Fisheries

A Census of Fishes and Everything They Eat: How the Census of Marine Life Advanced Fisheries Science

Ron O'Dor [a] , Andre M. Boustany [b] , Cedar M. Chittenden [c] , Mark J. Costello [d] , Hassan Moustahfid [e] , John Payne [f] , Dirk Steinke [g] , Michael J. W. Stokesbury [h] & Edward Vanden Berghe [i]

[a] Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4R2 E-mail:

[b] Nicholas School of the Environment, Duke University, Durham, NC, 27708

[c] Department of Arctic and Marine Biology, University of Tromsø, 9037, Tromsø, Norway

[d] Leigh Marine Laboratory, University of Auckland, Auckland, New Zealand

[e] U.S. Integrated Ocean Observing System, National Oceanic and Atmospheric Administration, Silver Spring, MD, 20910, USA

[f] Pacific Ocean Shelf Tracking, Vancouver Aquarium, Vancouver, British Columbia, Canada, V6G 3E2

[g] University of Guelph, Guelph, Ontario, Canada, N1G 2W1

[h] Department of Biology, Acadia University, Nova Scotia, Canada, B4P 2R6

[i] Ocean Biogeographic Information System, Rutgers University, New Brunswick, NJ, 08904

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Ron O'Dor

Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada. B3H 4R2. E-mail: Ron.ODor@Dal.Ca

Andre M. Boustany

Nicholas School of the Environment, Duke University, Durham, NC 27708

Cedar M. Chittenden

Department of Arctic and Marine Biology, University of Tromsø, 9037, Tromsø, Norway

Mark J. Costello

Leigh Marine Laboratory, University of Auckland, Auckland, New Zealand

Hassan Moustahfid

U.S. Integrated Ocean Observing System, National Oceanic and Atmospheric Administration, Silver Spring, MD 20910, USA

John Payne

Pacific Ocean Shelf Tracking, Vancouver Aquarium, Vancouver, British Columbia, Canada V6G 3E2

Dirk Steinke

University of Guelph, Guelph, Ontario, Canada N1G 2W1

Michael J. W. Stokesbury

Department of Biology, Acadia University, Nova Scotia, Canada B4P 2R6

Edward Vanden Berghe

Ocean Biogeographic Information System, Rutgers University, New Brunswick, NJ 08904

ABSTRACT: *The Census of Marine Life was a 10-year, international research effort to explore poorly known ocean habitats and conduct large-scale experimentation with new technology. The goal of Census 2010 in its mission statement was to describe what did live in the oceans, what does live in the oceans, and what will live in the ocean. Many of the findings and techniques from census research may prove valuable in making a transition, which many governments have publicly endorsed, from single-species fisheries management to more holistic ecosystem management. Census researchers sampled continental margins, mid-Atlantic ridges, ocean floor vents and seeps, and abyssal plains and polar seas and organized massive amounts of past and new information in a public online database called the Ocean Biogeographic Information System (www.iobis. org). The census described and categorized seamount biology worldwide for its vulnerability to fishing, advanced large-scale animal tracking with acoustic arrays and satellite archival tags, and accelerated species identification, including nearshore, coral reef, and zooplankton sampling using genetic barcoding and pyrotag sequencing for microbes and helped to launch the exciting new field of marine environmental history. Above all, the census showed the value of investing in large-scale, collaborative projects and sharing results publicly.*

Censo de peces y de todo aquello que comen: qué progreso aporta El Censo de la Vida Marina a la ciencia pesquera

RESUMEN: El Censo de la Vida Marina (Census, por su nombre en inglés) fue un esfuerzo internacional de investigación de diez años de duración diseñado para explorar hábitats oceánicos poco conocidos y experimentar a gran escala con nueva tecnología. El objetivo de Census 2010, declarado en su misión, era describir "qué vive y que vivirá en los océanos". Muchos de los hallazgos y técnicas generadas en Census pueden resultar valiosas para la transición de un manejo mono-específico a un manejo holístico, basado en el ecosistema; lo cual ha sido públicamente aprobado por muchos gobiernos. Los investigadores de Census muestrearon los márgenes continentales, las cordilleras oceánicas del Atlántico, ventilas hidrotermales del fondo marino, planicies abisales y mares polares; de igual forma organizaron cantidades formidables de información, tanto pasada como actual, en una base de datos pública y en línea llamada Sistema de Información de Biogeografía Oceánica. Census describe y categoriza la biología de los montes submarinos a nivel mundial para poder estimar su vulnerabilidad a la pesca; realiza marcado a gran escala de organismos utilizando técnicas avanzadas con arreglos acústicos y marcas satelitales; expide la identificación de especies, incluyendo muestreo costero de corales y zooplancton, basado en código genético de barras y secuencias de piro-marcaje para microbios; así mismo contribuyeron con el lanzamiento de la nueva disciplina "historia ambiental marina". Pero sobre todo, Census mostró las recompensas que deja la inversión en proyectos colaborativos de gran escala y la presentación pública de los resultados.

INTRODUCTION

The Census of Marine Life was originally conceived as a Census of Fishes (Ausubel 1997). Organizers quickly realized that the effort required to census fishes globally could concurrently census everything else in the ocean. If an icebreaker were sent to Antarctica, it could sample everything, not just fishes. After all, fisheries harvest a wide range of species, from invertebrates to mammals. Understanding fisheries dynamics in the ocean requires knowing what animals eat and what eats them. Thus, the Census of Fishes became the Census of Marine Life in 2000. On 22 May 2012 the census was the focus of the United Nations' International Day for Biological Diversity.

