (1995). Responses by four seabird species to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis*, 137(3), 329–339.
- Crawford, R., and Jahncke, J. (1999). Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. *South African Journal of Marine Science*, 21(1), 145–156.
- Crawford, R. J. M., et al. (2001). African penguins as predators and prey coping (or not) with change. *South African Journal of Marine Science*, 23(1), 435–447.
- Crawford, R. J. M., et al. (2006). The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*, 132(1), 119–125.
- Crawford, R. J. M., et al. (2007). An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*). *ICES Journal of Marine Science*, 64(3), 570–576.
- Crawford, R. J. M., et al. (2008). Influences of the abundance and distribution of prey on African penguins *Spheniscus demersus* off western South Africa. *African Journal of Marine Science*, 30(1), 167–175.
- Cresswell, K., et al. (2008). Can macaroni penguins keep up with climate and fishing-induced changes in krill? *Polar Biology*, 31(5), 641–649.
- Crowder, L. B., et al. (2000). Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science*, 66(3), 799–820.
- Croxall, J., et al. (2002). Environmental change and Antarctic seabird populations. *Science*, 297(5586), 1510–1514.
- Croxall, J., and Nicol, S. (2004). Management of Southern Ocean fisheries: Global forces and future sustainability. *Antarctic Science*, 16(4), 569–584.
- Cruz-Escalona, V., et al. (2007). Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. *Estuarine, Coastal and Shelf Science*, 72(1-2), 155–167.
- Csirke, J. (1980). Recruitment in the Peruvian anchovy and its dependence on the adult population. *Rapp. Proces-Verb. Réun. Cons. Int. Explor. Mer*, 177, 307–313.
- Csirke, J. (1988). Small shoaling pelagic fish stocks. In J.A. Gulland (ed.). *Fish population dynamics*. (pp. 271–302). New York: John Wiley & Sons.

- Csirke, J. (1989). Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. In D. Pauly and L. Tsukayama (Eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions* (pp. 207–243) ICLARM Studies and Reviews 18, 438 pp.
- Cury, P., et al. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, 57(3), 603–618.
- Cury, P., and Shannon, L. (2004). Regime shifts in upwelling ecosystems: Observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography*, 60(2-4), 223–243.
- Cury, P. et al. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science* 334(6063), 1703–1706.
- Cushing, D. (1971). The dependence of recruitment on parent stock in different groups of fishes. *ICES Journal of Marine Science*, 33(3), 340–362.
- Cushing, D. H. (1988). *The provident sea*. Cambridge, UK: Cambridge University Press.
- Dalsgaard, J., and Pauly, D. (1997). Preliminary mass-balance model of Prince William Sound, Alaska, for the pre-spill period, 1980–1989. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 1997*, 5(2), 33 pp.
- Daunt, F., et al. (2008). The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(3), 362–381.
- Davoren, G. K., and Montevecchi, W. A. (2003). Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series*, 258, 253–261.
- De la Mare, W.K. and Constable, A.J. (2000). Utilising data from ecosystem monitoring for managing fisheries: development of statistical summaries of indices arising from the CCAMLR Ecosystem Monitoring Program. *CCAMLR Science*, 7(2000), 101–117.
- de Moor, C. L., et al. (2008). Revised estimates of abundance of South African sardine and anchovy from acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine. *African Journal of Marine Science*, 30(2), 219–232.
- de Moor, C. L., et al. (2011). Is the management procedure approach equipped to handle short-lived pelagic species with their boom and bust dynamics? The case of the South African fishery for sardine and anchovy. *ICES Journal of Marine Science*, 68(10), 2075–2085.
- De Oliveira, J., et al. (1998). The application of a management procedure to regulate the directed and bycatch fishery of South African sardine *Sardinops sagax*. *South African Journal of Marine Science*, 19(1), 449–469.
- De Oliveira, J., and Butterworth, D. (2004). Developing and refining a joint management procedure for the multispecies South African pelagic fishery. *ICES Journal of Marine Science*, 61(8), 1432–1442.
- DeMartini, E. E. (1993). Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin*, 91, 414–414.
- Dichmont, C., et al. (2003). Application of a weekly delay-difference model to commercial catch and effort data for tiger prawns in Australia’s Northern Prawn Fishery. *Fisheries Research*, 65(1-3), 335–350.
- Dorman, J. G., et al. (2011). Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 northern California coastal populations: implications from a model study. *Geophysical Research Letters*, 38 (L04605), 5 pp.
- Dorn M.W. (2002). Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock–recruit relationships. *North American Journal of Fisheries Management*, 22(1), 280–300.
- Duarte, L. O., and Garcia, C. B. (2004). Trophic role of small pelagic fishes in a tropical upwelling ecosystem. *Ecological Modelling*, 172(2-4), 323–338.
- Ducklow, H. W., et al. (2007). Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1477), 67–94.
- Elliott, M. L., et al. (2007). Breeding biology and status of the California least tern *Sterna antillarum browni* at Alameda Point, San Francisco Bay, California. *Waterbirds*, 30(3), 317–325.
- Elmgren, R. (2001). Understanding human impact on the Baltic ecosystem: Changing views in recent decades. *Ambio*, 30(4-5), 222–231.
- Elmgren, R., and Hill, C. (1997). Ecosystem function at low biodiversity: the Baltic example. In R. F. G. Ormond, J. D. Gage, M. V. Angel, and C. Tickell (Eds.), *Marine Biodiversity Patterns and Processes*. (pp. 319–336). Cambridge, U.K.: Cambridge University Press.
- Erfan, A., and Pitcher, T. (2005). An ecosystem simulation model of the Antarctic peninsula. In M. L. D. Palomares, P. Pruvost, T. J. Pitcher, and D. Pauly, (Eds.) *Modeling Antarctic marine ecosystems*. (pp. 5–20). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2005*, 13(7), 98 pp.
- Essington, T. E. (2007). Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(4), 628–637.
- Faure, V., and Cury, P. (1998). Pelagic fisheries and environmental constraints in upwelling areas: How much is possible? In M. H. Durand, P. Cury, R. Mendelsohn, C. Roy, A. Bakun, and D. Pauly (Eds.), *Global versus Local Changes in Upwelling Systems*. Paris: ORSTOM, pp. 391–407.
