TRENDS, DRIVERS, AND ECOSYSTEM EFFECTS OF EXPANDING GLOBAL INVERTEBRATE FISHERIES

by

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "TRENDS, DRIVERS, AND ECOSYSTEM EFFECTS OF EXPANDING GLOBAL INVERTEBRATE FISHERIES" by Sean C. Anderson in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

Worldwide, finfish fisheries receive increasing assessment and regulation, slowly leading to more sustainable exploitation and rebuilding. In their wake, invertebrate fisheries are rapidly expanding with little scientific scrutiny despite increasing socio-economic importance. This thesis provides the first global analysis of the trends, drivers, and population and ecosystem consequences of invertebrate fisheries, in general, and sea cucumber fisheries, in particular, based on a global catch database in combination with taxa-specific reviews. Further, I developed new methods to quantify trends over space and time in resource status and fishery development. Since 1950, global invertebrate catches increased six-fold with 1.5 times more countries fishing and double the taxa reported. By 2004, 31% of fisheries were over-exploited, collapsed, or closed. New fisheries developed increasingly rapidly, with a decrease of six years (± three years) in time from start to peak from 1960 to 1990. Moreover, 71% of invertebrate taxa (53% of catches) are harvested with habitat-destructive gear, and many provide important ecosystem functions including habitat, filtration, and grazing. For sea cucumber fisheries, global catch and value has increased strongly over the past two to three decades, closely linked to increasing prices and demand on Asian markets. However, the catch of individual fisheries followed a boom-and-bust pattern, declining nearly as quickly as it expanded, and expanding approximately five times as quickly in 1990 compared to 1960. Also, new fisheries expanded increasingly far from their driving market in Asia, and encompassed a global fishery by the 1990s. One-third of sea cucumber fisheries experienced declines in average body size fished; half showed serial exploitation over space by moving further away from the coast; three-quarters showed serial exploitation from high- to low-value species; and two-thirds experienced population declines due to overexploitation with local extirpation in some cases. One-third of all sea cucumber fisheries remain unregulated. These findings suggest that the basis of marine food webs is increasingly exploited with limited stock and ecosystem-impact assessments, and a new management focus is needed to avoid negative consequences for ocean ecosystems and human well-being.

List of Abbreviations and Symbols Used

AIC	Akaike's information criterion
β_j	model parameter for country$_j$
CCAMLR	Conservation of Antarctic Marine Living Resources
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
C_m	simulated maximum catch value
CPUE	catch per unit effort
C_t	simulated catch at time t
DFO	Department of Fisheries and Oceans Canada
d_t	time to maximum development of the fishery
ϵ	error term
$\mathbb{E}$	estimate
e	exponent
F	median filtration rate
f	smooth function
FAO	Food and Agriculture Organization of the United Nations
GAM	generalized additive model
GCV	generalized cross-validation
GDP	gross domestic product
h	hour
ha	hectare
ICES	International Council for the Exploration of the Sea
IUU	illegal, unregulated, and unreported
kg	kilogram
km	kilometre
L	litre
lag	a shift of one time-series in time relative to another
LME	Large Marine Ecosystem

loess	locally weighted scatterplot smoothing
log	natural logarithm
$LogN$	log normal
m	metre
MM	multiple-model (estimation)
mm	millimetre
MSY	maximum sustainable yield
NA	not applicable
NAFO	Northwest Atlantic Fisheries Organization
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
p	probability
r	correlation coefficient
σ^2	standard deviation squared, i.e. variance
S-	supplementary figure or table
SCUBA	self contained underwater breathing apparatus
SPC	Secretariat of the Pacific Community
T	number of years in simulation
t	time
t	metric tonne
US	United States
USD	United States dollar
W	shell-free dry weight
Y	year
z_t	log-normally distributed random noise

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There are many people to thank for their assistance and support throughout my time working on this thesis. I am incredibly grateful to Heike K. Lotze who has shaped who I am as a scientist today from my early days as an undergraduate student. From discussions on science, the academic world, and life in general, to tireless, timely, and thoughtful editing of my writing — I couldn't have done it without you. Thank you to my committee members Joanna Mills Flemming, Nancy Shackell, Hal Whitehead, and Boris Worm whose comments at my Admission to Candidacy exam and on various aspects since have greatly improved this thesis. Ultimately it was Nancy in combination with the late Ransom Myers who started me on the path down low-trophic level fisheries many years ago. I thank Joanna Mills Flemming for guiding the statistical direction of this thesis, providing valuable advice on my academic path, and introducing me to the world of GAMs. I am also indebted to Chris Field, Trevor Branch, and especially Wade Blanchard for helping me get the statistics right. I owe thanks to Coilín Minto and Dan Ricard for opening my eyes to the value of repeatable research using open source tools, and showing me that, finally, it was cool to be a geek. The time Coilín invested in me early in my thesis deeply shaped my direction in science for the better. I gained immensely from discussions about science and statistics with Francesco Ferretti, Dan Boyce, and Bob Farmer. Bob repeatedly convinced me that I could get 'er done when I needed it most and his selfless upbeat attitude during tough times has inspired me. I am grateful to Catherine Muir for keeping us organized and repeatedly lending a sympathetic ear. The whole Myers-Worm-Lotze-Johnson lab group has been supportive and I've enjoyed working with you all. In addition to those mentioned earlier, a special thanks to Allison, Anna, Arliss, Camilo, Christine, Derrick, Diego, Greg, Marta, Rowan, Stephanie, Susan, Trevor, and Zoey.

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Chapter 1

Introduction

Over the past 50–100 years, exploitation has depleted many traditional finfish fisheries globally (e.g. Pauly et al. 2002; Myers and Worm 2003; 2005; Christensen et al. 2003; Frank et al. 2005). In recent decades these declines have spurred increasing assessment and regulation that are slowly leading to more sustainable exploitation and rebuilding of depleted finfish stocks in some regions (Worm et al. 2009). Concomitant with these declines has been a large-scale expansion of low trophic-level invertebrate fisheries. This trend has been observed through increasing catch (e.g. Pauly et al. 2002; FAO 2009*a*), increasing value (FAO 2009*a*), spatial expansion of selected fisheries (e.g. Berkes et al. 2006), and a declining trophic level of the overall fisheries catch (Pauly et al. 1998; 2001; Essington et al. 2006). In 2006, shrimp was the most valuable fishery at 16.5% of global fisheries value compared to 10% for all groundfish combined (FAO 2009*a*).

A variety of forces have been suggested as drivers of these increases, including changing market value (Botsford et al. 2004), local social and economic pressures (Roy 1996; Hamilton et al. 2004), and population increases caused by release from predation (Worm and Myers 2003; Heath 2005; Myers et al. 2007; Baum and Worm 2009). However, Jamieson (1993) suggested that invertebrate fisheries may not be as resistant to over-exploitation as once thought. My previous work has pointed to gaps in knowledge of population parameters such as growth rate, biomass, and geographic range in developing invertebrate fisheries on the east coast of Canada that may impair their management and the long-term viability of their fisheries (Anderson et al. 2008). Some invertebrate populations have already experienced severe declines (e.g. Tegner et al. 1996) and patterns of serial depletion have been suggested for some invertebrate fisheries such as crabs and shrimps (Orensanz et al. 1998), oysters (Kirby 2004), and chitons and sea urchins (Salomon et al. 2007) on regional scales and for sea urchins (Berkes et al. 2006) and sea cucumbers (e.g. Therkildsen and Petersen 2006) on a global scale. Thus, despite globally increasing total invertebrate catches, the underlying patterns of individual species may look less optimistic. Yet a synthetic analysis of the global status, trends and drivers of invertebrate fisheries has been lacking so far.

Many invertebrate species serve important roles in the marine ecosystem acting both as the base of the marine food web (e.g. Birkeland et al. 1982; Francour 1997) but also as habitat provision (e.g. Peterson et al. 2003), water filtration (e.g. Harrold and Pearse 1989), and algal grazing (e.g. Tegner and Dayton 2000) among other roles. These services are vital to healthy oceans, however, the ecosystem impacts of removing increasingly high volumes of low-trophic level species and of the gear used in these fisheries remains to be assessed on a global scale.

In addition to their ecological value, invertebrate fisheries are of great value to many coastal communities worldwide as sources of income (e.g. FAO 2008*a*;*b*) and nutrition (e.g. FAO 2009*a*; Smith et al. 2010). For example, entire coastal communities in the Solomon Islands (Nash and Ramofafia 2006) and Madagascar (Joseph 2005) are dependent on sea cucumber harvesting as a source of income. The potential for boom-and-bust trajectories of some invertebrate fisheries may be detrimental for the social structure and well-being of coastal communities (Berkes et al. 2006) — particularly in regions with weaker fisheries management and governance (Smith et al. 2010).

In this thesis I aim to analyze the trends and drivers of invertebrate fisheries around the world and interpret these findings in light of their potential population, ecosystem, and social impacts. Because of the generally poor data quality and quantity, I accomplish this through statistical approaches robust to outliers and methodological decisions; applying both meta-analytical methods across taxonomic groups and detailed analyses within taxa; and conducting a detailed review of available literature to verify data, trends, and identify further patterns hidden within the analysis of aggregated data.

In Chapter 2, I provide the first global analysis of the status and trends in invertebrate fisheries along with their drivers and ecosystem effects using a database of worldwide landings records. I develop robust methods to quantify the exploitation status of individual fisheries based on catch data, their spatial expansion relative to major markets, and their temporal rate of development. The results indicate an increasing proportion of invertebrate fisheries are overexploited or collapsed, and new fisheries are developing more rapidly and further away over time. Further, they reveal the potential consequences of harvesting invertebrates in terms of lost ecosystem services and fishing gear impacts. I therefore urge for a global management perspective to address global market drivers, scientific stock and ecosystem impact assessments, and local harvest regulations to avoid negative consequences for invertebrate populations, ocean ecosystems, and human well-being.

In Chapter 3, I build on the analysis in Chapter 2 and examine global fishery trends and drivers for one taxonomic group, sea cucumbers, in greater detail. I verify fishery trends by country to enable a more detailed analysis of global patterns of spatial expansion and rate of fishery development. I find that sea cucumber catches typically decline nearly as quickly as they expand, and that global patterns in fishery volume are linked to Asian market demand. Finally, I identify the prevalence of local issues of serial exploitation over space, from high- to low-value species, and decreasing body size via a literature survey of all major sea cucumber fisheries. The findings add quantitative evidence to anecdotally reported and suspected patterns that are central to forming international regulations and local management that can protect sea cucumber populations and the ecosystems and human communities who depend on them.

Both data chapters (Chapters 2 and 3) were written as manuscripts to be submitted for publication in scientific journals and were therefore written in the first person plural. "We" refers to myself and my co-authors (as outlined in the following paragraph). Due to the extensive development of new methods in Chapter 2 and the target journal format, the Materials and Methods (Section 2.3) and additional Supporting Tables and Figures appear after the Results and Discussion (Section 2.2).

I (S.C. Anderson) participated in a primary role in the conceptualization, analysis, and writing of this thesis. H.K. Lotze supervised and edited all chapters. H.K. Lotze and J. Mills Flemming guided the analysis and interpretation of Chapters 2 and 3. J. Mills Flemming and R. Watson assisted in editing Chapter 2 and comments from B. Worm enhanced its message. R. Watson, through the Sea Around Us Project, provided the global catch database upon which much of the analysis in Chapters 2 and 3 was based.

Chapter 2

Rapid Global Expansion of Invertebrate Fisheries: Trends, Drivers and Ecosystem Effects

2.1 Introduction

Global finfish catches peaked in the 1980s and have declined since the early 1990s, yet global invertebrate catches have continued to climb (FAO 2009*a*). Although some invertebrate fisheries have existed for centuries (Leiva and Castilla 2002; Kirby 2004; Lotze et al. 2006), many others have commenced or rapidly expanded over the past 2–3 decades (Berkes et al. 2006; Anderson et al. 2008). Today, shrimp has the largest share of the total value of internationally-traded fishery products (17% in 2006, including aquaculture), followed by salmon (11%), groundfish (10%), tuna (8%), and cephalopods (4%) (FAO 2009*a*). In several ways, invertebrate fisheries represent a new frontier in marine fisheries: they provide an alternative source of animal protein for people, job opportunities in harvesting and processing, and substantial economic windfall for communities due to their high value and expanding markets (Berkes et al. 2006; Anderson et al. 2008; FAO 2009*a*). Yet, while finfish fisheries (Worm et al. 2009) and some more established invertebrate fisheries (Breen and Kendrick 1997; Castilla and Fernandez 1998; Hilborn et al. 2005; Phillips et al. 2007) have received increasing assessment, regulation, and rebuilding, many invertebrate fisheries do not get the same level of attention or care. They are typically not assessed, not monitored, and often unregulated (Andrew et al. 2002; Leiva and Castilla 2002; Berkes et al. 2006; Anderson et al. 2008; FAO 2009*a*), which threatens their sustainable development despite their increasing social, economic, and high ecological importance (Perry et al. 1999; Anderson et al. 2008).

The increase in invertebrate fisheries is in part a response to declining finfish catches that let many fishermen switch to new target species, often further down in the food web (Pauly et al. 2002; Anderson et al. 2008). At the same time, the abundance and availability of many invertebrates may have increased due to release from formerly abundant finfish predators (Worm and Myers 2003). Once thought to be particularly resistant to over-exploitation (Jamieson 1993), an increasing number of historical (Kirby 2004; Lotze et al. 2006) and recent invertebrate fisheries (Andrew et al. 2002; Leiva and Castilla 2002; Berkes et al. 2006) tell a different story. Thus, in light of their increasing importance, we evaluated the current global status and trends of invertebrate fisheries, as well as their underlying drivers, and population and ecosystem consequences.

Stock assessments and research survey data that are available to evaluate many finfish populations (Worm et al. 2009) are often lacking for invertebrates (Perry et al. 1999; Andrew et al. 2002; Anderson et al. 2008). Therefore, we used the Sea Around Us Project's catch database (see Section 2.3 Materials and Methods) as the best available data source to analyze temporal and spatial trends in invertebrate fisheries on a global scale. It consists largely of a quality-checked version of the Food and Agriculture Organization's (FAO) catch database supplemented by regional and reconstructed datasets covering 302 invertebrate species or species groups (taxa) over 175 countries from 1950–2004 (Zeller and Pauly 2007). Wherever possible we have corroborated the observed patterns with recent taxa-specific global reviews (see Section 2.3 Materials and Methods).