This review highlights some of the most important fish-related findings of the census. In a report for the census, Eschmeyer et al. (2010) recently cataloged 16,764 species of marine fishes and estimated that there are still about 5,000 species to be discovered, mostly from the unexplored depths (Figure 1). This number is independently supported by statistical modeling of fish species description rates (Costello et al. 2012). Although taxonomic description takes too long to be able to attribute a number of new species directly to the census, it has been estimated that 100–150 new fish species per year were described during the census's decade of discovery (Ausubel et al. 2010). The census recognized this limitation from the beginning and adopted the "Barcode of Life" as an interim technology for distinguishing species using a short DNA sequence while waiting for taxonomy to catch up (Bucklin et al. 2011). The census's data system, the Ocean Biogeographic Information System (OBIS), contains 14 million distribution records for 17,000 fish species, of which over 7,000 species have been barcoded (Figure 2), including 62 previously overlooked species, since 2005 (Table 1). Although fish sampling has been biased to northern and coastal seas (Figure 2a) the selection of samples for barcoding has been more uniform and global (Figure 2b).

In addition to OBIS, the census included 14 field and two interdisciplinary projects (see www.coml.org, which defines the 17 projects in a few words; projects are indicated in the text below using capital letters). Twelve of the field projects were oriented toward discovering biodiversity (i.e., taxonomy) and especially toward quantifying biodiversity in the least-sampled parts of the ocean, including continental margins, the mid-Atlantic ridge, the abyssal plains, and seafloor vents and seeps. Two of the field projects focused on tracking the movements of fish and top marine predators. Interdisciplinary projects included Oceans Past, focused on historical records from diverse sources to estimate past abundances of exploited species, and Oceans Future, which modeled movements and the future abundances of exploited species. Hundreds of publications detail the census results (e.g., McIntyre [2010] contains downloadable project chapters) and many summarize it (Crist et al. 2009; O'Dor et al. 2009, 2010; Knowlton 2010; Snelgrove 2010). This fish-focused review is an effort to bring attention to results that may be useful steps toward ecosystem-based management, so that we can avoid future fisheries crises as ecosystems respond to global climate change.
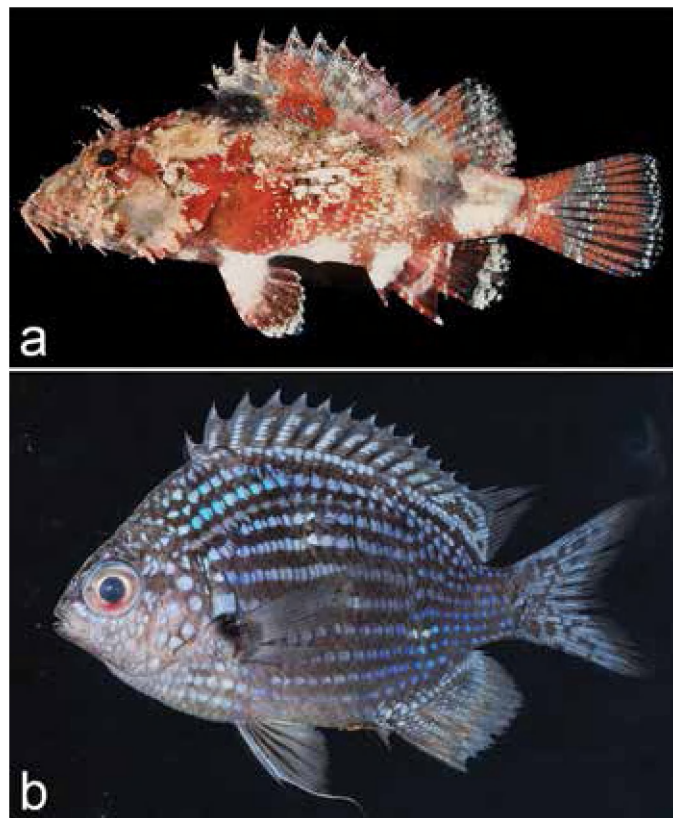

Figure 1. Red fish, blue fish, lots of new fish. (a) A new species of scorpion fish, *Scorpaenopsis vittapinna*, found in the Indo-Pacific area, one of a rapidly growing list of more than 17,000 marine fish species now logged in the Census of Marine Life database. [Photo credit: Bill Eschmeyer and John E. Randall] (b) An intensely blue fish that lives below 120 m, the newly discovered species *Chromis abyssus* was so named by scientists in recognition of its color and deep habitat and to honor the BBC documentary film project—Pacific Abyss—that supported the expedition to the Caroline Islands. [Photo credit: Richard Pyle, Bishop Museum.]

BIG FISH

Little is known about the ecology of even the most intensively harvested large marine fish species because of the difficulty in studying fast-moving, wide-ranging animals in the ocean. However, a combination of tagging technologies is now increasingly being used to gain an understanding of fish movement, migration, and ecological interactions throughout their life cycle. The census created two overlapping projects in the Pacific to test and demonstrate these technologies on a wide scale (Figure 3).

Tagging animals with electronic archival tags that are returned after capture or disengage from the animal, float to the surface of the ocean, and transmit data to satellite systems provides data that is not biased by fishing effort. The census supported the largest archival tagging program to date, driven over the decade largely by the Tagging of Pacific Predators (TOPP) project, which examined the environmental basis for the movement and behavior of large pelagic animals in the Pacific Ocean (Block et al. 2011). Tag technologies now allow researchers to monitor movement and distribution of animals at sea and simultaneously sample the physical properties of the water column

TABLE 1. Overview of fish barcoding studies showing the number of overlooked species that were flagged by DNA barcoding and then corroborated through morphological, geographical, and ecological data.