- Field, J. C., et al. (2006). Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography*, 68(2-4), 238–270.
- Field, J. C., and Francis, R. C. (2006). Considering ecosystem-based fisheries management in the California Current. *Marine Policy*, 30(5), 552–569.
- Field, J. C., et al. (2010). Estimating the impacts of fishing on dependent predators: a case study in the California Current. *Ecological Applications*, 20(8), 2223–2236.
- Food and Agriculture Organization of the United Nations (FAO). (2010). *The State of World Fisheries and Aquaculture 2010*. Rome: FAO.
- Forcada, J., and Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Global Change Biology*, 15(7), 1618–1630.
- Fowler, C. W. (2009). *Systemic management: Sustainable Human Interactions with Ecosystems and the Biosphere*. New York, NY: Oxford University Press.

- Francis, R. C., et al. (1998). Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, 7(1), 1–21.
- Frank, K. T., et al. (2011). Transient dynamics of an altered large marine ecosystem. *Nature*, 477(7362), 86–89.
- Frederiksen, M., et al. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea black legged kittiwakes. *Journal of Applied Ecology*, 41(6), 1129–1139.
- Frederiksen, M., et al. (2008). The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a longlived seabird. *Journal of Animal Ecology*, 77(5), 1020–1029.
- Fréon, P., et al. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulletin of Marine Science*, 76(2), 385–462.
- Froese, R. (2004). Keep it simple: Three indicators to deal with overfishing. *Fish and Fisheries*, 5(1), 86–91.
- Froese, R., et al. (2011). Generic harvest control rules for European fisheries. *Fish and Fisheries*, 12(3), 340–51.
- Fulton, E. A., et al. (2003). Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series*, 253, 1–16.
- Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, 81(1-2), 171–183.
- Furness, R. W., and Tasker, M. L. (2000). Seabird-fishery interactions: Quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, 202, 253–264.
- Furness, R. W. (2002). Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES Journal of Marine Science*, 59(2), 261–269.
- Furness, R. W. (2003). Impacts of fisheries on seabird communities. *Scientia Marina*, 67(Suppl. 2), 33–45.
- Gaichas, S., et al. (2009). A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. *Progress in Oceanography*, 81(1-4), 47–62.
- Gaines, S. D., et al. (2010). Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences*, 107(43), 18286–18293.
- Garcia, S. (1994). The precautionary principle: Its implications in capture fisheries management. *Ocean and Coastal Management*, 22(2), 99–125.
- Gasalla, M., and Rossi-Wongtschowski, C. (2004). Contribution of ecosystem analysis to investigating the effects of changes in fishing strategies in the South Brazil bight coastal ecosystem. *Ecological Modelling*, 172(2-4), 283–306.
- Gascuel, D., et al. (2009). Impact de la pêche sur l'écosystème marin de Guinée: modélisation EwE 1985/2005. (Fishing impact on the marine Guinean ecosystem: a 1985/2005 model using EwE). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2009*, 17(4), 60 pp.
- Gerber, L. R., et al. (2003). Population models for marine reserve design: a retrospective and prospective synthesis. *Ecological Applications*, 13(Suppl.1), 47–64.
- Gerrodette, T., et al. (2002). Precautionary management of marine fisheries: Moving beyond burden of proof. *Bulletin of Marine Science*, 70(2), 657–668.
- Gjøsaeter, H., et al. (2009). Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Marine Biology Research*, 5(1), 40–53.
- Grabowski, J. H., et al. (2010). Use of Herring Bait to Farm Lobsters in the Gulf of Maine. *PLoS One*, 5(4), 509–515.
- Gribble, N. A. (2005). *Ecosystem Modelling of the Great Barrier Reef: A Balanced Trophic Biomass Approach*. In Zenger, A. and Argent, R.M. (Eds.) MODSIM 2005 International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2005, pp. 170–176.
- Griffis, R. B., and Kimball, K. W. (1996). Ecosystem approaches to coastal and ocean stewardship. *Ecological Applications*, 6(3), 708–712.
- Guénette, S., and Morato, T. (2001). The Azores Archipelago in 1997. In: S. Guénette; V. Christensen and D. Pauly (Eds.), Fisheries impacts on North Atlantic ecosystems: models and analyses. (pp. 241–270). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2001*, 9(4), 344 pp.
- Guénette, S., et al. 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(11), 2495–2517.
- Halpern, B. S., et al. (2008). A global map of human impact on marine ecosystems. *Science*, 319(5865), 948–952.
- Hamre, J. (1994). Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. *Biodiversity and Conservation*, 3(6), 473–492.
- Hansson S., et al. (2007). Managing Baltic Sea fisheries under contrasting production and predation regimes: ecosystem model analyses. *Ambio*, 36(2-3), 265–271.
- Harvey, C. J., et al. (2003). An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine Science*, 60(5), 939–950.
- Hawkins, S. J., et al. (2003). Detection of environmental change in a marine ecosystem-evidence from the western English Channel. *Science of The Total Environment*, 310(1-3): 245–256.
- Hewitt, R., et al. (2004). Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. *CCAMLR Science*, 11, 81–97.
- Heymans, J. J. (2001). The Gulf of Maine, 1977–1986. In S. Guénette, V. Christensen, and D. Pauly (Eds.) Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses (pp. 128–150). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2001*, 9(4), 344 pp.
- Heymans, J.J., and Pitcher, T.J. (2002) A model of the marine ecosystem of Newfoundland and southern Labrador (2J3KLNO) in the time periods 1985–1987 and 1995–1997. In T.J. Pitcher, J.J. Heymans, M. Vasconcellos (Eds.), Ecosystem models of Newfoundland for the time periods 1995, 1985, 1900 and 1450. (pp. 5–43). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2002*, 10(5), 73 pp.
- Hilborn, R. (1985). A comparison of harvest policies for mixed stock fisheries. *Lecture Notes in Biomathematics*, 61, 75–87.
- Hilborn, R., and Walters, C. J. (1992). *Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty*. New York, NY: Chapman and Hall.