2.2 Results and Discussion

Since 1950, invertebrate fisheries have rapidly expanded on multiple scales, and today operate around the world (Figure 2.1A). In 2000–2004, the highest concentrations of catch per unit area by Large Marine Ecosystem (LME, http://www.lme.noaa.gov) were in the Yellow Sea, Northeast U.S. Continental Shelf, and the East China Sea (red), followed by the Newfoundland-Labrador Shelf, the Patagonian Shelf, and the South China Sea (yellow). The bulk of the catch in these areas consisted of bivalves, squids, and shrimps. Since 1950, the total reported catch of invertebrates has steadily increased six-fold from two to 12 million t (Figure 2.1B). In comparison, the catch of invertebrates and finfish combined increased five-fold over the same period, beginning to decline in the late 1980s (Pauly 2008). The increase in invertebrate catch is not driven by only a few countries, as the average catch per country has more than doubled (Figure 2.1B). Also, in 2004 there were 1.5 times more countries fishing for twice as many invertebrate taxa compared to 1950 (Figure 2.1C). This is in contrast to all finfish and invertebrate fisheries combined, where the number of countries reporting catch has been largely stable over the past 50 years (Figure 2.1C) and overall finfish catch has declined since the early 1990s (Pauly et al. 2002). Although increasing trends in invertebrate fisheries may be partly explained by increasing precision in reporting (see Section 2.3 Materials and Methods) (Figures 2.S-1, 2.S-2), there are clear underlying trends of expansion by catch, country, and taxa. This is corroborated by studies on individual fisheries where assessments or effort data are available (Jamieson and Campbell 1998).

The increase in invertebrate fisheries is driven not by a few major target species, but instead by increasing catch trends across all taxonomic groups (Figure 2.2, Figure 2.S-3). While catches have increased continuously since the 1950s for more

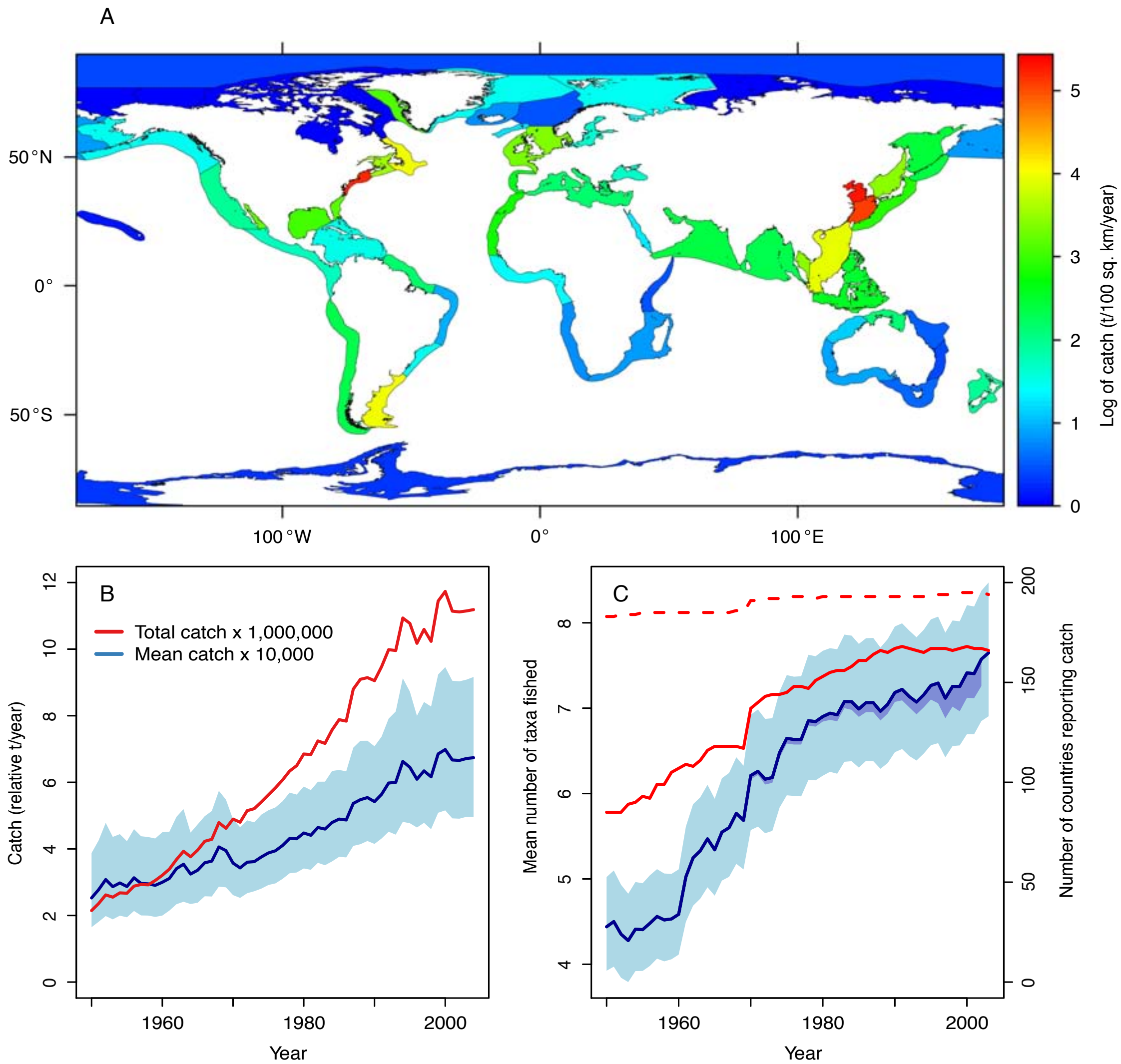

Figure 2.1: Spatial and temporal trends in catch, species diversity and countries involved in global invertebrate fisheries. (A) Mean annual invertebrate catch in each Large Marine Ecosystem (LME) from 2000–2004. (B) Trends in invertebrate catch globally (total catch, red) and per country (mean and standard error assuming a log-normal distribution, blue). (C) Trends in the number of countries reporting catch of invertebrates (solid red) and of all finfish and invertebrate species (dashed red, as a reference) since the 1950s, and number of invertebrate taxa fished by country (mean and standard error assuming a negative binomial distribution, blue). Thickness of dark blue line approximates false increase due to increased reporting precision (see Section 2.3 Materials and Methods).

traditionally fished crustaceans and bivalves, they rapidly increased in the 1980s and 1990s for often newly targeted cephalopods and echinoderms. Thus, already existing fisheries expanded and new fisheries were developed for species that had not been commercially fished before. Although overall catch trends for invertebrate fisheries paint a picture of continuing expansion (Figure 2.1B), catches in several groups (e.g. bivalves and echinoderms) have slowed or declined in recent years (Figure 2.2B and 2.2D). The picture of universal increase changes even more drastically if we look at individual invertebrate fisheries by country. Here, some countries are still expanding their catches while others peaked long ago (Figure 2.S-4).

Based on individual catch trajectories, we assessed the current status and patterns of depletion of invertebrate fisheries. To do this, we modified a technique of Froese and Kesner-Reyes (2002) to estimate the exploitation status of each invertebrate fishery from catch data (Figure 2.S-5). Our modifications overcome previous weaknesses of this method by accounting for high variability in catch, spurious peak catch years, and fisheries that are still expanding (see Section 2.3 Materials and Methods). Our results indicate that half of the fisheries had peaked as of 2004 (Figure 2.3A), with 19% fully exploited, 15% over-exploited or restrictively managed, and 16% collapsed or closed. This indicates that the globally increasing invertebrate catches (Figure 2.1B) are likely supplied by new taxa or new countries entering the fishery. We do not suggest that these patterns have been driven solely by high exploitation pressure. Declines in catch can also have natural (e.g. recruitment failure due to climate) and other human related (e.g. changing markets, restrictive management) drivers that can act in conjunction with each other (Shepherd et al. 1998).

Strong global markets may drive the expansion and serial depletion of some fisheries over space and time (Kirby 2004; Berkes et al. 2006; Salomon et al. 2007),

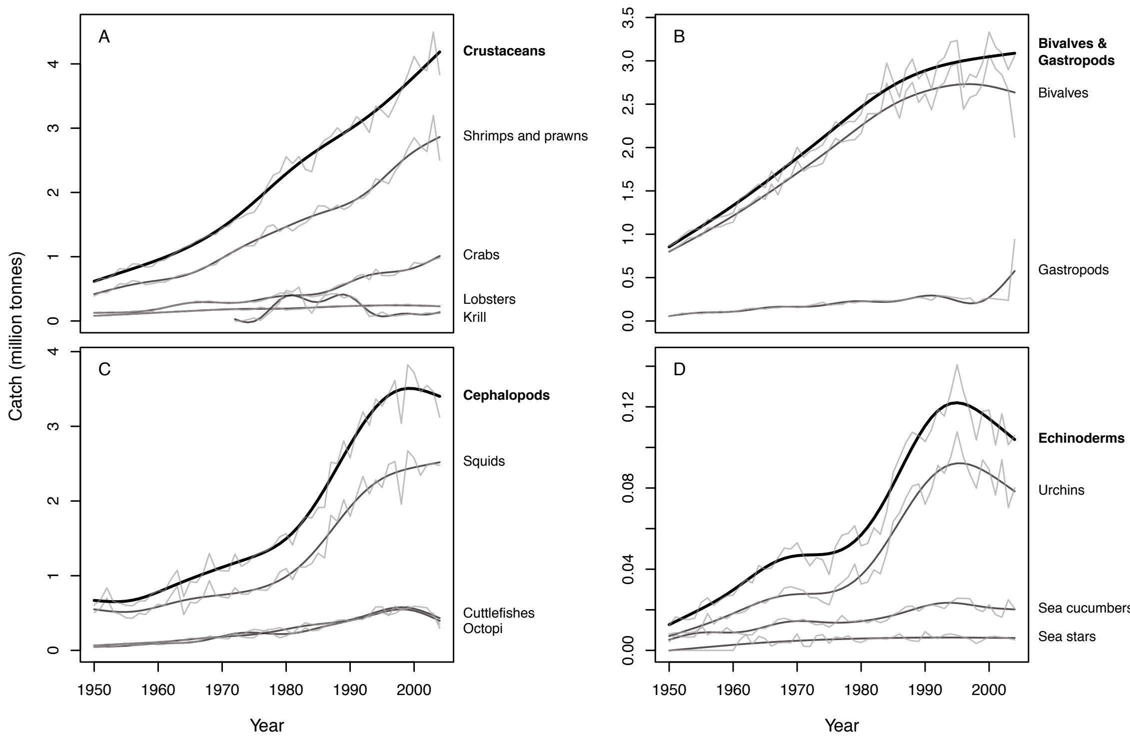

Figure 2.2: Expansion of invertebrate catch since the 1950s across taxa: (A) crustaceans, (B) bivalves and gastropods, (C) cephalopods, and (D) echinoderms. Upper lines indicate total catch for each group and underlying lines catch for subgroups. Dark lines represent smooth estimates obtained from generalized additive models. Light lines indicate the unfiltered catch trends.

particularly given the increasing availability of efficient fishing gear and rapid global transport. If a fishery is declining in one region, fishing companies move into other regions, usually further away, to supply the demand of global buyers (Berkes et al. 2006). Some new invertebrate fisheries have a single strong market as shown for sea urchins (Berkes et al. 2006), where the global catch is related to the value of the Japanese Yen (Botsford et al. 2004). For other taxa, single driving markets are less obvious. For example, squid has three main importing nations (Japan, Italy, and Spain), while others have even more (see Section 2.3 Materials and Methods).

However, the vast majority of global sea cucumber catch is exported to Hong Kong (or nearby Asian countries) (see Section 2.3 Materials and Methods) and the value of sea cucumber has risen dramatically in recent decades (FAO 2008*b*). To test whether spatial expansion has occurred, we used least-squares regression to compare the great-circle distance from Hong Kong with the year of peak sea cucumber catch for each country (see Section 2.3 Materials and Methods) and found a significantly positive relationship ($r = 0.62$, $p = 0.002$, Figure 2.3B). Given the generally poor stock status of sea cucumber fisheries (FAO 2008*b*), this may indicate a strong driving market where fisheries are sequentially exploited in relation to transportation cost. Such serial exploitation can have strong negative social and ecosystem consequences (Berkes et al. 2006).

If markets and prices increase, new fisheries may develop more rapidly over time. To test this, we compared the time when fisheries began or expanded with the time when they reached an initial peak in catch (see Section 2.3 Materials and Methods). We used an initial rather than overall peak in catch trajectories to treat new and old fisheries equally. Despite uncertainty in individual taxa, we found a significant overall reduction in time to peak for newer fisheries (Figure 2.3C). This corresponds to an approximate decrease of six years ($\pm$ three years) in time to peak when comparing 1960 to 1990. We suggest this may be a combined result of growing demand due to the increasing global human population, changes in diet preferences (e.g. the rise of Sushi restaurants in Western countries), declines in finfish fisheries, as well as more and more smaller fisheries being exploited, facilitated by global transport. Where a peak in catch represents a peak in fishery productivity, it is unlikely that management and research can keep up with this rate of expansion to ensure sustainable development (Berkes et al. 2006; Anderson et al. 2008).

The rapid expansion, and in some cases serial depletion, of global invertebrate fisheries may have strong ecosystem consequences due to the method of fishing and the functional roles invertebrates play in marine ecosystems. In 2000–2004, 53% of invertebrate catch by volume and 71% by taxa fished were caught by benthic trawling and dredging gear with these proportions remaining relatively stable since the 1950s (Figures 4A, B). This is largely driven by benthic trawling for crustacean and cephalopod species and dredging for bivalves. In comparison, benthic trawling and dredging accounted for only 20% of global finfish catch (57% of taxa, 2000–2004 mean). Such gear has substantive negative impacts on benthic habitat and communities by destroying three-dimensional structure, impacting spawning and nursery grounds, altering benthic community composition, and reducing future biomass, production, and species richness (Tillin et al. 2006). Moreover, together with midwater trawls, benthic trawls and dredges can incur a substantial portion of incidental by-catch (Alverson et al. 1994).