Study	Sample Size/No. of Species	Overlooked Species	Barcode of Life Database Project Code[a]
Fishes of Australia	754/207	5	FOA
Sharks/rays of Australia	945/210	4	FOASR
Fishes of Pacific Canada	1225/201	2	TZFPC
Reef associated fishes	1638/390	7	TZAIC
Arctic fishes of Western Pacific	684/114	3	DSFAL
Western Atlantic Starksia	59/13	7	STARK
Canadian skates	301/14	1	SCFAC
Antarctic fishes CEAMARC	538/68	2	EATF
Western Pacific Chromis	N/A	5	RPCHR
Southern Ocean skates	76/10	1	FNZC
Southern Ocean Macrourus	141/3	1	RATSO
Morid cods	62/4	1	HALAR
Fish North Atlantic/Australia	149/15	2	DSNSF
Asian sea bass	21/2	1	FOAGB
Australian Squalus	127/16	10	FOAS
South African and Australian fish	229/35	10	TZSAA
Total		62	

[a]Data and associated publications can be accessed through the respective public projects on BOLD: www.boldsystems.org; Ratnasingham and Hebert (2007).

(Costa et al. 2010). Tags have been used to provide information on stock structure that has proven important to management (Block et al. 2005) and to record animal interactions (see Cooke et al. 2011). Future technological developments may make it possible for ecological information from numerous organisms to be brought to shore by a few individuals (Stokesbury et al. 2009), generating biological economies of scale.

> Further investment in tagging technologies will help to alleviate our fundamental ignorance about movement patterns and ecological interactions and contribute to the development of management strategies that are robust to environmental change.

Economies of scale are critical when studying mobile resources in the ocean because simultaneous tagging of many species across a huge geographic area has indicated that animals are concentrated in distinct diversity hotspots in the open ocean. The California current is a hotspot for animals that range from the United States to Japan and from the tropics to the Gulf of Alaska. Gathering information from animals in these hotspots not only generates oceanographic information from undersampled areas but identifies multispecies critical habitat (McIntyre 2010). Another remarkable example of a general behavioral pattern that was only discovered because of extensive, simultaneous tagging of many species is that site fidelity and round-trip migrations are shown by most top predators, including great white sharks (Carcharodon carcharias), which occupy a common area offshore but return to coastal home territories (Jorgensen et al. 2010).

The TOPP project helped to advance the industrial engineering of tagging technology, including validation and standardization of data, which are necessary to answer applied questions in fisheries science. An example of the contribution of TOPP to applied fisheries science was the determination of migration routes and fishing mortality rates for Pacific bluefin tuna (Thunnus orientalis). TOPP has tagged 663 Pacific bluefin tuna to date, beginning in 2002, including a dozen individual tuna tracks lasting over 3 years that cross the Pacific. This tuna has one of the largest individual home ranges of any fish species (Collette and Nauen 1983). The only known spawning grounds for Pacific bluefin occur in the East China Sea and Ryukyo Islands in the spring and in the Sea of Japan in the summer months (Chen et al. 2006). Bluefin tagged off the Mexican and Southern Californian coasts show movements up and down the coast associated with seasonal peaks in primary productivity and sardines (Kitagawa et al. 2007; Boustany et al. 2010). Some bottom-up forcing was apparent: phytoplankton blooms had an aggregating effect on bluefin, with densities of tagged fish increasing in areas and times of high productivity and dropping as productivity subsided and fish dispersed. Bluefin feed in the eastern Pacific for several years before heading west after age 4 to 5 (Boustany et al. 2010). Beyond movement patterns, tagging studies have allowed examination of exploita-
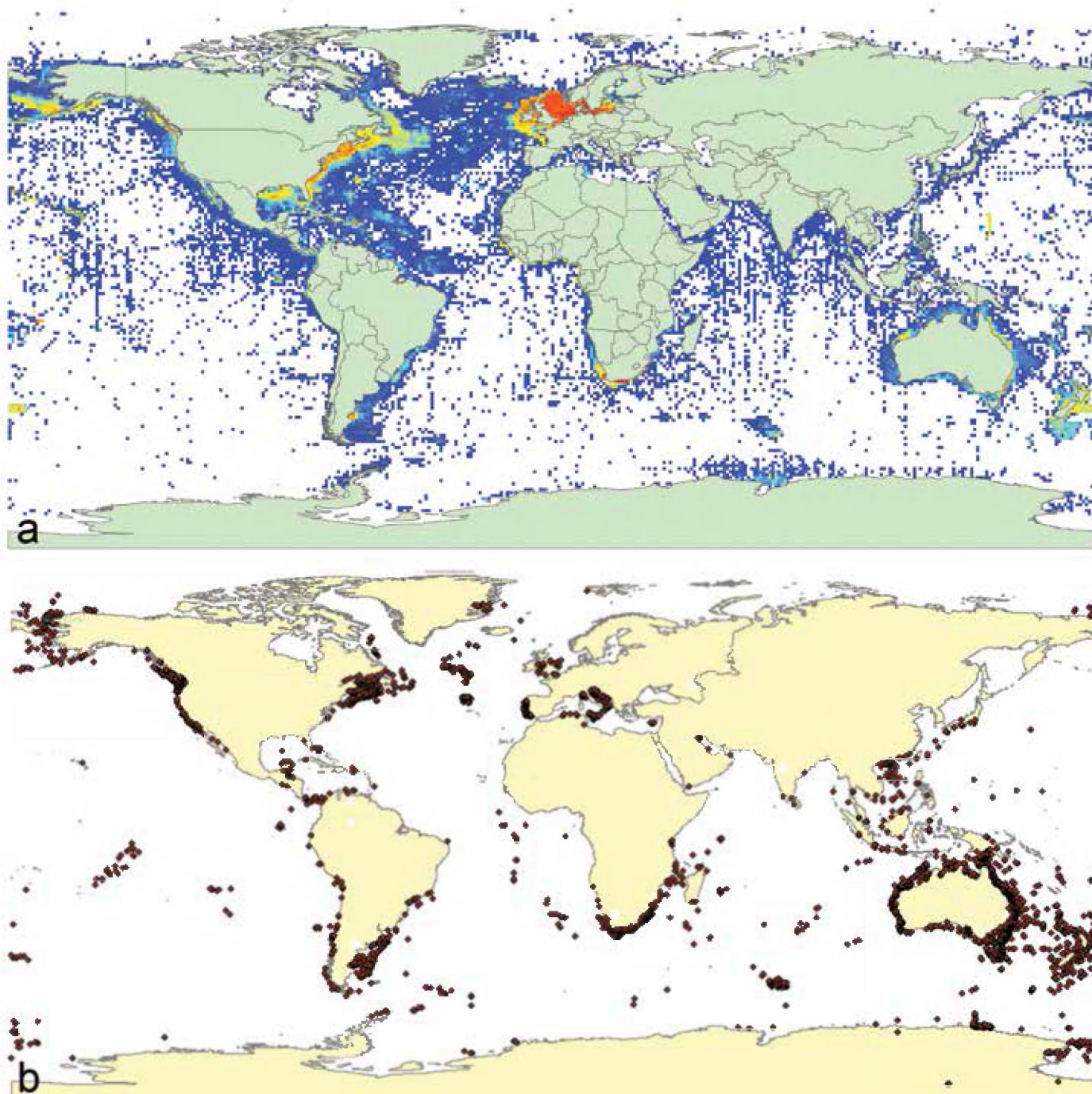
Figure 2. (a) On 20 November 2011, OBIS contained 13,691,333 fish records for 17,001 valid marine species in 536,412 unique locations, mapped in one-degree squares. Dark blue, one location per square; dark red, 17 locations per square. (b) For 7,279 of these species the Barcode of Life is also known, from locations shown as brown dots, plus an additional 4,721 freshwater fish species.