- Hilborn, R., and Liermann, M. (1998). Standing on the shoulders of giants: Learning from experience in fisheries. *Reviews in Fish Biology and Fisheries*, 8(3), 273–283.
- Hilborn, R. (2010). Pretty good yield and exploited fishes. *Marine Policy*, 34(1), 193–196.

- Hill, S. L., et al. (2009). The risk to fishery performance associated with spatially resolved management of Antarctic krill (*Euphausia superba*) harvesting. *ICES Journal of Marine Science*, 66(10), 2148–2154.
- Hjermann, D. Ø., et al. (2004). Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proceedings of the National Academy of Sciences*, 101(32), 11679–11684.
- Hockey, P., et al. (2005). *Roberts birds of southern Africa, 7th Edition*. Cape Town: John Voelcker Bird Book Fund.
- Hollings, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, 91(7), 385–398.
- Hollowed, A. B., et al. (2000). Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science*, 57(3), 707–719.
- Hollowed, A.B., et al. (2011). Experience with quantitative ecosystem assessment tools in the northeast Pacific. *Fish and Fisheries*, 12, 189–208.
- Hsieh, C., et al. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences-Research Across Boundaries*, 72(2), 165–178.
- Hunsicker, M. E., et al. (2010). The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries*, 11(4), 421–438.
- Hunt, G. L., and Megrey, B. A. (2005). Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas. *ICES Journal of Marine Science*, 62(7), 1245–1255.
- Hutchings, J. A. (2009). Avoidance of fisheries induced evolution: management implications for catch selectivity and limit reference points. *Evolutionary Applications*, 2(3): 324–334.
- Huyer, A. (1983). Coastal upwelling in the California Current system. *Progress in Oceanography*, 12(3), 259–284.
- International Council for the Exploration of the Sea (ICES). (2008). *Report of the Baltic Fisheries Assessment Working Group (WGBFAS)*. ICES Headquarters, Copenhagen, Denmark.
- ICES. (2010). *Report of the ICES Advisory Committee*. ICES Headquarters, Copenhagen, Denmark.
- ICES. (2010a). *Report of the Arctic Fisheries Working Group*. ICES Headquarters, Copenhagen, Denmark.
- ICES. (2010b). *Resolving climate impacts on fish stocks*. ICES Headquarters, Copenhagen, Denmark.
- ICES. (2011). *Capelin in Subareas I and II, excluding Division Ila west of 5W (Barents Sea capelin)*. ICES Headquarters, Copenhagen, Denmark.
- Iles, T. D. (1971). *The retention inside the Bay of Fundy of herring larvae spawned off the southwest coast of Nova Scotia*. International Commission for the Northwest Atlantic Fisheries. Res. Doc. 71/98.
- Iles, T. D. (1972). *Report of the herring working group*. Standing Committee on Research and Statistics Proceedings. App. II. Int. Comm. Northwest Atl. Fish. (ICNAF) Redb. Part 1. 1972: 43–66.
- The IndiSeas Project. Indicators for the seas. <http://www.indiseas.org/>
- Intergovernmental Panel on Climate Change (IPCC). (2007). *Climate change 2007: The physical science basis*. In S. Solomon, D. Qin and M. Manning (Eds.), *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 996). Cambridge, U.K.: Cambridge University Press.
- Jahncke, J., et al. (2004). Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography*, 13(3), 208–223.
- Jarre-Teichmann, A., and Christensen, V. (1998). Comparative modelling of trophic flows in four large upwelling ecosystems: global versus local effects. In M. H. Durand, P. Cury, R. Mendelsohn, C. Roy, A. Bakun, and D. Pauly (Eds.), *Global versus Local Changes in Upwelling Systems*. Paris: ORSTOM, 423–443.
- Jiang, H., et al. (2008). Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. *Ecological Modelling* 212, 492–503.
- Johannesson, K., et al. (2011). The Future of Baltic Sea Populations: Local Extinction or Evolutionary Rescue? *AMBIO: A Journal of the Human Environment*, 40(2): 179–190.
- Jung, S., and Houde, E. (2004). Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. *Fishery Bulletin*, 102(1), 63–77.
- Kanwit, J. K., and Libby, D. A. (2009). Seasonal movements of Atlantic herring (*Clupea harengus*): Results From a Four Year Tagging Study Conducted in the Gulf of Maine and Southern New England. *J. Northw. Atl. Fish. Sci*, 40, 29–39.
- Kawaguchi, S., and Nicol, S. (2007). Learning about Antarctic krill from the fishery. *Antarctic Science*, 19(02), 219–230.
- Kimmel, D. G., et al. (2009). Estuarine ecosystem response captured using a synoptic climatology. *Estuaries and Coasts*, 32(3), 403–409.
- Kirkman, S., et al. (2007). Making sense of censuses and dealing with missing data: Trends in pup counts of Cape fur seal *Arctocephalus pusillus pusillus* for the period 1972–2004. *African Journal of Marine Science*, 29(2), 161–176.
- Köster, F. W., et al. (2005). Baltic cod recruitment—the impact of climate variability on key processes. *ICES Journal of Marine Science*, 62(7), 1408–1425.
- Largier, J. L., et al. (2006). WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. *Deep Sea Research Part II: Tropical studies in Oceanography*, 53(25-26), 2833–2849.
- Levin, P. S., et al. (2009). Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology*, 7(1), 23–28.
- Liew, H., and Chan, E. (1987). *ECOPATH model of a tropical shallow-water community in Malaysia*. Fisheries and Marine Science Centre, Universiti Pertanian Malaysia, Kuala Terengganu.
- Lin, H. J., et al. (2006). Trophic structure and functioning in a eutrophic and poorly flushed lagoon in southwestern Taiwan. *Marine Environmental Research*, 62(1), 61–82.
- Link, J. S. (2005). Translating ecosystem indicators into decision criteria. *ICES Journal of Marine Science*, 62(3), 569–576.
- Link, J. S. (2010). *Ecosystem-Based Fisheries Management: Confronting Tradeoffs*. New York, NY: Cambridge University Press.
- Loeb, V., et al. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387(6636), 897–900.

- Lorenzen, K., and Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1486), 49–54.