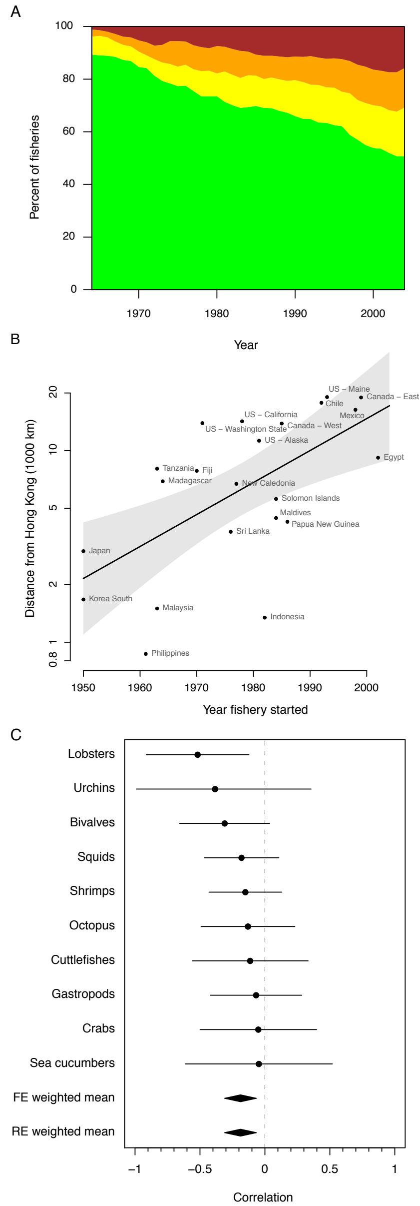

Figure 2.3: Status, drivers, and rate of development of invertebrate fisheries. (A) Estimated status of invertebrate fisheries over time as expanding (green), fully exploited (yellow), over-exploited or restrictively managed (orange), and collapsed or closed (brown). (B) Distance from Hong Kong vs. year of first peak in catch for sea cucumber fisheries in different countries. Line represents least squares regression ($r = 0.62$, $p = 0.002$), and shaded area represents 95% confidence interval. (C) Meta-analysis of correlation between fishery initiation year and time to peak catch across 10 invertebrate taxonomic groups. Dots represent median correlation coefficients, lines represent 95% confidence intervals, and diamonds represent fixed and random effect pooled estimates (see Section 2.3 Materials and Methods).

Beyond the predator-prey roles that most finfish play in marine ecosystems, invertebrates have more diverse functions and provide essential ecosystem services such as maintaining water quality (Newell 1988), regenerating nutrients (Uthicke 2001), providing nursery and foraging habitat (Peterson et al. 2003), and preventing algal overgrowth through grazing (Tegner and Dayton 2000) (Figure 2.4C). We aggregated mean catch per year from 2000–2004 by functional groups to assess the potential removal impact (Figure 2.4D, Table 2.S-4) (see Section 2.3 Materials and Methods). All invertebrate taxa form potentially important roles as prey for higher trophic levels while most cephalopods and crustaceans also perform predatory roles. Especially bivalve, but also krill and some sea cucumber fisheries, represent a substantial removal by volume (3 million t/year) of filter feeders. We estimate the removal of bivalves alone to equate to a loss of ∼11 million Olympic sized swimming pools in filtering capacity per day between 2000–2004 (see Section 2.3 Materials and Methods). In addition, many bivalves form beds, banks, or reefs that structure the seafloor and provide important habitat (Peterson et al. 2003). Invertebrate fisheries further remove ∼1 million t of detritivores and scavengers and ∼1 million t of herbivores annually. Although recruitment and re-growth will compensate for some of these losses, the direct and indirect short- and long-term ecosystem effects of such removals are largely unknown.

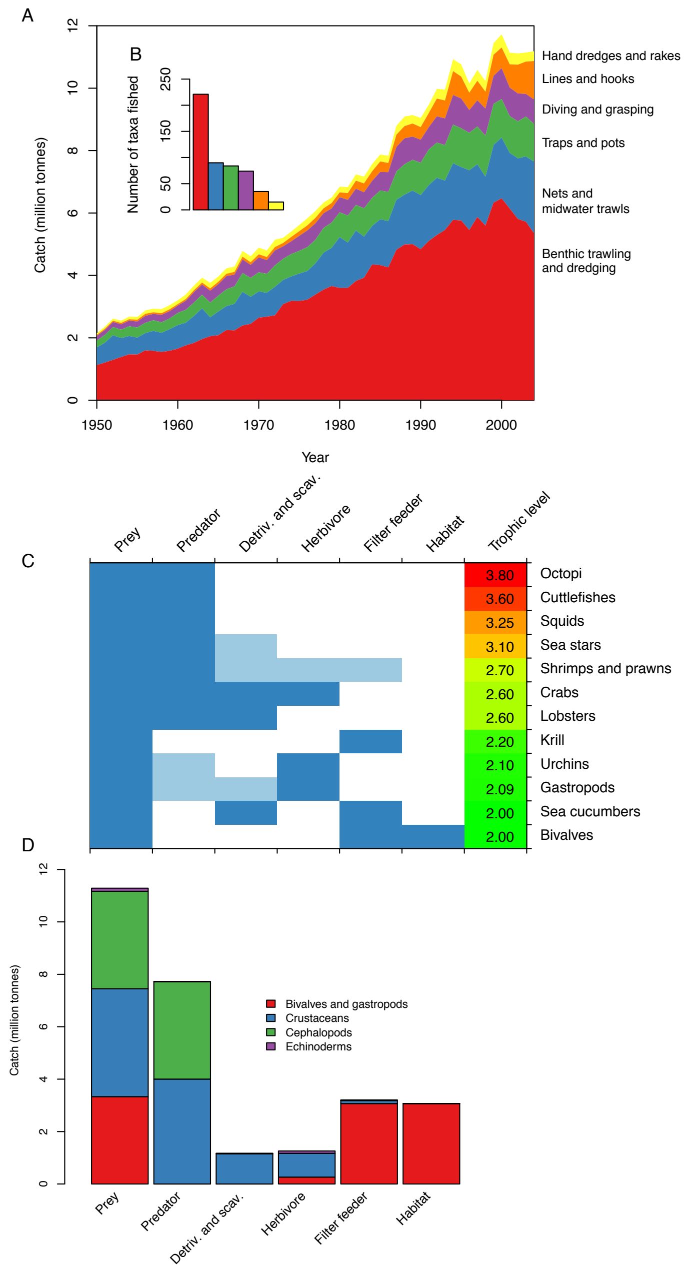

Figure 2.4: Potential ecosystem effects of invertebrate fisheries. Habitat impacts expressed as (A) total invertebrate catch and (B) number of taxa fished by different gear types. (C) Ecosystem role of invertebrate taxa belonging to different functional groups and trophic levels (see Section 2.3 Materials and Methods). Dark and light blue indicate primary and secondary roles respectively (see Section 2.3 Materials and Methods). (D) Removal impact expressed as total catch removed by functional group as categorized in (C).

Our results demonstrate that despite overall increasing catches, diversity, and country participation in global invertebrate fisheries, there is strong evidence that the underlying trends in many individual fisheries are less optimistic. An increasing percent of invertebrate fisheries are over-exploited, collapsed, or closed. Some invertebrate fisheries, such as the rock lobster fishery in western Australia, have existed for a long time and are well-managed (Phillips et al. 2007), yet even there factors beyond the management system, such as climate change, can present major challenges. However, the same is not true for many newer fisheries like those for sea urchins (Andrew et al. 2002; Berkes et al. 2006) and sea cucumbers (FAO 2008*b*). New fisheries develop further away and at an increasingly rapid rate, likely driven by strong market forces. This means that global industries, markets, and free trade may enable the rapid expansion of new fisheries before scientists and managers can step in and make sensible decisions to secure the long-term, sustainable use of these resources (Berkes et al. 2006). On the one hand, we risk losing some of the last remaining viable and financially lucrative fisheries; bringing financial and social hardship to a large number of small communities dependent on these fisheries for income or food. At the same time, the population and ecosystem consequences of many invertebrate fisheries are largely unknown and unassessed (Anderson et al. 2008), although there are notable exceptions (Breen and Kendrick 1997; Castilla and Fernandez 1998; Hilborn et al. 2005; Phillips et al. 2007). Whereas there is increasing concern about the sustainable management and conservation of finfish (Worm et al. 2009), many invertebrates do not enjoy the same awareness or attention. Many of the described patterns are reminiscent of an earlier phase in finfish fisheries in which the rate of finding new fishing areas, new target species, and more efficient gears masked overall catch trends. However, because of improved industrial fishing gear and global networks that allow rapid and accessible transport, we may be progressing through invertebrate fishery phases even faster.

In order to prevent further uncontrolled expansion and instead aim for a more sustainable development of invertebrate fisheries, we highlight the need for a global perspective in their management combined with local assessment, monitoring, and enforcement of fisheries regulations. A global perspective is essential to identify roving buyers, monitor foreign investments, and consider CITES (U.N. Convention on International Trade in Endangered Species) listing where appropriate (Berkes et al. 2006). Also, the displacement of fishing effort from highly- to less-regulated regions and illegal, unreported, and underreported (IUU) catches requires global regulations in invertebrates and finfish fisheries alike (Worm et al. 2009). On a regional and local scale, stock assessments are infrequently or not performed for many invertebrate fisheries and often lack adequate knowledge on the species biology, population status, and response to exploitation (Anderson et al. 2008). Invertebrates are rarely monitored in research trawl surveys (Worm et al. 2009) and independent research surveys to assess population trends, by-catch, and habitat impacts of invertebrate fisheries are rarely done for many newer fisheries (Andrew et al. 2002; Berkes et al. 2006; Anderson et al. 2008). Based on such limited knowledge, the sustainable exploitation of invertebrates for fisheries may be difficult to achieve (Perry et al. 1999).

In contrast, after many decades of increasing exploitation and fish stock depletion, concerted management efforts in several regions around the world achieved the reverse: a reduction in overall exploitation rate and an increase in stock biomass in several finfish fisheries (Worm et al. 2009). This was achieved by a combination of management tools adapted to local conditions as well as strong legislation and enforcement. Similar measures can be implemented in invertebrate fisheries to prevent current and future trajectories of depletion (Hilborn et al. 2005). As an example, the addition of co-management and property rights in Chilean artisanal gastropod fisheries solved many overexploitation concerns, substantially increasing catch per unit effort and mean individual size (Castilla and Fernandez 1998). Similarly, the New Zealand rock lobster fishery was on a path of declining abundance before a reduction in effort and change of seasons substantially increased abundance, catch rates, and profitability (Breen and Kendrick 1997). Such successes provide a great opportunity to inform the management of other newer fisheries. It is our hope that increasing awareness of the ecological and economic importance of invertebrates may spur more rigorous scientific assessment, precautionary management, and sustainable exploitation to ensure long-term resilience of invertebrate populations, ocean ecosystems, and human well-being.

2.3 Materials and Methods

2.3.1 Temporal and Spatial Catch Trends

Global catch data (i.e. reported landings) for all harvested invertebrate species were obtained from the Sea Around Us Project (http://seaaroundus.org) (Watson et al. 2005). The data are based on landings reported to FAO, but have been quality checked and where possible, replaced with more precise versions from regional organizations such as the Northwest Atlantic Fisheries Organization (NAFO), the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), and the International Council for the Exploration of the Sea (ICES) (Zeller and Pauly 2007). Known reporting errors, for example Chinese records (Watson and Pauly 2001), are corrected as best possible. All such corrections are documented (see http://seaaroundus.org/doc/saup_manual.htm#13).

The Sea Around Us catch data are recorded by (i) which country reported the catch and (ii) the assumed LME in which the fishing was completed, for which catches are assigned to 30 x 30 minute cells using a series of rules taking into account where the catch was reported caught, known species' distributions, and fishing access agreements (Watson et al. 2005). We mapped spatial patterns in global catches as the mean annual invertebrate catch per 100 km^2 in each LME from 2000–2004 (Figure 2.1A).

Temporal trends from 1950–2004 were derived for total invertebrate catch and mean catch per country per year (Figure 2.1B). Confidence intervals were calculated under the common assumption that the catch data followed a log-normal distribution (Haddon 2001). Trends were similar when we used the median instead. Wherever possible, we corroborated the observed trends with recent taxa-specific global reviews. These included sea cucumbers (Conand 2004; Toral-Granda et al. 2008; FAO 2008*b*), sea urchins (Andrew et al. 2002), squids (Payne et al. 2006), octopus and cuttlefishes (Boyle and Rodhouse 2005), shrimps (FAO 2008*a*), gastropods (Leiva and Castilla 2002), lobster, bivalve, and crab fisheries (FAO 2009*a*).

2.3.2 Estimating the Legitimate Increase in the Diversity of Species Fished

To some extent, the increasing diversity of taxa reported in the Sea Around Us Project database is a function of the increasing taxonomic precision of reporting over time (Figure 2.1C). For example, Malaysian crustacean catch was recorded as Crustacea until 1986 before being split and reported as Sergestidae and *Panulirus*. There appeared to be a slowing or leveling of the mean number of species or group-level taxa reported per year since about 1980 (Figure 2.S-1). Therefore, we approximated the degree to which the increasing diversity reflected a true trend of an increasing number of species being targeted by fisheries.

As a first step, we excluded small fisheries because (i) we wished to focus on major fisheries and (ii) small fisheries were more likely to appear and disappear in the catch series (assuming some are experimental) thereby confusing the issue of diversity of fisheries. Thus, we included only those fisheries in which catch surpassed 1000 t/year since 1950 and which had at least five consecutive years of data. To exclude years in which a taxa or species was minimally fished, we excluded years in which a country reported catching less than 0.5 t of a taxa or species.

We then flagged a fishery as potentially halting due to increased taxonomic precision if (i) the catch trend ended with over 1000 t/year before the end of the dataset (2004) and (ii) the taxonomic precision was broader than a species level designation (e.g. "Crustacea"). These were cases in which catch might have been reported for an aggregated group but was then reported in multiple more specific taxonomic divisions. We summed these instances cumulatively assuming that on average each instance resulted in a division from one broader category to two, three, or four specific categories (Figure 2.S-2). Each instance of a possible transition from an aggregated group to a species level designation division would have to result in at least three or four additional specific taxonomic divisions to affect the overall trend (Figure 2.S-2).

We note that this method does not account for instances where a country started reporting a fishery at a species level designation and continued to report that species in a group level designation. However, we see no method of discerning these instances on a global scale.

2.3.3 Taxonomic Grouping

Globally, over 1200 taxonomic groups and species are reported caught in invertebrate or finfish fisheries, however, only the top species (based on cumulative catch since

1950) are recorded individually by the Sea Around Us Project with the remaining aggregated into groups such as "crustaceans" and "mollusks" (http://seaaroundus.org/doc/saup_manual.htm#8.6). Further, the Sea Around Us Project has aimed to disaggregate catch reported in aggregated taxonomic groups, where possible, based primarily on taxonomic catch distribution in surrounding areas and known species' distributions, limiting the candidate taxa to those reported by the same country in other years or by countries in the same LME (http://seaaroundus.org/doc/saup_manual.htm#8.4.5).