tion levels of Pacific bluefin, with estimated fishery mortality rates (0.02–1.92 quarter^{-1}) two to six times higher than natural mortality rates (Whitlock et al., 2012).

Further investment in tagging technologies will help to alleviate our fundamental ignorance about movement patterns and ecological interactions and contribute to the development of management strategies that are robust to environmental change.

SMALL FISH

Small fish, including the juveniles of larger species, are abundant, important in oceanic food chains, and particularly difficult to study in situ. A recent report by the Lenfest Foundation suggested that forage fish may be overharvested worldwide (Pikitch et al. 2012). The other census tracking project, Pacific Ocean Shelf Tracking (POST), pioneered the use of large-scale arrays of acoustic receivers to study the movements of fish (McIntyre 2010). The research was driven at first by the de-

sturgeon (Acipenser medirostris), which was central to legal designation of critical habitat for that species; exploratory studies of sixgill sharks (Hexanchus griseus), salmon sharks (Lamna ditropis), Humboldt squid (Dosidicus gigas), and other predators; and studies of bottom fish, including rockfish, lingcod (Ophiodon elongates), and English sole (Parophrys vetulus; McIntyre 2010).

A series of studies used the POST array to estimate tag effects (Melnychuk 2009), evaluate the impact of management actions in a hydropower system, and examine the differences between hatchery-raised and wild fish. An investigation into the genetic and environmental effects of hatchery rearing on young coho salmon (Oncorhynchus kisutch) found that rearing environment had much more of an effect on phenotype than any genetic differences between hatchery- and wild-born fish (Chittenden et al. 2010a, 2010b) and that various physical differences were correlated with the timing of their ocean entry and migration routes in the ocean (Chittenden et al. 2008).

In sum, the advent of large-scale acoustic arrays has created exciting new research opportunities to study the movement and mortality of fish, both small and large.

MANAGING HUMANS IN ECOSYSTEMS RATHER THAN FISH

The census made significant contributions in relation to (1) poorly explored habitats; (2) baseline (historical, pre-fishery) abundances of populations; (3) the distributions and movements of marine species and the forces that drive those patterns; (4) abundances, distribution, and biology of species not targeted by fisheries; (5) species interactions; (6) how species respond to multiple impacts (e.g., how distributions, migration timing, and available habitat may shift in response to climate and thereby change an ecosystem's vulnerability to human exploitation; Cooke et al. 2011); and (7) how to manage multiple human activities that affect species and ecosystems simultaneously at many scales.