- MacCall, A. (1976). Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. *CalCOFI Report*, 18, 136–148.
- MacCall, A. D. (1990). *Dynamic geography of marine fish populations*. Seattle, WA: Univ. Washington Press.
- Mace, P. M., et al. (1988). *A generalised bioeconomic simulation model for fish population dynamics*. Wellington, NZ: MAFFish, NZ Ministry of Agriculture and Fisheries.
- Mackinson, S., and Daskalov, G. (2007). An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. *Sci. Ser. Tech Rep. Cefas Lowestoft*, 142 pp.
- Mangel, M. (1998). No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters*, 1(2), 87–90.
- Mangel, M. (2000a). Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bulletin of Marine Science*, 66(3), 663–674.
- Mangel, M. (2000b). On the fraction of habitat allocated to marine reserves. *Ecology Letters*, 3(1): 15–22.
- Mangel, M., et al. (2002). Requiem for Ricker: unpacking MSY. *Bulletin of Marine Science*, 70(2), 763–781.
- Mangel, M. (2006). *The theoretical biologist's toolbox*. Cambridge, UK: Cambridge University Press.
- Mangel, M. (2010). Scientific inference and experiment in Ecosystem Based Fishery Management, with application to Steller sea lions in the Bering Sea and Western Gulf of Alaska. *Marine Policy*, 34(5), 836–843.
- Mangel, M., et al. (2010). Reproductive ecology and scientific inference of steepness: A fundamental metric of population dynamics and strategic fisheries management. *Fish and Fisheries*, 11(1), 89–104.
- Manickchand-Heileman, S., et al. (1998a). Energy flow and network analysis of Terminos Lagoon, SW Gulf of Mexico. *Journal of Fish Biology*, 53, 179–197.
- Manickchand-Heileman, S., et al. (1998b). A preliminary trophic model of the continental shelf, south-western Gulf of Mexico. *Estuarine, Coastal and Shelf Science*, 46(6), 885–899.
- Manickchand-Heileman, S., et al. (2004). A trophic model for exploring possible ecosystem impacts of fishing in the Gulf of Paria, between Venezuela and Trinidad. *Ecological Modelling*, 172(2-4), 307–322.
- Martin, J. M. (2005). *The distribution, abundance and trophic ecology of the fishes of Darwin Harbour mangrove habitats*. PhD Thesis Charles Darwin University.
- Maryland Sea Grant. (2009). *Menhaden species team: background and issue briefs*. Paper presented at the Ecosystem Based Fisheries Management for Chesapeake Bay, College Park, MD.
- McClatchie, S., et al. (2010). Re-assessment of the stock-recruit and temperature-recruit relationships for Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Sciences*, 67(11), 1782–1790.
- McClintock, J., et al. (2008). Ecological responses to climate change on the Antarctic Peninsula. *American Scientist*, 96(4), 302–310.
- McEvoy, A. F. (1986). *The fisherman's problem: Ecology and law in the California fisheries*. New York, NY: Cambridge University Press.
- McGinley, M. (2008). North Sea large marine ecosystem. In C. J. Cleveland (Ed.), *Encyclopedia of Earth*. Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment.
- McLeod, K., et al. (2005). Scientific consensus statement on marine ecosystem-based management. *Signed by 219*.
- Mendoza, J. (1993). A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. In V. Christensen and D. Pauly (Eds.) *Trophic models of aquatic ecosystems*. (pp. 285–297). ICLARM Conf. Proc. 26, 390 p.
- Mendy, A. (1999). *Trophic modeling as a tool to evaluate and manage Iceland's multispecies fisheries*. Report of the Marine Research Institute of Iceland. M5
- Mendy, A. N. (2004). Addendum: The Gambian continental shelf ecosystem in 1992 and 1995. In M.L.D. Palomares and D. Pauly (Eds.), *West African Marine Ecosystems: models and fisheries impacts*. (pp. 89–94). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(7), 221 pp.
- Moffitt, E. A., et al. (2009). Marine reserve networks for species that move within a home range. *Ecological Applications*, 19(7), 1835–1847.
- Mohammed, E. (2001). A model of the Lancaster Sound region in the 1980s. In S. Guenette, V. Christensen, and D. Pauly (Eds.), *Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses*. (p. 99–110). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2001*, 9(4), 344 pp.
- Monaghan, P., et al. (1989). The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. *Journal of Animal Ecology*, 58(1), 261–274.
- Mori, Y and Boyd, I.L. (2004). The behavioural basis for non-linear functional responses: the case of the Antarctic fur seal. *Ecology*, 85, 398–410.
- Morissette, L., et al. (2003). Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). *Can. Tech. Rep. Fish. Aquat. Sci.* 2497, 94 pp.
- Muck, P., and Pauly, D. (1987). Monthly anchoveta consumption of guano birds, 1953 to 1982. In D. Pauly and I. Tsukayama (Eds.), *The peruvian anchoveta and its upwelling ecosystem: three decades of change*. (pp. 219–233). ICLARM Studies and Reviews 15, 351 pp.
- Mullon, C., et al. (2005). The dynamics of collapse in world fisheries. *Fish and Fisheries*, 6(2), 111–120.
- Munch, S. B., et al. (2005). A unified treatment of top down and bottom up control of reproduction in populations. *Ecology Letters*, 8(7), 691–695.
- Munch, S., and Kottas, A. (2009). A Bayesian modeling approach for determining productivity regimes and their characteristics. *Ecological Applications*, 19(2), 527–537.
- Murawski, S. A. (2000). Definitions of overfishing from an ecosystem perspective. *ICES Journal of Marine Science*, 57(3), 649–658.
- Murphy, E., et al. (1998). Interannual variability of the South Georgia marine ecosystem: Biological and physical sources of variation in the abundance of krill. *Fisheries Oceanography*, 7, 381–390.

- Murphy, E., et al. (2007). Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1477), 113–148.
- Murphy, G. I. (1967). Vital statistics of the Pacific sardine (*Sardinops caerulea*) and the population consequences. *Ecology*, 48(5), 731–736.
- Murphy, G. I. (1977). Clupeoids. In J. A. Gulland (Ed.), *Fish Population Dynamics*. London: J. Wiley and Sons.