Thus, we obtained catch data for a total of 302 "taxa" (including 213 species). For our analyses, we looked at the number of taxa (species or species groups) fished over time (Figure 2.1C), and catches for each of four aggregated taxonomic groups (crustaceans, bivalves, echinoderms, cephalopods), and 12 species groups (bivalves, crabs, cuttlefishes, gastropods, krill, lobsters, octopus, sea cucumbers, sea stars, shrimps and prawns, squids, and urchins) (Figure 2.2).

2.3.4 Increasing Number of Countries Fishing

We extracted the number of countries reporting invertebrate catch from 1950–2004 as an indicator of the number of countries participating in invertebrate fisheries. One problem is that in the Sea Around Us Project database the designation of countries can change over time. For example, Samoa became independent from New Zealand in 1962 and appears independently in the data set from 1978 onwards. The overall classification of countries is not static. Such changes in the number of countries reporting catches over time are reflected in the overall number of countries reporting any catch for both finfish and invertebrate species. We have included this trend as a reference line (Figure 2.1C, dashed red line).

Overall, the country designation variation was small compared to the much larger changes of increasing participation in invertebrate fisheries. Nonetheless, we took this overall reporting trend into account and scaled the number of countries reporting catch of different invertebrate taxonomic and species groups to the total number of countries fishing finfish or invertebrates in any given year (Figure 2.S-3).

2.3.5 Assessment of Fishery Status from Catch Trends

Although overall catch of invertebrate fisheries has been increasing, individual fisheries by taxa and country show a less optimistic picture (Figure 2.S-4 for example). Previous attempts have been made to categorize the status of fisheries using catch data (FAO 2009*a*; Froese and Kesner-Reyes 2002; Sumaila et al. 2007; Pauly 2007) as underdeveloped (prior to reaching 10% of maximum catch), expanding (prior to 50% of maximum catch), fully exploited (50% to 100% of maximum catch), over-exploited (descended to 10% to 50% of maximum catch), and collapsed or closed ($<$ 10% of maximum catch). However, these approaches (i) can incorrectly categorize a fishery as over-exploited or collapsed due to single or multiple years of anomalous high catch and (ii) require all non-declining fisheries to be categorized as fully-exploited by the end of the time series. Analysis of fishery status from catch trends will always remain an approximate science since catch can be affected by many variables other than stock status (Harley et al. 2001). However, since catch is the only consistent metric we have for the vast majority of invertebrate fisheries, we developed a modified method for defining fishery status (Figure 2.S-5) designed to take into account two shortcomings of the above technique.

(i) *An anomalous year of high reported catch could potentially induce false "collapses"* (Branch 2008). Given the variability in fisheries catches, even a stationary catch series will at some point exhibit a year of relatively high catch with subsequent years then categorized as over-exploited (or collapsed/closed). To reduce the effect of such anomalous high values, we filtered catch using a smoother that is robust to outliers — a loess smoother (Cleveland 1979; Cleveland and Devlin 1988; Cleveland et al. 1992) from the function *loess* in the R statistical package (R Development Core Team 2009). This smooths the catch series, thereby down-weighting the impact of any outlying values. Such an approach is conservative in that it will require more evidence than a single high catch value before categorizing a fishery as over-exploited. We demonstrate the conservativeness of our approach using simulated data (Section 2.3.6).

(ii) *Previous analyses categorized all fisheries that hadn't declined as fully developed by the end of the catch series.* This is likely untrue in the majority of cases, especially for newly emerging or expanding invertebrate fisheries that have not yet reached a peak and are still expanding. Therefore, if a catch series had not peaked within five years of its end, we categorized the fishery as expanding.

An important feature of our analysis was that we determined a fishery's current status based on only the data obtained up until that point. If alternatively we had used the entire catch series then we would have generated the false perception that more and more fisheries have become fully- or over-exploited in recent years. For example, what may have appeared to be a peak in catch after 10 years may not have appeared so if we had observed and smoothed the data over an additional 30 years (see Section 2.3.8). Essentially our approach enabled us to treat old and recent fisheries equally as they developed.

We note that our method necessitated a different definition of "fully exploited". Previously (Froese and Kesner-Reyes 2002; Pauly 2007; Sumaila et al. 2007; FAO 2009*a*), a retrospective approach was taken and considered a fishery fully exploited if the catch was anywhere above 50% of the maximum catch. With our dynamic approach, we defined fully exploited as anywhere after a peak in catch and before catch fell below 50% of that peak (Figure 2.S-5).

2.3.6 Verification of Fishery Status Estimation Using Simulated Data

Since a criticism of previous fishery status estimation approaches has been the incorrect finding of an increasing number of collapses due to data variability or anomalous years of catch (Branch 2008), we demonstrate the robustness of our method to assigning false collapses or declines using simulated data. Our simulated catch series (C_t) last 55 years (T). They start at zero tonnes in the first year and increase according to the first quarter of a sine wave before leveling off at a maximum catch value (C_m) randomly selected from a log-normal distribution. The period of the wave, i.e. the time to maximum development of the fishery (d_t), was randomly selected from a uniform distribution varying between zero and 30 years based on the approximate ranges observed in the Sea Around Us Project's catch data for invertebrate fisheries. We added varying levels of multiplicative log-normally distributed random noise (z_t) to the simulated catch trends (Fig. 2.S-6):

$$z_t = LogN(0, \sigma^2)$$

$$C_t = \begin{cases} \sin(\pi t/2d_t) \cdot C_m \cdot z_t & \text{if } t = 0 \ldots d_t \\ C_m \cdot z_t & \text{if } t = d_{t+1} \ldots T \end{cases}$$

We demonstrate our method applied to data with log standard deviation of 0.10, 0.25, and 0.50 (Figures 2.S-6 and 2.S-7). At each of these three levels of variation we ran our simulation 1000 times and found the false positive rate (categorizing a fishery as "over-exploited" or "collapsed" when it should be "expanding" or "fully exploited") low at 0%, 0%, and ~1% respectively. We note that the variation in this simulated data greatly exceeds the variation seen in the Sea Around Us Project catch database for invertebrates. Therefore, the false positive rate due to anomalous values in our simulated data should exceed that in the Sea Around Us Project's catch data.

2.3.7 Correlation of Distance from Hong Kong With Fishery Initiation Year

When a resource becomes locally depleted, fisheries often respond by expanding the fishing area. On a global scale, this could mean that if one country has depleted its resource, other countries may start fishing it. Over time, the resource is fished further and further away from its original country or countries. Such spatial expansion and depletion has been suggested for global sea urchin fisheries (Berkes et al. 2006). We were interested in whether other invertebrate fisheries followed this trend. Few species, however, have a single strong market, making such detection difficult. We chose to investigate sea cucumbers because they have one strong market in Asia. Additionally we investigated squids, which have three main markets (Sonu 1989; FAO 2009*b*), but we were unable to locate historical import statistics for squid fisheries of sufficient length for all major importing nations.

For sea cucumbers, the majority of catch (64% of the cumulative import volume since 1950, see Table 2.S-1) is imported by Hong Kong where it is processed before most of it is then directed to China (Jaquemet and Conand 1999; Toral-Granda et al. 2008). The vast majority of the remaining import volume is imported by nearby Asian countries (Table 2.S-1). We reasoned that great circle distance could be used as a proxy for the spatial distance, and therefore cost, between the exporting and importing nations.

For each country, we determined the great circle distance between its city with the largest population (as a proxy for the city with the largest cargo airport) and the main Hong Kong freight operator, Hong Kong Air Cargo Terminals, at Hong Kong International Airport (Table 2.S-2), which handles over 70% of Hong Kong's air cargo (Hong Kong General Chamber of Commerce 2009). City population data (as of January 2006) and latitude and longitude were obtained from the dataset *world.cities*, which is part of the R (R Development Core Team 2009) package *maps* (Becker et al. 2009). Although the largest cargo airport may not always be found in the largest city by population, most countries are small enough geographically (compared to their distance from Hong Kong) to not affect our results. In the case of the United States and Canada, however, east and west coast regions started fishing at different times, and, due to the width of the continent, are of substantially differing distances from Hong Kong. Here we used the coordinates of the largest city (by population) in each Canadian region (west and east coast) or US state as the assumed location of the largest air cargo airport. We natural log transformed the distance data for both ease of visual interpretation and normality of the linear regression residuals.

To determine a starting year for each fishery (Table 2.S-2) we calculated the year at which catch (smoothed via a loess curve as outlined earlier) passed 10% of its first peak in catch (see proceeding Section 2.3.8). For the east and west coast Canadian fisheries, catch trends and 10% starting years were calculated based on governmental reports (DFO 1996; 2002; Hand et al. 2008; Rowe et al. 2009). For the United States, where separate catch trends were unavailable, we used the reported years of directed fishery initiation from the literature (Bruckner 2005; Therkildsen and Petersen 2006).

2.3.8 Analysis of Fishery Development Time

We were interested in whether there was evidence that newer fisheries were developing more rapidly than in the past. We assessed this by checking for a relationship between when invertebrate fisheries began and the time when they achieved their first peak in catch ("initial peak catch").

Here, a fishery was defined as one of the 10 larger taxonomic groupings (Figure 2.3C) as reported by an individual country. We excluded sea stars and krill due to the limited number of countries with substantial fisheries. To focus on substantial fisheries, we discarded all fisheries that didn't surpass 1000 t/year. We made an exception for the lower volume sea urchin and sea cucumber fisheries for which we took a minimum catch of 250 t. Our overall conclusions were invariant to choices of cutoffs from 500–2000 t (for the higher volume fisheries).

Catch trajectories can have multiple smaller local peaks together with an overall peak. For example, Figure 2.S-4 shows world bivalve fisheries by country. If we naively calculated the peak catch from the entire available catch trajectory we would be more likely to be measuring local peaks (rather than overall peaks) with fisheries that started more recently. This alone would falsely generate the trend for which we were testing. To avoid this time based bias we calculated the time it took for each fishery to develop to the first peak in catch.

For each year, a loess curve was fit to the data (as outlined earlier). A fishery was only evaluated if there were at least five years of data to ensure there would be enough data to conclude a peak had occurred. Fisheries with less than five years of data were considered censored.

For each year, the smoothed catch trajectory was built and catch was considered to have reached initial peak catch if (Figure 2.S-8):

1. a maximum in catch occurred and was not within three years of the end of the catch series at that step (so we had enough subsequent data to ensure a peak),

2. a maximum in catch was at least half of our cutoff for considering the fishery

— 500 t for most taxa and 125 t for sea cucumbers and sea urchins (to avoid small peaks during the variable catch portion at the start of the fishery), and

3. a maximum in catch was at least 10% greater than the catch at the end of the catch series at that step (to ensure a peak and not a stationary catch series).

If even one of these criteria was not met, then our knowledge of peak catch for that fishery was considered censored as of that year.

We considered the year in which smoothed catch surpassed 10% of the smoothed peak catch as the starting year. This approximates when the fishery became a substantial directed fishery. If a fishery was censored then we took 10% of the maximum observed smoothed catch as the initiation year. We removed all fisheries that began at greater than 10% of the maximum catch (i.e. fisheries that began prior to 1950). This simplified our analysis and allowed us to make inferences for fisheries that began between 1950 and 2000.

Central to this analysis, we had to deal with the censored fisheries that had yet to achieve peak catch. The possible range of censored fishery time to peak catch values increases over time — it could be anywhere in a missing triangle above the known data (Figure 2.S-9).

To account for these censored fisheries we assumed the null hypothesis that there had been no change in the distribution of times to peak for recent fisheries compared to fisheries that began between 1950–1970 (Figure 2.S-9). For fisheries in which there was no precedence (fisheries that had lasted longer than any other fishery in that taxa and still had not peaked), we assigned the maximum observed time for that taxa (Figure 2.S-10). We chose this approach to be most conservative. If we had assigned the maximum length for which we had observed each fishery as the time to peak we would have had more slower developing older fisheries. This would have created a linear downward trend in time to peak — the trend we were testing for. We proceeded to determine if we could still detect a pattern in the correlation coefficients using linear regression despite assigning simulated values to the censored fisheries (Figure 2.S-10).

We repeated our correlation analysis 1000 times, each time resampling the censored fisheries. This approach generates two kinds of uncertainty in our correlation estimates: uncertainty due to the resampling of censored values ("missingness") and uncertainty on each individual correlation coefficient. For each taxa, we derived the combined standard error by taking the median of the individual standard errors. We show the median correlation coefficients and 95% confidence intervals (Figure 2.3C). We combined the median correlation coefficients using inverse-variance weighted meta-analysis (Cooper and Hedges 1994). We estimated a change in time to peak between 1960 and 1990 by repeating our analysis with slope estimates (instead of correlation coefficients) and using the meta-analytic slope estimate to predict on the year scale. The approximate range of possible time to peak values was based on a 95% confidence interval.

Our overall results were robust to both our choice of peak catch algorithm and smoothing function. We tested our analysis with loess functions with smoothing spans ranging from 0.25 to 0.9 and with running medians of length three through nine. Finally, the overall trend remained when we tested our analysis substituting robust regression (iterated re-weighted least squares using MM-estimation (Huber 1981; Venables and Ripley 2002)) for least squares regression.

2.3.9 Potential Habitat Impacts

To assess the potential habitat effects of different invertebrate fisheries, we calculated the total invertebrate catch and the number of taxa fished by different gear types

(Figures 4A, B). The Sea Around Us Project derived gear associations for taxonomic groups primarily from books, journals, and Internet sources (Watson et al. 2006). Where unavailable, gear associations were interpolated based on the type of organism, country fished, and FAO area where the gear was used (Watson et al. 2006).

There were 19 types of fishing gear recorded for invertebrates, which we grouped into six broader groups based on their potential habitat impact (Table 2.S-3). Hand dredges or rakes can have short term effects (up to a year) on marine habitat and its associated community but these effects are unlikely to remain on longer time scales unless long lived species are present (Kaiser et al. 2001; MacKenzie and Pikanowski 2004). Lines and hooks represent a substantive bycatch concern for threatened sea turtle (Lewison et al. 2004; Lewison and Crowder 2007) and seabird populations (Lewison and Crowder 2003) among other taxa. Diving and grasping likely has the least impact on habitat and bycatch but is used in a small proportion of the fisheries by taxa and especially by volume (Figures 4A, B). Traps and pots are unlikely to have significant marine habitat impacts (Eno et al. 2001) although present an issue of marine mammal entanglement (Johnson et al. 2005). Nets and midwater trawls, while avoiding the benthic habitat damage of benthic trawling and dredging have substantial bycatch issues with taxa such as cetaceans (Fertl and Leatherwood 1997), sea turtles (Crowder et al. 1994), and sharks (Stevens et al. 2000). Benthic trawling and dredging, which combined comprised 53% of invertebrate catch by volume and 71% of the species or species groups fished, can have great impact on benthic habitat and communities (see Section 2.2 Results and Discussion) (Hiddink et al. 2006; Tillin et al. 2006).