Poorly Explored Habitats

The census emphasized exploration of the unknown, with many projects that collected fauna from poorly sampled habitats. One project with major implications for fisheries was Seamounts, which coordinated and facilitated research globally. Seamounts have become a target for fisheries worldwide, and researchers created the first integrated public database of global seamount biological data (Seamounts Online 2012). They compiled available data, new surveys, and the latest modeling methods in the first global seamount classification identifying regions most vulnerable to fishing and climate change (Tittensor et al. 2009; Clark et al. 2011). Their data showed that seamount communities are vulnerable to fishing and that these communities, particularly those with hard corals, have high sensitivity and low resilience to bottom trawling. In addition, there was plausible evidence that seamounts are step-

Figure 3. Ocean Tracking Network (OTN) Canada student, Will Roberts, holds an Atlantic sturgeon (*Acipenser oxyrinchus*) with a surgically implanted VEMCO coded acoustic telemetry tag that could last up to 10 years. He will add a one-year Wildlife Computer MK10 Popup Archival Tag (PAT) tag to combine short-term, high-resolution information with long-term patterns in a Bay of Fundy tidal hydropower study off the coast of Nova Scotia by Acadia University. OTN and other telemetry networks around the globe are building on ground-breaking research performed by POST and TOPP during the Census of Marine Life (Cooke et al. 2011). [Photo credit: Montana McLean.]

sire to understand the mortality patterns of juvenile Pacific salmon, because many salmon stocks in the Pacific Northwest are threatened or endangered. Salmonids as small as 10 cm in length were tagged with acoustic tags transmitting individual ID numbers, and several individual salmon were tracked over 2,500 km from release sites far inland on rivers, up the continental shelf to Alaska. A baseline collection of early marine mortality estimates was collected for a large group of salmon stocks in Canada and the United States for the first time (Melnychuk 2009; Welch et al. 2011). The results suggest that large arrays can be used to estimate mortality of migrating fish with acceptable accuracy and may improve our understanding of where and why mortality occurs, especially when the arrays are used in conjunction with manipulative experiments (Donalsdon et al. 2008). Although salmon behavior was plastic and mortality patterns were inconsistent between stocks and years, a core message was that juvenile salmon often suffered significant mortality far into the open ocean. This preliminary finding complicates efforts to predict the size of returning salmon cohorts, because it suggests that we require more information on salmon offshore.

During the census, the POST array tracked 18 marine species, big and small (Figure 3). Interesting results included discovery of surprisingly extensive movements in green

ping stones for dispersal, oases of abundance and biomass, and hotspots of species richness. They supported emerging theories that individual seamount communities are structurally unique, that populations of invertebrates on seamounts are the source of propagules for nearby margins, and that seamounts can act as biological refugia from large-scale catastrophic environmental events (Rowden et al. 2010).

Baseline Data

The Oceans Past project gleaned data on the past abundance of marine species from archeological digs of bones and shell middens, fish-scale records from sediment cores, and thousands of historical documents, including catch and trade records, restaurant menus, and whaling logs. They were pioneering in showing that such data can provide credible estimates of fish harvest and sometimes abundance (Starkey et al. 2008). Several examples of major resource extraction dating back more than 2,000 years were found in heavily populated areas such as the Mediterranean and demonstrated that preindustrial technologies could put marine animal populations under severe stress. A review of 256 exploited marine populations estimated that, on average, those populations had declined 89% from historical abundance levels (Lotze and Worm 2009). Historically, anthropogenic threats to ocean ecosystems were local or regional, but they are now pervasive and compounded by the global threat of climate change.

Distribution and Movements

As described briefly above, the POST and TOPP tagging projects showed that large-scale use of electronic tags was cost effective. Oceanographic data collected by animals wearing sophisticated new tags will help to explain the preferences and physiological limits that drive changes in animal distributions, as species respond to changes such as shoaling and expansion of the oxygen minimum layer in the central Pacific and increasingly acidic ocean waters.

Biology of Nonexploited Species

The U.S. National Marine Fisheries Service reported that 60% of exploited stocks (545 stocks) lacked assessments sufficient to evaluate stock status relative to overfishing (Mace et al. 2001), and the situation for nonexploited stocks is undoubtedly worse. The census made huge contributions to basic taxonomic exploration of lesser-known species and habitats and to the development of techniques such as standardized sampling (McIntyre 2010) and genetic barcoding (Table 1), but the basic biology and abundance of most nontarget species remains poorly known.

Species Interactions

Genetic barcoding, plankton surveys (McIntyre 2010), and taxonomic work of the census all contribute to the ability to interpret diet studies. The POST and TOPP tagging projects hint at the possibility of using tags to study species interactions on a

larger scale in the future, in part by using large-bodied species to monitor small species (Cooke et al. 2011). Another census project recently pioneered a new use of waveguide sonar technology that made it possible to instantaneously visualize all of the fish in an area 250 miles on a side. The school of 250 million Atlantic herring (Clupea harengus) described in the Gulf of Maine represented the largest assembly of animal biomass ever recorded on earth (Makris et al. 2009). Nevertheless, to study species interactions on a large scale will require the best of our existing genetic, taxonomic, and telemetry technologies, and tagging and acoustic technology will have to be advanced significantly before the dream becomes a reality.

How Species Respond to Multiple Impacts

Recent high-profile papers have called for more holistic approaches to marine resource management and adoption of ecosystem-based management (EBM; Larkin 1996; Link 2010). EBM differs from traditional resource management, defining management strategies for entire systems, not individual components of the ecosystem (Link 2010). Central to this ecosystem-based perspective is accounting for all factors that can influence a fisheries stock, including ecological interactions.

Forage fish species (prey) can occupy middle trophic levels that link lower trophic level energy or biomass to upper trophic levels by being common prey for a range of species. They can be an important source of standing biomass in an ecosystem and are often subject to both predation pressure and commercial harvesting. Various authors have found that when consumption of particular forage species is calculated, the predation mortality for the species that had been assumed as a part of the total natural mortality in traditional stock assessments was underestimated (e.g., Hollowed et al. 2000; Moustahfid et al. 2009b). Unsurprisingly, predation mortality is temporally and ontogenetically variable as well (Tsou and Collie 2001).