- Myers, R. A., et al. (1999). Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(12), 2404–2419.
- Myers, R. A., et al. (2002). Inferring Bayesian priors with limited direct data: applications to risk analysis. *North American Journal of Fisheries Management*, 22(1), 351–364.
- Naylor, R., and Burke, M. (2005). Aquaculture and ocean resources: Raising tigers of the sea. *Annu. Rev. Environ. Resour.*, 30, 185–218.
- Naylor, R. L., et al. (2009). Feeding aquaculture in an era of finite resources. *Proceedings of the National Academy of Sciences*, 106(36), 15103–15110.
- Neira, S., et al. (2004). Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. *Ecological Modelling*, 172(2–4), 233–248.
- Neumann, T. (2010). Climate-change effects on the Baltic Sea ecosystem: a model study. *Journal of Marine Systems*, 81(3): 213–224.
- National Marine Fisheries Service (NMFS). (1998). *Magnuson-Stevens Act Provisions, National Standards Guidelines: Final Rule. Code of Federal Regulations*.
- NMFS. (2003). Supplement to the Endangered Species Act-Section 7 Consultation. Biological opinion and incidental take statement of October 2001. Silver Spring, MD.
- NMFS. (2009). *Our living oceans. Report on the status of U.S. living marine resources*.
- National Oceanic and Atmosphere Administration (NOAA). (2009). Species of concern: River herring (alewife and blueback herring). <http://www.nmfs.noaa.gov/pr/species/concern>
- National Research Council (NRC). (2003). *Decline of the Steller Sea Lion in Alaskan Waters: Untangling Food Webs and Fishing Nets*. Washington, DC: National Academies Press.
- Okey, T., and Pauly, D. (1999). Trophic Mass-Balance Model of Alaska's Prince William Sound Ecosystem, for the Post-Spill Period 1994–1996. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 1999*, 7(4), 136 pp.
- Okey, T. A., et al. (2004). Simulating community effects of sea floor shading by plankton blooms over the West Florida Shelf. *Ecological Modelling*, 172(2–4), 339–359.
- Olsen, E., et al. (2007). The Norwegian ecosystem-based management plan for the Barents Sea. *ICES Journal of Marine Science*, 64(4), 599–602.
- Olsen, E., et al. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES Journal of Marine Science*, 67(1), 87–101.
- Olson, R. J., and Watters, G. M. (2003). A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. *Bulletin, Inter-American Tropical Tuna Commission*, 22(3), 133–217.
- Örek, H. (2000). *An application of mass balance Ecopath model to the trophic structure in the Black Sea after anchovy collapse*. MSc thesis, Middle East Technical University, Turkey.
- Österblom, H., et al. (2007). Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems*, 10(6), 877–889.
- Overholtz, W., et al. (2000). Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES Journal of Marine Science*, 57(4), 1147–1159.
- Overholtz, W. (2002). The Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*): spatial pattern analysis of the collapse and recovery of a large marine fish complex. *Fisheries Research*, 57(3), 237–254.
- Overholtz, W. (2006). Atlantic herring. http://www.nefsc.noaa.gov/sos/spsyn/pp/herring/archives/22_AtlanticHerring_2006.pdf
- Overholtz, W., et al. (2008). An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine-Georges Bank Atlantic herring complex. *North American Journal of Fisheries Management*, 28(1), 247–257.
- Parke, G. (2000). Precautionary fisheries management: the CCAMLR approach. *Marine Policy*, 24(2), 83–91.
- Parrish, R. A., et al. (1983). Monsoon-induced seasonality in the comparative climatology of selected processes in relation to eastern boundary currents pelagic fish reproduction. In G.D. Sharp and J. Csirke (Eds.), *Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, 18–29 April 1983*. (pp. 731–777). FAO Fisheries Report No. 291(3).
- Patterson, K. (1992). Fisheries for small pelagic species: an empirical approach to management targets. *Reviews in Fish Biology and Fisheries*, 2(4), 321–338.
- Patterson, K. (1999). Evaluating uncertainty in harvest control law catches using Bayesian Markov Chain Monte Carol virtual population analysis with adaptive rejection sampling and including structural uncertainty. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 208–221.
- Paula e Silva, et al. (1993). The Maputo Bay Ecosystem (Mozambique). In V. Christensen and D. Pauly (Eds.) *Trophic models of aquatic ecosystems*. (p. 214–223). ICLARM Conf. Proc. 26, 390 pp.
- Pauly, D., et al. (2009). Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, 616(1), 67–85.
- Pedersen, S.A. (1992). Multispecies interactions on the offshore West Greenland shrimp grounds. ICES Cm 1994/P2.
- Peterson, W. T., and Schwing, F. B. (2003). A new climate regime in northeast pacific ecosystems. *Geophysical Research Letters*, 30(17), 1896–1899.
- Piatt, J.F., et al. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352, 221–234.
- Pichegru, L., et al. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*, 6(4), 498–501.
- Pikitch, E., et al. (2004). Ecosystem-based fishery management. *Science*, 305(5682), 346–347.
- Pinsky, M. L., et al. (2011). Unexpected patterns of fisheries collapse in the world's oceans. *Proceedings of the National Academy of Sciences*, 108(20), 8317.
- Pitcher, T. (1995). The impact of pelagic fish behaviour on fisheries. *Scientia Marina*, 59(3), 295–306.

- Plagányi, É. E., and Butterworth, D. (2004). A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *African Journal of Marine Science*, 26(1), 261–287.
- Plagányi, É. E., and Butterworth, D. S. (2005). Indirect fishery interactions. In J. E. Reynolds, W. F. Perrin, R. R. Reeves, S. Montgomery and T. J. Ragen (Eds.), *Marine Mammal Research: Conservation Beyond Crisis* (pp. 19–45). Baltimore, Maryland: John Hopkins University Press. 223 pp.
- Plagányi, É. E. (2007). *Models for an Ecosystem Approach to Fisheries*. Food and Agriculture Organization of the United Nations. Fisheries Technical Paper No. 477.