2.3.10 Functional Group Analysis

To evaluate the potential food-web and ecosystem impacts of different invertebrate fisheries, we assigned functional groups to larger taxonomic groupings (Figure 2.4C). Functional groups were assigned as primary or secondary roles within that functional group according to the primary literature and reference books (Table 2.S-4). Trophic levels were obtained from the Sea Around Us Project.

In order to quantify the ecosystem effect, we extracted the overall removal (catch) of each primary functional group. Based on Figure 2.4C, we amassed the total catch per functional group averaged over 2000–2004 (the five most recent years available) (Figure 2.4D). This does not include renewal of resources via recruitment and re-growth.

2.3.11 Estimation of Bivalve Filtering Capacity

We estimated the consequence of removing filter feeding bivalves from the ocean, in terms of their capacity to filter water, using filtration rates reported in the literature. Newell (1988) estimated the filtering capacity of American oysters (*Crassostrea virginica*) in Chesapeake Bay (US) to be 5 $L \cdot g^{-1} \cdot h^{-1}$. We applied this value to the mean global catch of bivalves for the last five years of our data (2000–2004, 2.72 million t) to estimate the removal of filtering capacity per year. We converted wet weight landings to shell-free dry weight by the median value reported in the literature for all bivalves (8.6% of wet weight) as reported by Ricciardi and Bourget (1998). We converted these values into Olympic sized swimming pools for comparison. We estimated the volume of a pool as $2.5 \cdot 10^6$L: pool volume $= 50m \cdot 25m \cdot 2m$.

Newell's estimate of filtration capacity (Newell 1988) was made for one bivalve species in one geographic region. Therefore, we checked our results using filtration rates compiled by Riisgard (2001), which were obtained under ideal laboratory conditions and should typically represent similar values to what would be observed in nature across a range of bivalve species (Riisgard 2001). We used the median filtration rate (F) reported by Riisgard: $F = 6.47W^{0.72}$, where W is the shell-free dry weight. To simplify the analysis, we assumed an individual bivalve to be on average 1 g shell-free dry weight or $\sim$11.6 g wet weight (Ricciardi and Bourget 1998). Under these assumptions, we calculated the loss of filtration capacity to be $\sim$14.5 million pools per day, a similar result to our estimate using Newell's approximation. We report the more conservative estimate in Section 2.2 Results and Discussion.

2.4 Supporting Tables

Table 2.S-1: Percentage of cumulative sea cucumber catch volume imported by nation from 1950–2004. Only nations with greater than 1% of cumulative import volume are shown. Data from (FAO 2007).

Country	Percentage imported
Hong Kong	63.5
Taiwan	11.9
Singapore	7.9
Malaysia	7.2
Republic of Korea	4.4
China	4.1

Table 2.S-2: Distance and starting year of sea cucumber fisheries by country. Listed are each country's largest city (by population) with an international airport, its location, its distance from Hong Kong, the starting year of the sea cucumber fishery, and a verification reference.

Country	Largest city	Latitude (°)	Longitude (°)	Distance (1000 km)	Start (year)	Reference
China/Hong Kong	HK Int. Airport	22.34	114.01	0	NA	NA
Philippines	Manila	14.62	120.97	0.87	1961	Schoppe 2000, Gamboa et al. 2004
Indonesia	Jakarta	-6.18	106.83	1.34	1982	Tuwo 2004
Malaysia	Kuala Lumpur	3.16	101.71	1.50	1963	Baine and Sze 1999
Korea South	Soul	37.56	126.99	1.67	1950	Choo 2008*a*
Japan	Tokyo	35.67	139.77	2.99	1950	Akamine 2004
Sri Lanka	Colombo	6.93	79.85	3.77	1976	Kumara et al. 2005
Papua New Guinea	Port Moresby	-9.48	147.18	4.25	1986	Kinch et al. 2008*a*
Maldives	Male	4.17	73.50	4.45	1984	Joseph 2005
Solomon Islands	Honiara	-9.43	159.91	5.60	1984	Nash and Ramofafia 2006
New Caledonia	Noumea	-22.27	166.44	6.71	1977	Conand and Byrne 1993
Madagascar	Antananarivo	-18.89	47.51	6.92	1964	Rasolofonirina et al. 2004
Fiji	Suva	-18.13	178.43	7.84	1970	Ferdouse 2004, Uthicke and Conand 2005
Tanzania	Dar es Salaam	-6.82	39.28	8.05	1963	Jiddawi and Ohman 2002 Mmbaga and Mgaya 2004
Egypt	Cairo	30.06	31.25	9.19	2002	Lawrence et al. 2004 Ahmed and Lawrence 2007
US - Alaska	Anchorage	61.18	-149.19	11.28	1981	Bruckner 2005, Hamel and Mercier 2008
Canada West	Vancouver	49.28	-123.13	13.86	1985	Hamel and Mercier 2008, Hand et al. 2008
US - Washington State	Seattle	47.62	-122.35	13.93	1971	Bruckner 2005, Hamel and Mercier 2008
US - California	Los Angeles	34.11	-118.41	14.24	1978	Bruckner 2005, Hamel and Mercier 2008
Mexico	Mexico City	19.43	-99.14	16.35	1998	Ibarra and Soberón 2002, Toral-Granda 2008*a*
Chile	Santiago	-33.46	-70.64	17.77	1992	Toral-Granda 2008*a*
Canada East	Halifax	44.67	-63.61	18.95	1999	Therkildsen and Petersen 2006 Hamel and Mercier 2008, Rowe et al. 2009
US - Maine	Portland	43.66	-70.28	19.04	1993	Bruckner 2005, Hamel and Mercier 2008

Table 2.S-3: Major gear groupings of gear categories from the Sea Around Us Project catch database.

Major gear grouping	Minor gear categories
Hand dredges and rakes	hand dredges
	raking devices
Lines and hooks	lines
	squid hooks
Diving and grasping	by diving
	grasping with hand
	tongs
	without gear
Traps and pots	box-like traps
	traps
	pots
Nets and midwater trawls	driftnets
	gillnets
	ring nets
	bagnets
	purse seines
	mid-water trawls
Benthic trawling and dredging	bottom trawls
	dredges

Table 2.S-4: Classification of invertebrate taxonomic groups into primary and secondary functional groups. Taxa are ordered approximately by decreasing trophic level.

Taxa	Primary	Secondary	Reference
Octopus	Prey, Predators		Boyle and Rodhouse 2005, Hickman et al. 2006
Cuttlefishes	Prey, Predators		Boyle and Rodhouse 2005, Hickman et al. 2006
Squids	Prey, Predators		Boyle and Rodhouse 2005, Hickman et al. 2006
Sea stars	Prey, Predators	Scavengers	Hickman et al. 2006
Shrimps and prawn	Prey, Predators	Herbivores, Filter feeders, Scavengers/Detritivores	Ruppert et al. 2004, Hickman et al. 2006
Crabs	Prey, Scavengers, Herbivores, Predators		Pearse et al. 1987
Lobsters	Prey, Predators, Scavengers		Pearse et al. 1987
Krill	Prey, Filter feeders		Ruppert et al. 2004
Urchins	Prey, Herbivores	Predators	Ruppert et al. 2004
Gastropods	Prey, Herbivores	Scavengers, Predators	Hickman et al. 2006
Sea cucumbers	Prey, Detritivores, Filter feeders		Ruppert et al. 2004, Hickman et al. 2006
Bivalves	Prey, Filter feeders, Habitat	Detritivores	Hickman et al. 2006

2.5 Supporting Figures

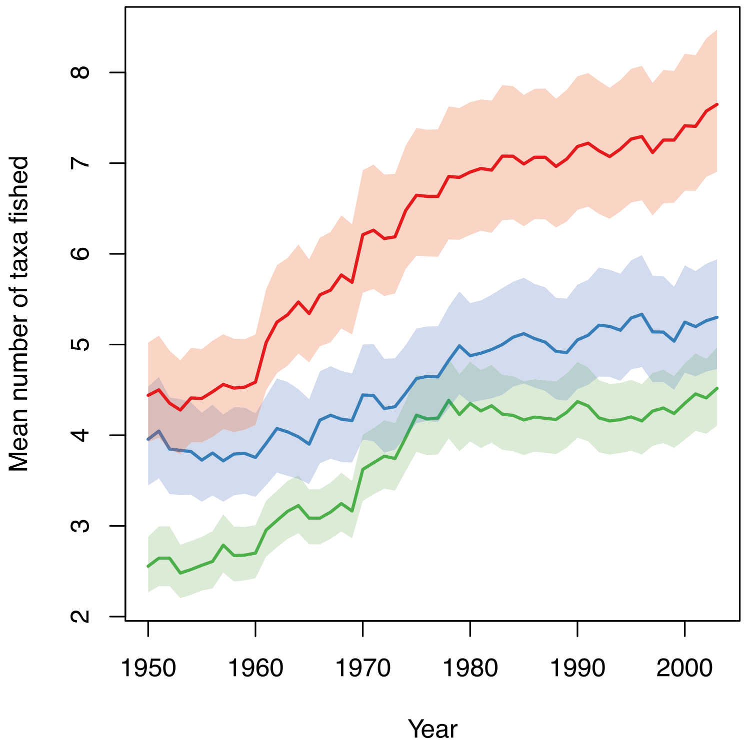

Figure 2.S-1: Increasing reporting of invertebrate taxa fished divided into species level (blue), larger grouping level (green), and combined (red). Dark lines represent mean and shaded region represents standard error assuming a negative binomial distribution of the data.

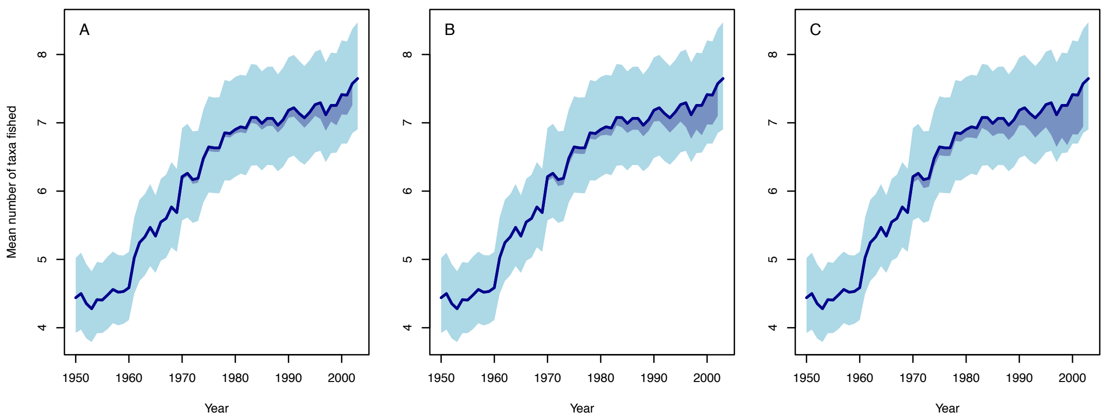

Figure 2.S-2: Estimated mean number of invertebrate taxa fished per country assuming different penalties for increased taxonomic precision. Dark blue line indicates estimate, light blue shaded region indicates standard error assuming a negative binomial distribution of the data, and the dark blue shaded regions indicate an estimated trend adjusted for increasing taxonomic precision in reporting. (A) Assumes each loss of an aggregated group results in two new species level designations, (B) assumes three, and (C) assumes four.

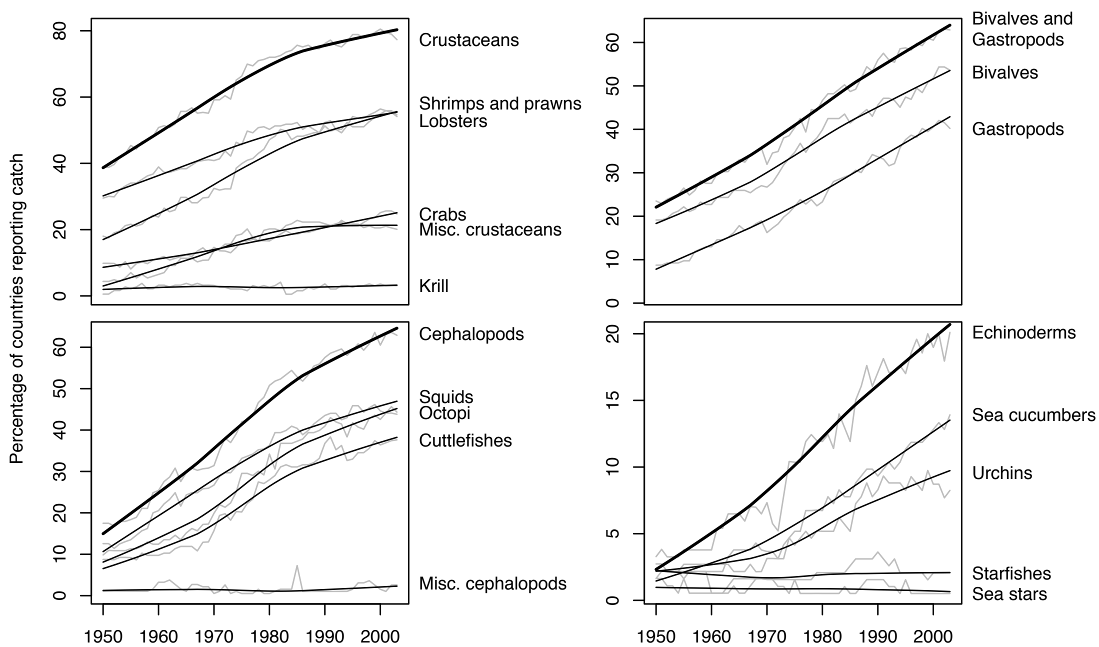

Figure 2.S-3: Percentage of all countries reporting catch of various invertebrate taxonomic and species groups. Dark lines represent smooth estimates obtained from generalized additive models. Light lines represent unfiltered data.