Another consensus among scientists is that for forage species in particular, careful examination of traditional assumptions regarding predation mortality is needed because the abundance of their major predators (e.g., demersal fish, large pelagics, marine mammals, birds, etc.) can reasonably be expected to increase in the next several years as stocks are rebuilt to meet legal requirements (e.g., Overholtz et al. 2008; Moustahfid et al. 2009a). Figure 4 illustrates the trade-offs between predators and fisheries to be made when managing forage species like the longfin squid (Loligo pealeii) in the North Atlantic. It is clear that if timing of high commercial exploitation and predatory removals are out of sync and dynamic over the year, traditional single-species models that assume constant natural mortality rates will overestimate the stock's recovery potential (e.g., Moustahfid et al. 2009a, 2009b).

Managing Multiple Human Impacts

One census legacy was the exchange of ideas and experiences. It became clear to the thousands of participants that human impacts on the ocean are increasing (Costello et al.

2010b). Although exploitation is certainly important, participants realized the need to acknowledge other influences, including increased noise, light, ship traffic, chemical pollution, agricultural runoff and siltation, species introductions, oil exploration and extraction, undersea mining, tourism, heat and CO2 transfer from the atmosphere, temperature change, and acidification, among myriad factors.

FISH, FISH FOOD, AND EVERYTHING ELSE

A census is the most basic step toward understanding an ecosystem: it answers the question "What are the system's biological components?" From census results we know we cannot answer that question definitively for most marine ecosystems. Because the depth of less than 10% of the ocean seabed has been measured from ships (Costello et al. 2010a), we may assume that significantly less seabed biodiversity has been sampled. About 75% of the ocean area is between 3,000 and 6,000 m depth and yet most sampling is along shallow coasts (Figure 2a). Even some deepwater habitats that are more accessible are poorly known: in recent samples from the Australian continental margins, 90% of 365 species of eastern slope isopods and 30% of western slope decapods were new to science. In some cases, we cannot yet come close to naming species. Coral reefs have been estimated to contain over one third the diversity of all marine life, but the Reefs project was unable to even estimate the number of unknown species by the end of its 10-year mission because their new data showed the inadequacy of existing sampling. They found little overlap in species composition between adjacent sites, and 40% to 60% of reef species in most samples and sites were represented by a single specimen (McIntyre 2010). The finding that "rare is common" became a census theme that the Reefs project showcased better than any other, illustrating the extreme need to develop taxonomic expertise.

In microbial communities, where individuals are abundant and difficult to define as species, researchers found a long tail of rare DNA-defined taxa (McIntyre 2010). Although microbes are key components of geochemical cycles, we do not understand how their communities will respond to climate change, but we do know that rare kinds include a variety of recently discovered metabolic pathways and that a major turnover in species could alter ecosystem functioning and impact fish and fisheries.

Fish Diversity in Perspective

The major effort of the census to count and identify organisms from lower taxa helped to put the taxonomic diversity of fishes in perspective with diversity in the lower orders that are fish prey and was also the basis for revised estimates of total biodiversity on Earth. Fish are by far the most diverse chordates, inhabiting all habitats in the oceans and most in freshwaters. After birds, mammals, and reptiles, they are among the best known groups on Earth, particularly because of their importance as food for humans. Yet, in the ocean, there are already far more species of crustaceans, molluscs and other invertebrates, and plants known to science (around 240,000; Appeltans et al. 2011), and the proportion of undiscovered species in these groups is far higher than it is for fish (Figure 5).

Fish prey constitute essentially all taxonomic groups that are smaller-bodied than fish. Most fish are dietary generalists that eat anything that fits in their mouths, and many prey species are so small that they are only eaten by planktonic fish larvae. The census helped to highlight challenges faced in estimating the distributions of small organisms. The microbes and at least some of the meiofauna are unlike larger species in several respects. Bacteria exchange DNA both frequently and rapidly, which helps them adapt to new situations. This means that the species concept, as applied to multicellular organisms, does not apply well. There may be millions of kinds of bacteria but there appear to be only thousands of species that do not interbreed.

Because of their small size, bacteria, single-celled organisms, and some multicelled organisms are easily dispersed by air, water, and larger animals (O'Dor et al. 2009). If they can survive environmental conditions that are not ideal during dispersal, they may proliferate when they arrive in a suitable location, thus giving the appearance of a discontinuous distribution. High dispersal rates and adaptability to poor conditions also allow organisms to be cosmopolitan, occurring wherever environmental conditions are suitable (Patterson and Lee 2000).

A key aspect of landscape (and seascape) ecology is the relationship of local to regional diversity. For a given regional number of species (i.e., gamma diversity), a taxon may show (1) high alpha- (local) but low beta- (between-location differences) diversity or (2) low alpha- but high beta-diversity. Microbes may be a good example of (1) and invertebrates of (2). Beta-diversity is closely related to diversity of habitats in a landscape. Failing to appreciate these patterns is a reason some authors extrapolated from high alpha-diversity to estimate that many millions of species may exist (reviewed by Costello and Wilson 2011; Costello et al. 2012).