- Plagányi, É. E., and Butterworth, D. (2011). The Scotia Sea krill fishery and its possible impacts on dependent predators—modelling localized depletion of prey. *Ecological Applications*, in press.
- Plagányi, É. E., et al. (2011). Assessing the adequacy of current fisheries management under changing climate: a southern synopsis. *ICES Journal of Marine Science*, 68(6), 1305–1317.
- Polovina, J. J. (1984). Model of a coral reef ecosystem. *Coral reefs*, 3(1), 1–11.
- Pew Oceans Commission (POC). (2003). *America's Living Oceans: Charting a course for sea change*. Arlington, VA.
- Pruvost, P., et al. (2005). An ecosystem model of the Kerguelen Islands' EEZ. In M.L.D Palomares, P. Pruvost, T. Pitcher, and D. Pauly (Eds.), *Modeling Antarctic Marine Ecosystems*. (p. 40–64). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2005*, (13)7, 98 pp.
- Punt, A. E., et al. (2010). Integrating size-structured assessment and bioeconomic management advice in Australia's northern prawn fishery. *ICES Journal of Marine Science*, 67(8), 1785–1801.
- Reid, K. (2001). Growth of Antarctic krill *Euphausia superba* at South Georgia. *Marine Biology*, 138(1), 57–62.
- Reid, K., et al. (2005). Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science*, 62(3), 366–373.
- Reid, R., et al. (1999). *Essential fish habitat source document: Atlantic herring, Clupea harengus, life history and habitat characteristics*. National Ocean and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center. Report NMFS-NE-200.
- Restrepo, V., and Powers, J. (1999). Precautionary control rules in US fisheries management: specification and performance. *ICES Journal of Marine Science*, 56(6), 846–852.
- Richardson, A. J., et al. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, 24(6), 312–322.
- Richerson, K., et al. (2010). Accounting for indirect effects and non-commensurate values in ecosystem based fishery management (EBFM). *Marine Policy*, 34(1), 114–119.
- Rindorf, A., et al. (2000). Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series*, 202, 241–252.
- Roberts, C. (2007). *The Unnatural History of the Sea*. Washington, DC: Island Press.
- Rosado-Solórzano, R., and Del Proo, G. (1998). Preliminary trophic structure model for Tampamachoco lagoon, Veracruz, Mexico. *Ecological Modelling*, 109(2), 141–145.
- Rose, K. A., and Cowan, J. H. (2003). Data, models, and decisions in US marine fisheries management: lessons for ecologists. *Annual Review of Ecology, Evolution, and Systematics*, 34, 127–151.
- Rose, K. A., et al. (2010). End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 2(1), 115–130.
- Ruhl, H. A., and Rybicki, N. B. (2010). Long-term reductions in anthropogenic nutrients link to improvements in Chesapeake Bay habitat. *Proceedings of the National Academy of Sciences*, 107(38): 16566–16570.
- Ryan, P., et al. (2010). Parlous conservation status of African penguins provides the correct wider context. *Biology Letters*, eLetter, comment on Pichegru et al. 6(4), 498–501.
- Samb, B., and Pauly, D. (2000). On 'variability' as a sampling artefact: the case of *Sardinella* in north western Africa. *Fish and Fisheries*, 1(2), 206–210.
- Samb, B., and Mendy, A. (2004). Dynamique du réseau trophique de l'écosystème sénégalais en 1990. West African marine ecosystems: models and fisheries impacts. In M.L.D. Palomares and D. Pauly (Eds.), *Fisheries Centre Research Reports 12(7)*, 57–70. [in French].
- Sánchez, F., and Olaso, I. (2004). Effects of fisheries on the Cantabrian Sea shelf ecosystem. *Ecological Modelling*, 172(2–4), 151–174.
- Schaefer, M. B. (1970). Men, birds and anchovies in the Peru Current-dynamic interactions. *Transactions of the American Fisheries Society*, 99(3), 461–467.
- Schwartzlose, R., et al. (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21(1), 289–347.
- Schweder, T., et al. (2000). Direct and indirect effects of minke whale abundance on cod and herring fisheries: A scenario experiment for the Greater Barents Sea. *NAMMCO Scientific Publications*, 2, 120–132.
- Shannon, L. J., et al. (2003). Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems*, 39(1–2), 83–116.
- Shannon, L., et al. (2009). Impacts of fishing and climate change explored using trophic models. In D. Checkley, J. Alheit, Y. Oozeki, and C. Roy (Eds.), *Climate change and small pelagic fish*. (pp. 158–191). Cambridge, U.K.: Cambridge University Press.
- Shelton, A. O., and Mangel, M. (2011). Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences*, 108(17), 7075–7080.
- Sherman, K., and Alexander, L.M. (1986). *Variability and Management of Large Marine Ecosystems*. American Association for the Advancement of Science Selected Symposium 99. Boulder, CO: Westview Press. 391 pp.
- Sherman, K. (2003). Physical, Biological and Human Forcing of Biomass Yields in Large Marine Ecosystems. ICES CM 2003/P: 12.
- Sidi, M.T., and Diop, M.S. (2004). Modèle écotrophique du banc d'arguin (mauritanie) dans la période 1988 à 1998. In M.L.D. Palomares and D. Pauly (Eds.), *West African Marine Ecosystems: models and fisheries impacts*. (pp. 4–11). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(7), 221 pp. [in French].

- Silvestre, G., et al. (1993). Preliminary trophic model of the coastal fisheries resources of Brunei Darussalam, South China Sea. In V. Christensen and D. Pauly (Eds.), *Trophic models of aquatic ecosystems*. (pp. 300–307). ICLARM Conference Proceedings, Manila, Philippines. 390 pp.
- Smith, A. D. M., et al. (2011). Impacts of fishing low-trophic level species on marine ecosystems. *Science*, 333(6046), 1147–1150.
- Smith, J. W. (1999). *Distribution of Atlantic menhaden, Brevoortia tyrannus, purse-seine sets and catches from southern New England to North Carolina, 1985–96*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Report (NMFS-TR-144).
- Smith, P.E. (1993). Balancing sampling precision and fisheries management objectives: minimal methods. *Bulletin of Marine Science*, 53(2): 930–935.