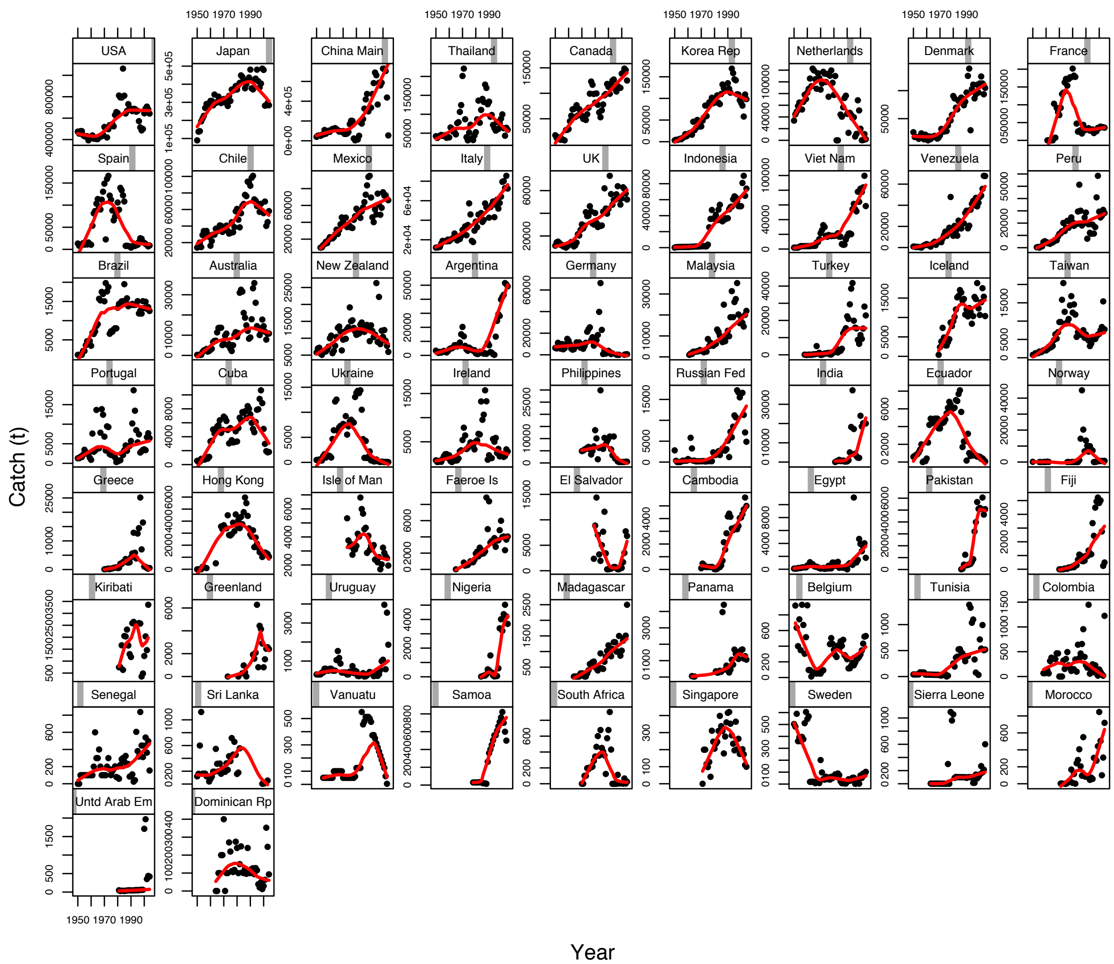

Figure 2.S-4: An example invertebrate catch series arranged by country for one invertebrate taxa: bivalves. Red lines indicate loess smoothed fits. Plots are ordered by cumulative catch since 1950. Vertical grey bars in title bars indicate log transformed cumulative catch, with bars near the right indicating the greatest cumulative catch and bars near the left indicating the least cumulative catch.

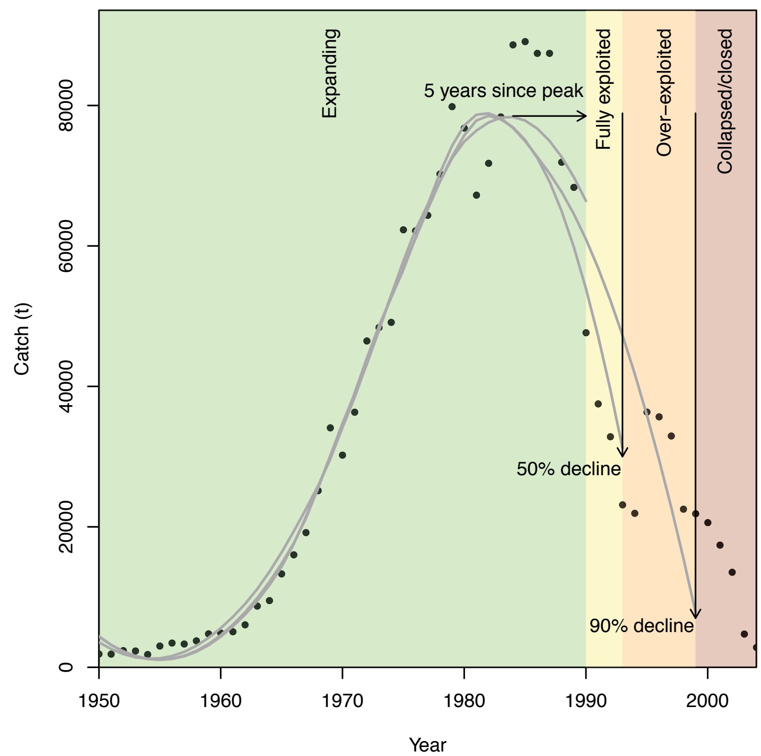

Figure 2.S-5: Illustration of our algorithm for dynamically assigning fishery status. Dots represent raw catch values, grey lines represent three of the loess functions fit to the data. Loess functions were built dynamically for each year but for clarity we show only the three functions which resulted in a change in status. By default a fishery was categorized as "expanding" until one of the following criteria was met: when there was at least five years since a maximum in the smoothed catch the fishery was classified as "fully exploited", when smoothed catch fell below 50% of maximum smoothed catch the fishery was classified as "over-exploited", and when smoothed catch fell below 90% of maximum catch the fishery was classified as "collapsed or closed".

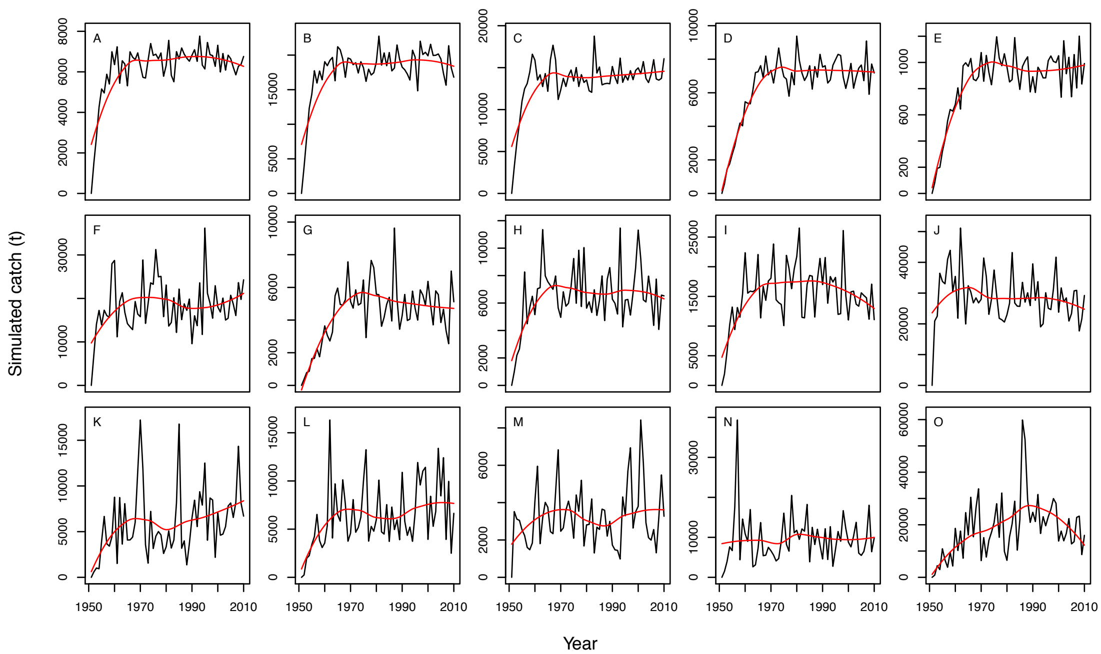

Figure 2.S-6: Example simulated increasing and then stationary catch series with multiplicative log-normal error about a random mean: log standard deviation of error of 0.10 (A-E), 0.25 (F-K), and 0.50 (K-O). Black lines indicates unfiltered catch. Red lines indicate loess smoothed fits.

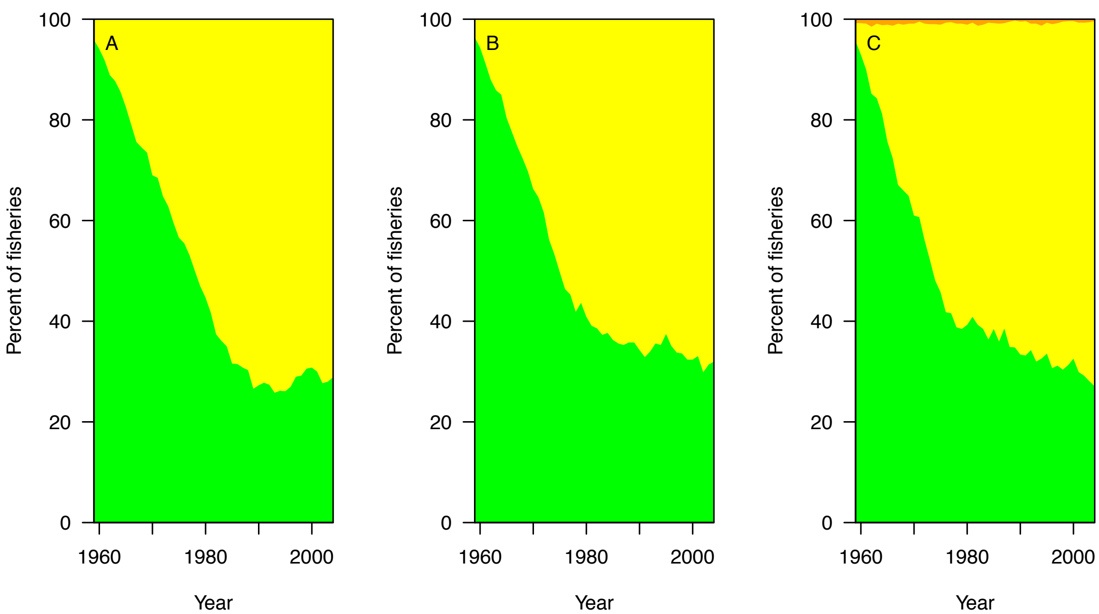

Figure 2.S-7: Predicted stock status (expanding = green, fully exploited = yellow, over-exploited or restrictively managed = orange) from simulated data showing the robustness of our method to variability in the data. The simulated data follow increasing and then stationary catch trends with log-normally distributed multiplicative error with a log standard deviation of 0.10 (A), 0.25 (B), and 0.50 (C).

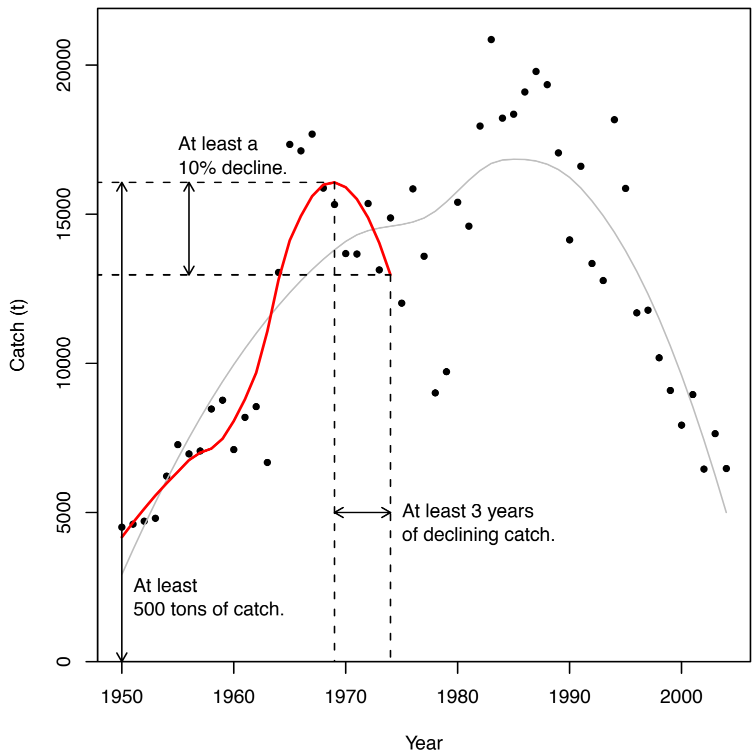

Figure 2.S-8: Illustration of our algorithm for assigning year of initial peak catch. Dots represent raw catch values, grey line represents loess function fit through the entire catch series, and red line indicates loess function fit through data up to the year of initial peak catch. A fishery was considered to have peaked if there was at least 500 tonnes of catch, at least a 10% decline from peak catch, and at least three years of data after the peak in catch. This algorithm was applied dynamically each year until the first instance of peak catch was observed.

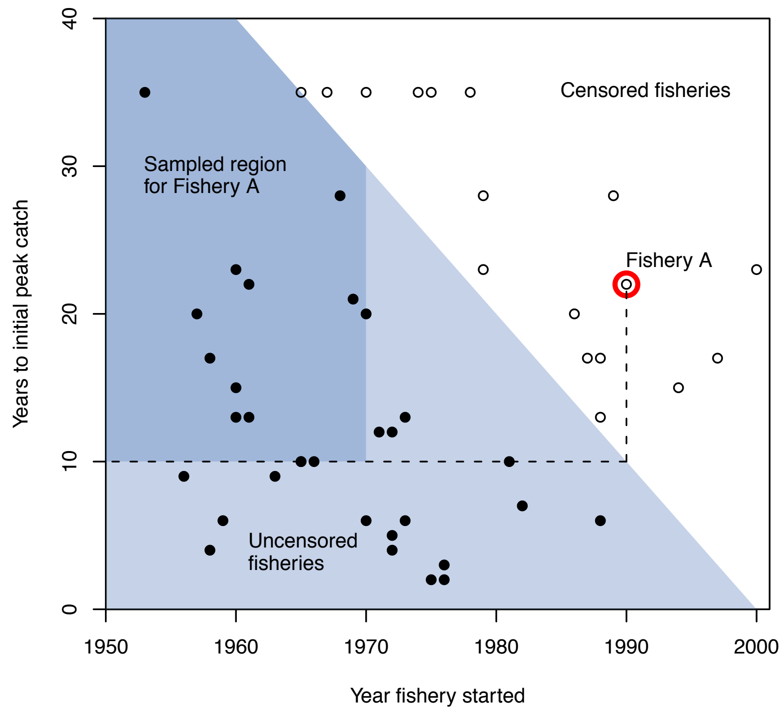

Figure 2.S-9: Illustration of sampling time to peak for one censored fishery (Fishery A, red circle). Fisheries for which time to peak could be calculated are shown with solid dots in the shaded blue triangle. Censored fisheries for which time to peak was sampled are shown with open dots. Vertical dashed line indicates known year in which Fishery A surpassed 10% of its maximum observed catch. Fishery A could therefore have been assigned a time to peak from any value above 10 years, as indicated by horizontal dashed line, and before 1970 (dark blue shaded region). This sampling was repeated 1000 times.