The resilience of microbes to environmental stressors means that they have low extinction rates. One may thus expect there to be an enormous number of microbial species because they have lived longer on Earth than any other organisms. However, their good dispersal means that populations regularly interbreed and so new species are not formed (similar mechanisms also affect animals and plants). One of the reasons there are fewer species in the ocean than on land is that there are fewer barriers to dispersal and ocean currents disperse eggs, larvae, and adults. Thus, there are relatively few planktonic and pelagic species, compared to a larger number of stationary benthic species (Gibbons et al. 2010). The formation of new species requires some separation of populations, typically by a physical barrier such as distance or a land bridge separating oceans or, alternatively, microhabitat specialization.
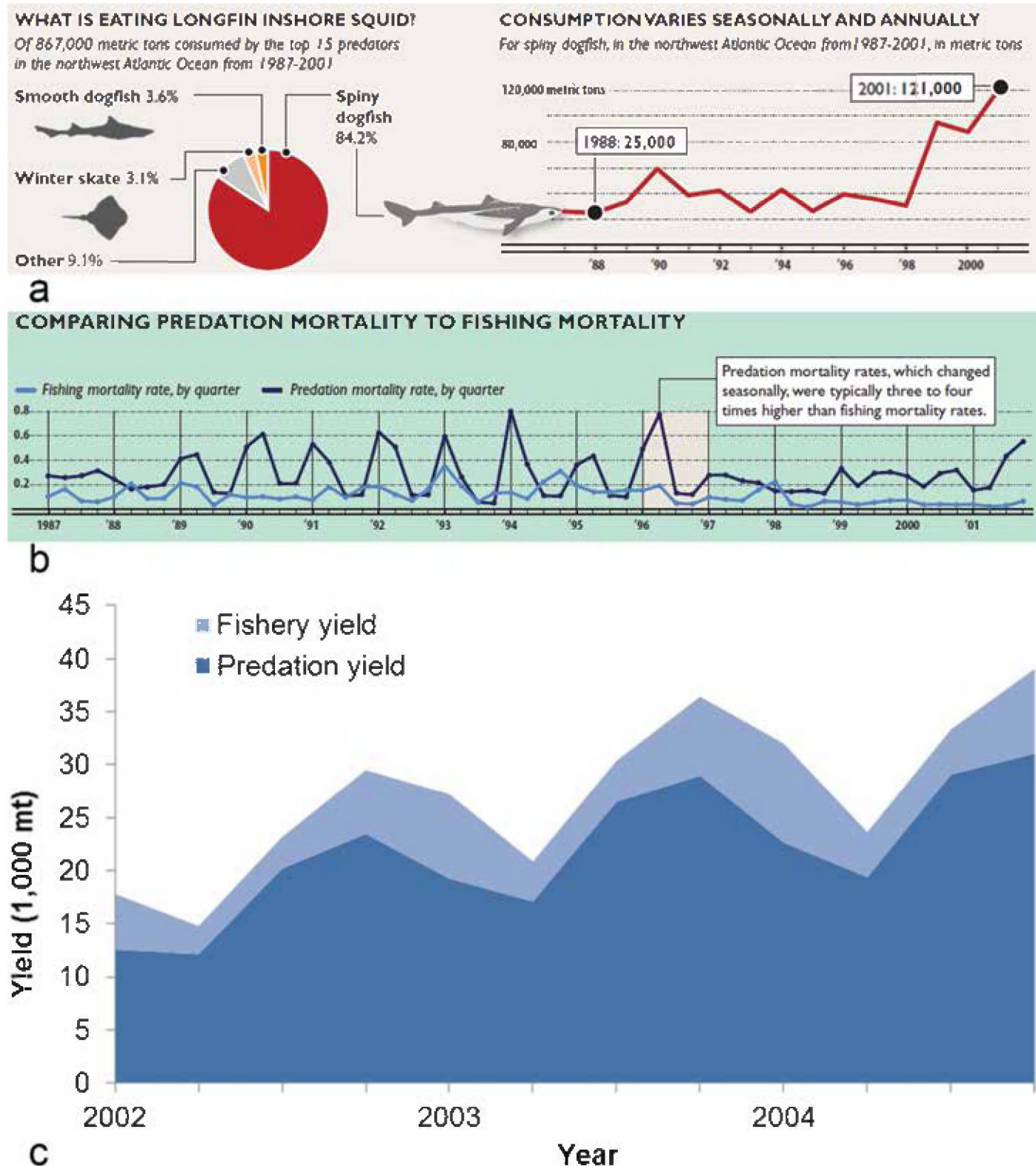
Figure 4. Fish predation on longfin squid, a case study. (a) Consumption estimates, (b) predation mortality versus fishing mortality (Lenfest Ocean Program Research Series, June 2011; Moustahfid et al. 2009a), and (c) projected quarterly yield (thousands of metric tons, mt) of Northwest Atlantic longfin squid in the fishery (light blue) and in predation removals (dark blue) for the 5-year average of total mortality (Moustahfid et al. 2009a).

Marine Species Diversity as a Component of the Earth's Total Species Diversity

Fish are diverse in species, but their food is almost 10 times more diverse. Marine species discovery rates have been relatively high compared to terrestrial discovery rates since the 1950s, and the number of scientists involved in describing species has never been so great (Eschmeyer et al. 2010; Costello et al. 2012). The apparent linear trend in the rate of description of new marine species may be due to increased taxonomic effort offsetting an increasing difficulty in discovering species new to science. The continued high rate of species description may reflect scientists' improved abilities to sample new habitats, remote locations, and/or more taxonomically difficult taxa, rather than an unending supply of species waiting to be discovered.

Of the estimated 1.5 million described species, only about 240,000 are marine (Costello et al. 2012). We suggest that this relatively low proportion of marine species reflects reality, not an artifact of the oceans being less explored. The ocean has fewer species than land for two primary reasons. First, plants have provided a complex, long-lived habitat and food source that covers much of the land and enabled the evolution of insects, which comprise about 60% of all species on Earth (Hamilton et al. 2010). In contrast, the insects' ancestors in the oceans, the crustaceans, find large plants (seaweeds) only around the coastline; these plants feed only a few herbivorous species. Second, the greater dispersal of organisms in the oceans (Kinlan and Gaines 2003) mitigates against forming new species.