- Smith, R. C., et al. (1999). Marine ecosystem sensitivity to climate change. *BioScience*, 49(5), 393–404.
- Smith, R. C., and Stammerjohn, S. E. (2001). Variations of surface air temperature and sea-ice extent in the western Antarctic Peninsula region. *Annals of Glaciology*, 33(1), 493–500.
- Spencer, E. E. (2009). *Factors controlling alewife (Alosa pseudoharengus) Population Abundance Among Four Rivers in Mid-Coast Maine*. M.S. Thesis. University of Maine. 49 pp.
- Spies, A. E., and Lewis, R. (2001). The Turner Farm fauna: five thousand years of hunting and fishing in Penobscot Bay, Maine. *Occ Publ Maine Archeol*, 11, 1–120. Maine State Museum, Maine Historic Preservation Commission and Maine Archaeological Society.
- Springer, A., and Speckman, S. (1997). A forage fish is what? Summary of the symposium. In *Forage Fishes in Marine Ecosystems*. Alaska Sea Grant Report No. 97-01. (pp. 773–805). Fairbanks, AK.: University of Alaska.
- Stammerjohn, S., et al. (2008b). Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research*, 113, C03S90.
- Stammerjohn, S. E., et al. (2008a). Sea ice in the western Antarctic Peninsula region: spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(18-19), 2041–2058.
- Stanford, R. et al. (2004). A Preliminary Ecosystem Model for the Atlantic coast of Morocco in the Mid-1980s. In S. Guénette, V. Christensen, and D. Pauly (Eds.), *Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses*. (pp. 314–344). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 9(4), 221 pp.
- Stanford, R., and Pitcher, T. (2004). Ecosystem simulations of the English Channel: climate and trade-offs. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(3), 103 pp.
- Steele, J. H. (1985). A comparison of terrestrial and marine ecological systems. *Nature*, 313(6001), 355–358.
- Stefansson, G., and Palsson, O. K. (1998). Points of view: A framework for multispecies modelling of Arcto-boreal systems. *Reviews in Fish Biology and Fisheries*, 8(1), 101–104.
- Steneck, R. S., et al. (2004). Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, 7(4), 323–332.
- Steneck, R., et al. (2011). Creation of a Gilded Trap by the High Economic Value of the Maine Lobster Fishery. *Conservation Biology*, 25(5), 904–912.
- Stephenson, R. L. (1997). The Other F: Forage Considerations in Fisheries Management. In *Forage Fishes in Marine Ecosystems*. Alaska Sea Grant Report No. 97-01. (pp. 645–654). Fairbanks, AK: University of Alaska.
- Stephenson, R. L., et al. (2009). Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence. *ICES Journal of Marine Science*, 66(8), 1733–1739.
- Stergiou, K. (1998). Variability of fish catches in different ecosystems. In M. H. Durand, R. Mendelssohn, D. Pauly and C. Roy (Eds.), *Global versus local changes in upwelling systems. Séries Colloques et Séminaires*. (pp. 359–370). Paris: ORSTOM Editions.
- Stobberup, K., et al. (2004). Ecopath model of the Cape Verde coastal ecosystem. In D. Pauly, M. Palomares and J. Vakily (Eds.), *West African marine ecosystems: models and fisheries impacts*. (pp. 39–56). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(7), 221 pp.
- Sumaila, U. R., et al. (2007). A global ex-vessel fish price database: construction and applications. *Journal of Bioeconomics*, 9(1), 39–51.
- Sunada, J., et al. (1981). The brown pelican as a sampling instrument of age group structure in the northern anchovy population. *CalCOFI Report*, 22, 65–68.
- Sydeman, W. J., et al. (2001). Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography*, 49(1-4), 309–329.
- Tacon, A. G. J., and Metian, M. (2008). Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects. *Aquaculture*, 285(1-4), 146–158.
- Tam, J., et al. (2008). Trophic modeling of the northern Humboldt Current Ecosystem, Part I: comparing trophic linkages under La Niña and El Niño conditions. *Progress in Oceanography*, 79(2-4), 352–365.
- Taylor, M. H., et al. (2008). Trophic and environmental drivers of the Sechura Bay Ecosystem (Peru) over an ENSO cycle. *Helgoland Marine Research*, 62 (Suppl. 1), S15-S32.
- Thompson, G. G. (1993). A proposal for a threshold stock size and maximum fishing mortality rate. In S. J. Smith, J. J. Hunt, and D. Rivard (Ed.), *Risk evaluation and biological reference points for fisheries management* (pp. 303–320): Canadian Special Publication of Fisheries and Aquatic Sciences, 120, 442 pp.
- Tong, L., et al. (2000). A preliminary approach on mass-balance Ecopath model in the Bohai Sea. *Chinese Journal of Applied Ecology*, 11(3), 435–440.
- Trathan, P., et al. (2007). Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1488), 2351–2365.
- Trites, A. W. et al. (1999). Ecosystem Change and the Decline of Marine Mammals the Eastern Bering Sea: Testing the Ecosystem Shift and Commercial Whaling Hypotheses. The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 1999*, 7(1), 106 pp.
- Trivelpiece, W. Z., et al. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences*, 108(18), 7625–7628.

- Tsukayama, I., and Palomares, M. L. D. (1987). Monthly catch and catch composition of Peruvian anchoveta (*Engraulis ringens*) (Northern-Central Stock, 4-14 S), 1953 to 1982'. In D. Pauly and L. Tsukayama (Eds.), *The peruvian anchoveta and its upwelling ecosystem: three decades of change*. ICLARM Studies and Reviews, 15, (pp. 89–108).
- Turner, J., et al. (2005). A positive trend in western Antarctic Peninsula precipitation over the last 50 years reflecting regional and Antarctic-wide atmospheric circulation changes. *Annals of Glaciology*, 41(1), 85–91.
- Turner, R. E., et al. (2008). Gulf of Mexico hypoxia: alternate states and a legacy. *Environ. Sci. Technol.*, 42(7): 2323–2327.
- Tyrrell, M., et al. (2011). The importance of including predation in fish population models: Implications for biological reference points. *Fisheries Research*, 108(1), 1–8.