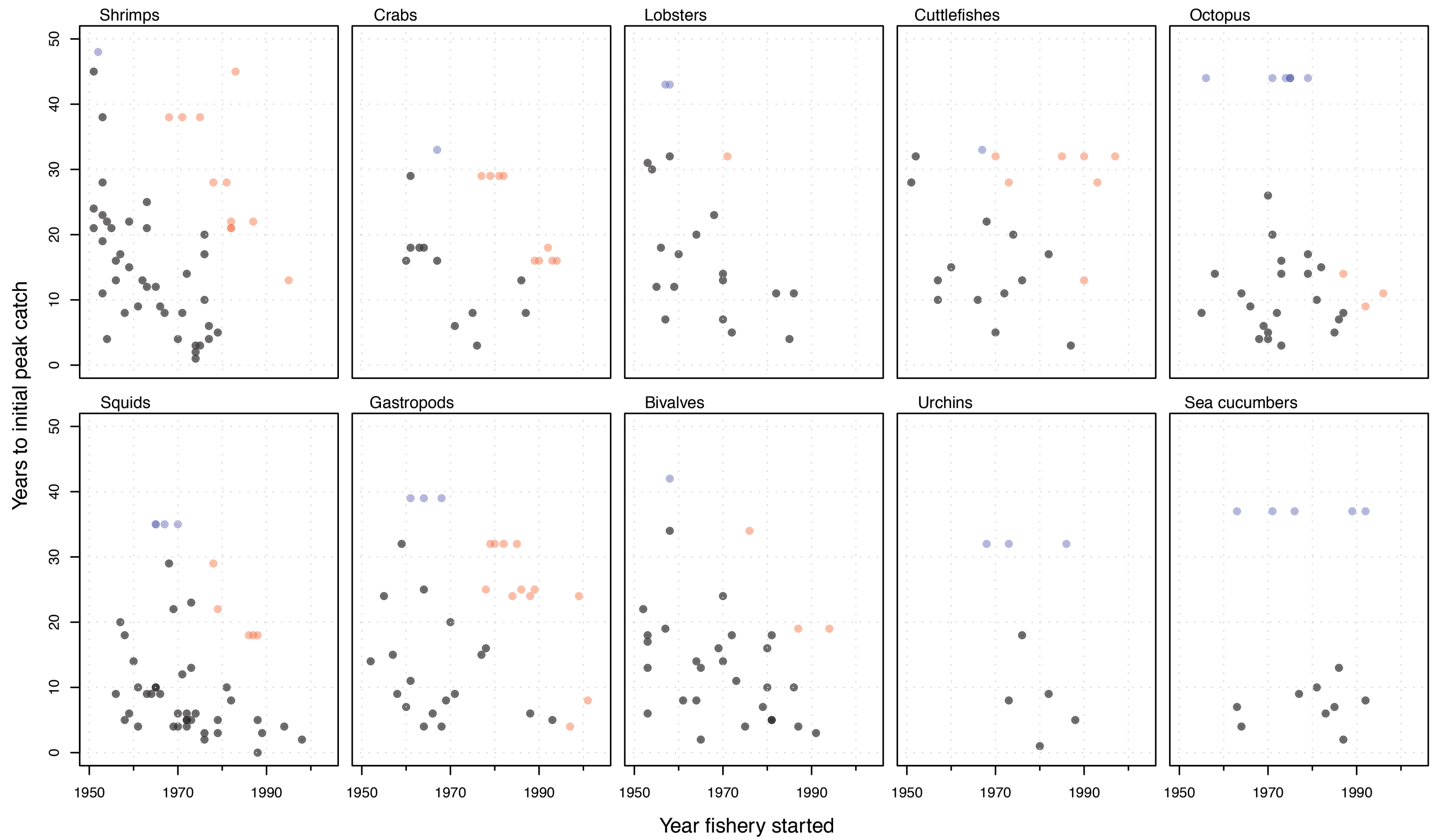

Figure 2.S-10: An example of time to peak catch vs. year of fishery initiation by taxonomic grouping for one random sampling of censored fisheries (red dots). Black dots represent known data points. In our analysis, the red dots were resampled 1000 times from possible time to peak values. Blue dots represent fisheries for which there were no fisheries to sample from. These were set to the maximum observed number of years for the earliest fishery affected (the left most blue dot).

Chapter 3

Serial Exploitation of Global Sea Cucumber Fisheries

3.1 Introduction

Over the past century we have witnessed both the decline of many traditional finfish fisheries as well as the expansion of existing and establishment of new invertebrate fisheries (FAO 2009*a*). The increase in invertebrate fisheries has been attributed to increasing demand (e.g. Clarke 2004; Berkes et al. 2006), the need for new resources to harvest (e.g. Pauly et al. 2002; Anderson et al. 2008) and the increasing abundance of invertebrates due to their release from predation (e.g. Worm and Myers 2003; Heath 2005; Savenkoff et al. 2007; Baum and Worm 2009).

Despite the overall global increase in invertebrate catches and target species (Chapter 2), many individual fisheries have shown severe depletion or even collapse. For example, sea urchin fisheries have followed a boom-and-bust cycle around the world (Andrew et al. 2002; Berkes et al. 2006), oysters have been serially depleted along the coasts of the United States and eastern Australia (Kirby 2004), and shrimp and crab populations have been serially depleted in the Greater Gulf of Alaska (Orensanz et al. 1998).

One invertebrate fishery that has shown one of the most remarkable worldwide expansions in terms of catch and value over the past 2–3 decades is the fishery for sea cucumbers (e.g. Conand and Byrne 1993; Conand 2004; FAO 2008*b*). Sea cucumbers (class Holothuroidea) are elongated tubular or flattened soft-bodied marine benthic invertebrates, typically with leathery skin, ranging in size from a few millimetres to a meter (Bell 1892; Backhuys 1977; Lawrence 1987). They encompass ∼14000 known species (Pawson 2007) and occur in most benthic marine habitats worldwide, in both temperate and tropical oceans, and from the intertidal zone to the deep sea (Uthicke et al. 2004; Hickman et al. 2006).

Sea cucumbers have been fished for thousands of years (Conand and Byrne 1993) but their fisheries have expanded substantially in recent decades. Since at least the 16th century, they have been fished and traded in Asian and Indo-Pacific regions (Akamine 2004), driven primarily by Chinese demand (Akamine 2004; Clarke 2004). They are usually fished by hand, spear, hook, or net while wading or diving with snorkel or SCUBA gear. In some regions, and especially for less valuable species, they are also trawled (Aumeeruddy and Payet 2004; Kumara et al. 2005; Choo 2008*a*). They are consumed both dried (called trepang or bêche-de-mer) and in a wet form, with muscles cut in strips and boiled (Sloan 1984). In recent years, reports have documented both the rapid climb in value of traded sea cucumbers and the spread and increase of their fisheries around the world (e.g. FAO 2004; 2008*b*).

Sea cucumber populations are particularly vulnerable to overfishing for two primary reasons. First, the ease and effectiveness with which shallow water holothurians can be harvested makes them susceptible to overharvesting (Uthicke and Benzie 2000; Bruckner et al. 2003). As a result, overfishing has severely decreased the biomass of many sea cucumber populations (e.g. Skewes et al. 2000; Lawrence et al. 2004; Conand 2004). Second, their late age at maturity, slow growth, and low rates of recruitment make for slow population replenishment (Uthicke et al. 2004; Bruckner 2005). Moreover, at low population densities, their broadcast spawning may induce an Allee effect (Allee 1938; Courchamp et al. 1999), resulting in population collapse and inhibiting recovery (Uthicke and Benzie 2000; Bruckner 2005). Other broadcast spawning invertebrate populations that have been severely depleted, such as pearl oysters in the South Pacific, have not recovered 50–100 years later (Dalzell et al. 1996). Thus far, even with harvesting closures, sea cucumber stocks seem slow to recover (D'Silva 2001; Uthicke et al. 2004; Ahmed and Lawrence 2007); potentially on the order of decades (Uthicke et al. 2004).

The depletion of sea cucumber populations may entail a substantial loss in the ecosystem functions and services they provide in terms of their ecological roles in the ecosystem as well as their social and economic importance to people. Ecologically, holothurians form an important role as suspension feeders and detritivores. For example, in kelp forests (Velimirov et al. 1977; Harrold and Pearse 1989) and coral reefs (Birkeland 1989) they consume a combination of bacteria, diatoms, and detritus (Yingst 1976; Moriarty 1982; Massin 1982*a*). Their presence as filter feeders can be substantial. For example, two species of holothurians alone represent nearly half of the filter feeding biomass in South African kelp forests (Velimirov et al. 1977). They are also important prey in coral reef and temperate food webs (Birkeland et al. 1982; Birkeland 1989) both in shallow and deep water (Jones and Endean 1973; Massin 1982*b*), where they are consumed particularly by fishes, sea stars, and crustaceans (Francour 1997).

In addition to their role as prey and consumer, deposit feeding sea cucumbers change the size of ingested particles and turn over sediment via bioturbation, thereby altering the stratification and stability of muddy and sandy bottoms (Massin 1982*b*), often in a substantial manner. For example, on coral reefs, healthy sea cucumber populations could bioturbate the entire upper five mm of sediment once a year (4600 kg dry weight year^{-1} 1000 m^{-2}) significantly reducing the microalgal biomass in the sediment (Uthicke 1999) and playing a substantial role in the recycling of nutrients in oligotrophic environments where nutrients would otherwise remain trapped in the sediment (Uthicke 2001). Bruckner et al. (2003) noted that the extirpation of holothurians has resulted in the hardening of the sea floor, thereby eliminating potential habitat for other benthic organisms. Finally, suspension feeding sea cucumbers are important in regulating water quality by affecting the carbonate content, carbon dioxide cycle, and pH of the water (Massin 1982*b*).

Sea cucumber fisheries are of great social and economic importance to many coastal communities. For example, in the Maldives, sea cucumbers became the most highly valued fishery outside the tuna fishing season, representing 80% of the value of all non-fish marine products just a few years after starting (Joseph 2005). Sea cucumber fisheries form the only source of income for many coastal communities in the Solomon Islands (Nash and Ramofafia 2006) and are relied upon by 4000–5000 families in Sri Lanka (Dissanayake et al. 2010). Perhaps the most important economic aspect of sea cucumber fisheries is their decentralized nature. While their total global value is low compared to other higher volume fisheries (Ferdouse 2004) economic benefits are obtained immediately at a village level (Kinch et al. 2008*b*). In contrast, other high-value fisheries, such as tuna fisheries, have high initial costs and bring wealth to a more centralized group of people (Kinch et al. 2008*b*).

Despite their ecological and social importance, the evaluation of the global status of sea cucumber populations is difficult. There is generally a lack of abundance data; catch, import, and export statistics are often incomplete; and the complexities of their trade remain immense (see Baine 2004; FAO 2004; 2008*b*). Nonetheless, reports such as FAO (2004) and FAO (2008*b*), and the SPC Beche-de-mer Information Bulletin[1]

[1] An unrefereed academic journal: http://www.spc.int/coastfish/News/BDM/bdm.htm

have assimilated much of the available knowledge on the status and management of sea cucumber fisheries around the world. So far, there has been discussion of country specific sea cucumber fisheries (see Table 3.1) and insight into the dynamics of the global sea cucumber trade (e.g. Baine 2004; Clarke 2004; Conand 2004; Ferdouse 2004; Uthicke and Conand 2005; FAO 2008*b*). However, a quantitative analysis of the typical trajectory, drivers, and combined spatial and temporal dynamics of sea cucumber fisheries around the world has been lacking. Therefore, the aim of this paper is to extend the existing knowledge to gain a quantitative global perspective.

Using a global catch database and available regional fishery assessments, our objectives are to (1) quantitatively synthesize the current status and trends in sea cucumber fisheries worldwide, (2) analyze their underlying drivers, (3) test for patterns of serial exploitation, and (4) assess the state of management of these fisheries to determine where improvements can be made. Our overall goal is to provide a global synthesis of sea cucumber fisheries in order to better inform the development of global trade regulations and of local and regional management strategies that ensure a more long-term and sustainable harvesting of sea cucumbers worldwide.

3.2 Methods

3.2.1 Catch Data Sources

Abundance data for sea cucumber populations are largely unavailable (see FAO 2004; 2008*b*). Therefore, to form a globally consistent database for our analysis, we obtained catch data (reported landings by country) for sea cucumber fisheries from the Sea Around Us Project, based out of the Fisheries Centre at the University of British Columbia, Canada (Watson et al. 2005). These data span from 1950 to 2004 and are largely derived from the Food and Agriculture Organization's (FAO) catch database.

The Sea Around Us Project supplements these data with regional and reconstructed datasets where possible (Zeller and Pauly 2007).

Not all catches reported to the FAO are reliable (Clarke 2004; Watson et al. 2005). Therefore, we have compared these catch data against regional records wherever possible (Table 3.1). We aimed at getting the most reliable estimate for the characteristics of the catch trends we were interested in, including starting years and years of peak catch as well as general patterns of increase and decline in catches.

Since there are a number of distinct reasonably high volume fisheries for sea cucumbers throughout the United States and Canada, and these countries are large geographically, we separated the catch trends into regions. Canada reports sea cucumber catches to FAO as "benthic invertebrates" (Hamel and Mercier 2008). Therefore, catch data for British Columbia and the Atlantic provinces of Canada were extracted from Hamel and Mercier (2008) who obtained the data from regional governmental offices. For southeast Alaska, catch data were obtained from Clark et al. (2009), and for Maine from the State of Maine Department of Marine Resources.[2] Catch data for Washington and California were obtained from the Pacific Fisheries Information Network.[3] Data for Australia were extracted from Uthicke (2004) and were originally obtained from the Queensland Fisheries Service. They represent the gutted weight of *Holothuria nobilis* on the Great Barrier Reef throughout the recent revival of the fishery since the mid 1980s. Sea cucumbers were previously heavily fished in the region in the late 1800s and early 1900s (Uthicke 2004).