Recent studies suggest that once we include the as-yet-undiscovered species, there may be as few as 5 plus or minus 3 million species on Earth and fewer than 1 million in the oceans (Hamilton et al. 2010; Costello et al. 2012). These estimates are far lower than

previous estimates of 10–100 million marine species alone (Costello and Wilson 2011). These are still extraordinary numbers of species that amaze the public, but providing exaggerated estimates of undiscovered diversity can make efforts to discover all species appear futile. They can also exaggerate estimates of the rate of species extinction, because these are partly based on the estimated number of all species on Earth (Stork 2010). By using more realistic estimates of biodiversity, it becomes possible to prepare a plan to explore, discover, and describe all biodiversity, including fish, within this century. During the census decade, the World Register of Marine Species has recorded descriptions of almost 2,000 new marine species each year (Appeltans et al. 2011). The last decade had nearly as many species described as the same decade a century earlier. The census was not able

19% Crustacea
(including crabs, lobsters, shrimp, and barnacles)

17% Mollusca
(including squid, octopuses, clams, snails, and slugs)

12% Pisces
(fish, including sharks)

10% Protists
(unicellular microorganisms)

10% algae and plant-like organisms

7% Annelida
(segmented worms)

5% Cnidaria
(including sea anemones, corals, and jellyfish)

3% Platyhelminthes
(including flatworms)

3% Echinodermata
(sea stars, sea urchins, sea cucumbers)

3% Porifera
(including sponges)

2% Bryozoa
(mat or "moss animals")

1% Tunicata
(including sea squirts)

Figure 5. Species representation by phylum in OBIS in 2010. Most species biodiversity falls into a dozen groups, including crustaceans and molluscs, fewer fishes, and only 2% other vertebrates (mainly whales, seals, and walruses). Not surprisingly, new species discoveries were more common among small organisms than large, but each image is a new census species (Costello et al. 2010b). [Photo credits: Russ Hopcroft, Gary Cranitch, Julian Finn, Larry Madin, John Huisman, Katrin Iken, Bernard Picton, and Piotr Kuklinski.]

to involve all countries or regions of the world (Costello et al. 2010b), but given improved coordination and greater participation, the next few decades could result in such progress that it will become demonstrably harder to discover new species in the oceans. Such a situation will enable better understanding of ocean ecosystems and resources and vastly improve communication to explain what needs conservation and why. It is difficult to argue for the protection of species that have not been shown to exist.

SUMMARY

The census repeatedly showed the value of investing in integrated, large-scale efforts such as the global seamount survey, the acoustic and satellite tagging efforts, the drive to barcode all marine species, and the value of sharing expertise and data. It found that human impacts are everywhere: Census researchers found more garbage than life in some deep-sea trawls (McIntyre 2010). It is also clear that humans impacted ocean biodiversity significantly earlier than previously thought and that there is not an endless supply of biodiversity. Reefs, deep-sea, Arctic, and Antarctic systems are particularly in need of work due to changing climate. It is clear that many large species need protection but also that species can rebound when given the opportunity. Many species may have homing behavior that makes them susceptible to harvesting, and we are beginning to identify concentrations of high species abundance where conservation efforts may yield larger-than-expected dividends. The census helped to advance technologies such as automated image processing, acoustic tracking of small fish on the continental shelves, satellite archival tags that allow large fish to collect environmental data, acoustic imaging of huge areas, genetic barcoding to speed up species identification in samples, and integrated data management. It seems that we are closer than ever to being able to do some of the things we have only dreamed of for generations, such as tracking species interactions in situ. Although many census projects could have succeeded on local scales with national funding, the census enabled collaboration in marine biology on a global scale, demonstrating the scientific benefits and cost efficiencies of international collaboration. It is the hope of all of us who were touched by the census that science institutions and countries will continue to explore and discover ocean biodiversity by collaborating internationally.

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COVER ILLUSTRATION

Census investigators explored on and beneath polar ice. Their aircraft remotely sensed animals through properties of scattered light. Marine animals carried tags that stored records of their travels and dives and communicated with satellites. Fish carried tags that revealed their migration past acoustic listening lines. Sounds that echoed back to ships portrayed schools of fish assembling, swimming, and commuting up and down. Standardized frames and structures dropped near shores and on reefs provided information for comparing diversity and abundance. Manned and unmanned undersea vehicles plus divers photographed seafloors and cliffs. Deep submersibles sniffed and videotaped smoking seafloor vents. And, nets and dredges still caught specimens, shallow and deep, for closest study. Photo credit: E. Paul Oberlander, Woods Hole Oceanographic Institution.

From the Archives

Bordering the Great Lakes are six States having a population of about fourteen millions of people. The fisheries of these Great Lakes, as their product enters into the general commerce of the country, cannot be regarded as the concern of the six States--they are of national importance. If the fish captured in these lakes were consumed along their shores I grant that the States would have no special claim upon the general Government for taking part in maintaining such fisheries, or helping in any way to their re-establishment. This was the condition of affairs once; but with the modern facilities of rapid communication and improved methods of transportation, their product is marketed all over the country, and for that reason the States bordering the Great Lakes have, in my judgment, as good a right to assistance from the General Government, in the directions I shall presently mention, as the fisheries of the Atlantic and Pacific Oceans.

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