- Ulltang, Ø. (1976). *Catch per unit of effort in the Norwegian purse seine fishery for Atlanto-Scandian (Norwegian spring spawning) herring*. FAO Fisheries Technical Papers (FAO) 155, 91–101.
- Ulrich, C., et al. (2002). A multi-species multi-fleet bioeconomic simulation model for the English Channel artisanal fisheries. *Fisheries Research*, 58(3): 379–401.
- Underhill, L., et al. (2006). Regionally coherent trends in colonies of African penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987–2005. *African Journal of Marine Science*, 28 (3&4), 697–704.
- UNEP. (2005). Lääne, A., et al. Global International Waters Assessment: Baltic Sea, GIWA Regional Assessment 17. Kalmar, Sweden: University of Kalmar. <http://www.unep.org/dewa/giwa/publications/r17.asp>
- United States Commission on Ocean Policy (USCOP). (2004). *An ocean blueprint for the 21st century. Final report to the President and Congress*. Washington, DC.
- Ursin, E. (1982). Stability and variability in the marine ecosystem. *Dana*, 2, 51–67.
- Utne-Palm, A. C., et al. (2010). Trophic structure and community stability in an overfished ecosystem. *Science*, 329(5989), 333–336.
- Van der Lingen, C., et al. (2006). 8 Resource and ecosystem variability, including regime shifts, in the Benguela Current System. *Large Marine Ecosystems*, 14, 147–184.
- Vasconcellos, M., and Watson, R. (2004). Mass balance of Atlantic oceanic systems. In M.L.D. Palomares and D. Pauly (Eds.), *West African Marine Ecosystems: models and fisheries impacts*. (pp. 171–204). The Fisheries Centre, University of British Columbia. *Fisheries Centre Research Reports 2004*, 12(7), 221 pp.
- Vaughan, D. S., et al. (2007). Gulf menhaden (*Brevoortia patronus*) in the U.S. Gulf of Mexico: fishery characteristics and biological reference points for management. *Fisheries Research*, 83(2-3), 263–275.
- Vega-Cendejas, M., and Arreguín-Sánchez, F. (2001). Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. *Ecological Modelling*, 137(2-3), 119–133.
- Velarde, E., et al. (2004). Seabird ecology, El Niño anomalies, and prediction of sardine fisheries in the Gulf of California. *Ecological Applications*, 14(2), 607–615.
- Wade, P. R. (1998). Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, 14(1), 1–37.
- Wagner, E. L., and Boersma, P. D. (2011). Effects of Fisheries on Seabird Community Ecology. *Reviews in Fisheries Science*, 19(3), 157–167.
- Walters, C., et al. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, 7(2), 139–172.
- Walters, C. J., and Martell, S. J. D. (2004). *Fisheries ecology and management*. Princeton, NJ: Princeton Univ Press.
- Walters, C. J., et al. (2006). A stochastic approach to stock reduction analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(1), 212–223.
- Walters, C., et al. (2008). An Ecosim Model for Exploring Gulf of Mexico Ecosystem Management Options: Implications of Including Multistanza Life-History Models for Policy Predictions. *Bulletin of Marine Science*, 83(1), 251–271.
- Wanless, S., et al. (2007). Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. *Progress in Oceanography*, 72(1), 30–38.
- Watson, R., et al. (2004) Mapping global fisheries: sharpening our focus. *Fish and Fisheries*, 5, 168–177.
- Watters, G.M., et al. (2008). *A risk assessment to advise on strategies for subdividing a precautionary catch limit among small-scale management units during stage 1 of the staged development of the krill fishery in Subareas 48.1, 48.2 and 48.3*. CCAMLR document WG-EMM-08/30.
- Witherall, D. (1999). Incorporating ecosystem considerations into management of Bering Sea groundfish fisheries. *Ecosystem Approaches for Fisheries Management* (pp. 315–327). Fairbanks, AK: University of Alaska Sea Grant. Report No. AK-SG-99-01. 728 pp.
- Wolf, N., and Mangel, M. (2008). Multiple hypothesis testing and the declining-population paradigm in Steller sea lions. *Ecological Applications*, 18(8), 1932–1955.
- Wolff, M. (1994). A trophic model for Tongoy Bay—a system exposed to suspended scallop culture (Northern Chile). *Journal of Experimental Marine Biology and Ecology*, 182(2), 149–168.
- Wolff, M., et al. (1996). A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. Modelo piloto trófico para el Golfo Dulce, Costa Rica, un tipo de fiordo tropical. *Revista de Biología Tropical*, 44(3), 215–231.
- Wolff, M., et al. (1998). A trophic flow model of the Golfo de Nicoya, Costa Rica. *Revista de biología tropical*, 46, 63–80.
- Wolff, M., et al. (2000). A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuarine, Coastal and Shelf Science*, 50(6), 789–803.
- Wood, R. J., and Austin, H. M. (2009). Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(3), 496–508.
- Worm, B., et al. (2009). Rebuilding global fisheries. *Science*, 325(5940), 578–585.
- Xue, H., et al. (2000). A model study of the seasonal circulation in the Gulf of Maine. *Journal of Physical Oceanography*, 30(5), 1111–1135.
- Zeller, D., et al. (2011). The Baltic Sea: Estimates of total fisheries removals 1950–2007. *Fisheries Research*, 108(2-3), 356–363.
- Zetina-Rejon, M. J. et al. (2003). Trophic structure and flows of energy in the Huizache-Caimanero lagoon complex on the Pacific coast of Mexico. *Estuarine, Coastal and Shelf Science*, 57(5-6), 803–815.



Lenfest Ocean Program:
Protecting Ocean Life Through Marine Science
901 E Street NW, 10th Floor, Washington, DC 20004
ph: 202.552.2000 • fx: 202.552.2299
email: info@lenfestocean.org • www.lenfestocean.org

Printed on stock made with an average of 100% de-inked recycled fiber and an average of 50% post-consumer waste, which is processed chlorine free and designated Ancient Forest Friendly™ using EcoSmart™ certified inks.

Paper manufactured using electricity that is offset with Green-e® certified renewable energy certificates and printed using Clean Currents (wind power) by an EPA Green Power partner.