We made the following two alterations to the data: (1) To avoid long tails of initial minimal catch from driving the models, as it is likely that catch of this minimal volume was inconsistently reported across countries, we removed years at the

[2] http://www.maine.gov/dmr/commercialfishing/historicaldata.htm
[3] http://pacfin.psmfc.org/

Table 3.1: Countries and regions included in different analyses[a] and their sources.

Country	Sources	Traj[b]	Dist	Exp	Pop	Spat	Spp	Size	IUU	Lack reg
Australia	Uthicke and Benzie 2000; Uthicke 2004; Uthicke et al. 2004	×	×	NA	1	1	1	1	?	0
Canada - East	Hamel and Mercier 2008; Rowe et al. 2009	—	×	0	0	?	NA	?	?	0
Canada - West	Hand et al. 2008; Hamel and Mercier 2008	—	×	0	0	?	NA	1	?	0
Chile	Toral-Granda 2008*a*	×	×	?	?	?	?	?	?	1
Egypt	Lawrence et al. 2004; Ahmed and Lawrence 2007	×	×	1	1	1	1	1	1	0
Fiji	Ferdouse 2004; Uthicke and Conand 2005	×	×	1	1	?	1	?	1	0
Indonesia	Tuwo 2004; Choo 2008*a*	×	×	1	1	1	1	1	1	1
Japan	Akamine 2004	—	×	0	0	?	?	?	?	0
Madagascar	Rasolofonirina et al. 2004	×	×	1	1	1	1	1	1	0
Malaysia	Baine and Sze 1999; Choo 2004	×	×	1	1	1	1	1	1	1
Maldives	Joseph 2005	×	×	1	1	1	1	1	?	1
Mexico	Ibarra and Soberón 2002; Toral-Granda 2008*a*	×	×	1	1	?	NA	?	1	0
New Caledonia	Conand and Byrne 1993	×	×	1	1	1	1	?	?	1
Papua New Guinea	Kinch et al. 2008*a*	×	×	1	1	1	1	1	1	0
Philippines	Schoppe 2000; Gamboa et al. 2004; Choo 2008*b*	×	×	1	1	1	1	1	1	1
Republic of Korea	Choo 2008*a*	×	×	?	?	?	?	?	?	?
Solomon Islands	Nash and Ramofafia 2006	×	×	1	1	1	1	1	?	0
Sri Lanka	Kumara et al. 2005; Dissanayake et al. 2010	×	×	1	1	1	1	?	1	1
Tanzania	Jiddawi and Ohman 2002; Mmbaga and Mgaya 2004	×	×	1	1	1	1	1	1	1
US - Alaska	Hamel and Mercier 2008; Clark et al. 2009	—	×	0	0	?	NA	0	?	0
US - California	Schroeter et al. 2001; Hamel and Mercier 2008	×	×	?	1	?	?	?	?	0
US - Maine	Chenoweth and McGowan 1995; Hamel and Mercier 2008	—	×	?	?	?	NA	?	?	0
US - Washington State	Bruckner 2005; Hamel and Mercier 2008	×	×	0	1	?	NA	?	1	0
Cambodia and Vietnam	del Mar Otero-Villanueva and Ut 2007	—	—	1	1	1	1	?	?	1
China	Chen 2004; Choo 2008*a*	—	—	1	1	?	NA	?	?	0
Ecuador - Galápagos	Hearn et al. 2005; Toral-Granda 2008*b*	—	—	1	1	1	1	?	1	0
Ecuador - Mainland	Toral-Granda 2008*b*	—	—	1	1	?	NA	?	1	1
Kenya	Samyn 2000	—	—	1	1	1	1	?	?	1
Peru	Toral-Granda 2008*a*	—	—	?	1	?	1	?	1	1
Russia	Konstantinova 2004; Hamel and Mercier 2008	—	—	?	1	?	?	1	?	0
Saudi Arabia	Hasan 2008; 2009	—	—	1	1	?	1	?	1	0
Seychelles	Aumeeruddy and Conand 2008	—	—	1	1	1	1	?	1	0
Sultanate of Oman	Al-Rashdi and Claereboudt 2010	—	—	1	1	1	1	1	?	1
Thailand	Choo 2008*a*	—	—	1	1	1	1	?	1	0
Torres Strait Islands	D'Silva 2001	—	—	1	1	?	?	?	?	0
VietNam	del Mar Otero-Villanueva and Ut 2007; Choo 2008*a*	—	—	1	1	1	?	?	1	1
Yemen	Hasan 2009	—	—	1	1	?	1	?	1	?

[a] × = included, — = not included, 0 = absent, 1 = present, ? = unknown or not mentioned, NA = not applicable

[b] Traj = Trajectory and time to peak analyses, Dist = Distance from Asia analysis, Exp = Overexploited, Pop = Population decline, Spat = Spatial expansion, Spp = Species expansion, Size = Size depletion, IUU = Illegal, Unregulated and Unreported fishing, Lack reg = Lack regulations

beginning of the catch series in which catch was less than one tonne (this affected Indonesia, Fiji, Philippines, and Maldives). (2) We removed four years (1994–1997) of anomalously high catch from Madagascar which were three times greater than then next highest year of catch and did not match the trajectory reported by Rasolofonirina et al. (2004) who studied the fishery in detail. We also removed anomalously high catch records at the beginning of the catch series for Madagascar from 1964 to 1971; again, they did not follow the trajectory reported by Rasolofonirina et al. (2004).

There is discrepancy about which countries report sea cucumber catch as wet weight and which as dry weight (Ferdouse 2004; Choo 2008*a*). However, wet ungutted sea cucumbers weigh anywhere from 6–25 (Skewes et al. 2004) or 8–25 (Purcell et al. 2009) times more than dried sea cucumbers. This makes a direct comparison of catch weights difficult, and at this time, the problem remains intractable. Therefore, throughout our analyses we do not compare absolute volumes of catch.

Since many of the records in the catch database are erratically reported, of short duration, and low volume, we focused on the more substantial fisheries when investigating catch trends. We investigated fisheries that surpassed 250 t (wet or dry weight, since this was the only measure we had) for more than one year (to account for outlying years).

3.2.2 Typical Trajectory of Sea Cucumber Fisheries

Under ideal fisheries management, a fishery would develop as a gradual increase towards a plateau near maximum sustainable yield (MSY) (Hilborn and Sibert 1988). However, sea cucumber fisheries are often reported to follow boom-and-bust patterns (e.g. Bremner and Perez 2002; Baine 2004; Uthicke 2004). Therefore, we tested whether individual sea cucumber fisheries followed a similar trajectory of rapid increase, short peak, and subsequent decline. Further we tested whether this increase and decrease were symmetric about the peak. We note that declining catch trends in the investigated fisheries may reflect declines in abundance due to overexploitation (see Section 3.3.7 in the Results), or declines in catches due to restrictive management and changes in effort, or a combination of these.

To enable us to calculate a typical trajectory, we lagged the catch series so that each country's catch reached a maximum in the same year (relative year 0). In some fisheries this corresponded to a peak with a subsequent decline and in others a plateau. We obtained these peak years from loess smoothed curves of catch series (Cleveland 1979; Cleveland and Devlin 1988; Cleveland et al. 1992; R Development Core Team 2009) (smoothing span = 75% of the data) so that our estimates were robust to outliers.

For this typical trajectory analysis, we focused on fisheries that had peaked or reached a plateau and excluded fisheries that were still expanding since we did not know when they would peak or plateau in catch. We did not include Japan since Japan has a long established fishery that started long before the 1950s and has declined in catch in recent years solely due to management decisions (Akamine 2004).

Absolute catch was not comparable between all investigated regions for several reasons: (1) the units of catch are not comparable (some wet, some dry weight), (2) the harvestable area is not comparable, and (3) the ecological productivity/virgin biomass is not comparable. We therefore investigated the relative trajectory of sea cucumber fisheries irrespective of volume. To do this, we scaled the catch for each country by subtracting the mean and dividing by the standard deviation (Figure 3.1). However, when showing our results by country we transformed our results back to the original scale of tonnes.

We used an additive model (Hastie and Tibshirani 1990; Wood 2004; 2006) to determine the typical trajectory of sea cucumber fisheries. Additive models provide a framework that allows both parametric and non-parametric terms to be included in a model, allowing for fits to non-standard relationships. In our additive models, a smooth function f was fit to the years Y_i relative to the years of peak catch Y_{peak} determined by the loess smooth. Additionally, we allowed the scaled catch from each country j to vary as a parametric factor β. This was necessary in addition to scaling the data since the range of relative year values about the peak in catch varied between countries (Figure 3.1). We fit three models: the full model,

$$\mathbb{E}[Catch_i] = \beta_j + f(Y_i - Y_{peak}) + \epsilon_i,\ \epsilon \sim Gaussian \tag{3.1}$$

the asymmetric model,

$$\mathbb{E}[Catch_i] = \beta_j + f(|Y_i - Y_{peak}|) + f_{after\ peak}(|Y_i - Y_{peak}|) + \epsilon_i,\ \epsilon \sim Gaussian \tag{3.2}$$

and the symmetric model,

$$\mathbb{E}[Catch_i] = \beta_j + f(|Y_i - Y_{peak}|) + \epsilon_i,\ \epsilon \sim Gaussian \tag{3.3}$$

where ϵ represents the normally distributed error. Since fisheries catch tends to be log-normally distributed (e.g. Haddon 2001), we fit alternate versions of these models on the multiplicative scale. For example:

$$\mathbb{E}[Catch_i] = e^{\beta_j + f(Y_i - Y_{peak}) + \epsilon_i},\ \epsilon \sim Gaussian \tag{3.4}$$

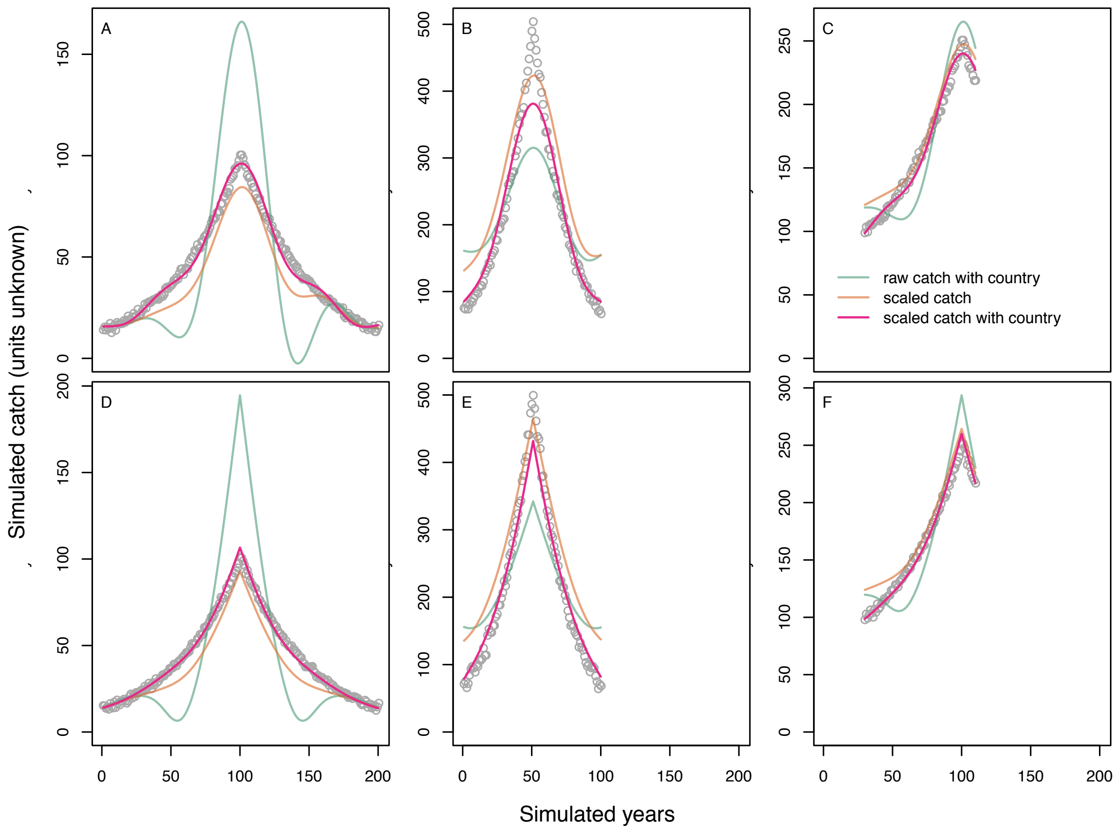

Figure 3.1: Simulated catch series to test the effects of scaling catch (subtracting the mean and dividing by the standard deviation) and including a parametric term in the model for country. Shown for catch series of varying volume (B, C, E, F), slope (B, E), and duration of recording (C, F) compared to A and D. The dots represent simulated catch that expands and declines exponentially and has minimal variability for clarity. Each panel represents a different country. Top panels (A–C) represent full additive models (Equation 3.1) and lower panels (D–F) represent symmetric additive models (Equation 3.3). Green lines represent unscaled catch with a parametric term for country; yellow lines, scaled catch without a parametric term for country; and pink lines, scaled catch with a parametric term for country (as was used in this study). Importantly, when comparing the two scaled catch versions (yellow and pink), the range of year values about the peak differs between panels.

where the errors ϵ_i were normally distributed when on the exponential scale. We compared the fit of these models to models 3.1, 3.2, and 3.3 shown above. We show Bayesian credible intervals (specifically two standard errors above and below the estimate) to approximate the interval for which there is a 95% probability that the estimated fit lies within (Wood 2006).

We verified the trends observed in the additive model using a regression tree. Regression trees provide an established method of partitioning data that requires few assumptions about the distribution of the data (Breiman et al. 1984; Clark and Pregibon 1992). We used the *rpart* package (Therneau et al. 2009) from the R statistical package (R Development Core Team 2009). Clark and Pregibon (1992) and Venables and Ripley (2002) describe these functions in detail. Since we were only interested in the shape of the trajectory and did not require the country parameters in addition to scaling to improve the model fit, we show a regression tree predicting scaled catch based only the relative year.

We pruned the tree via cost-complexity pruning (Breiman et al. 1984) using 10-fold cross-validation to balance the complexity of the tree against predictive accuracy. We chose the smallest tree with a cross-validation error rate within one standard error of the minimum error rate (Breiman et al. 1984).

3.2.3 Drivers of Sea Cucumber Fisheries

The majority of global sea cucumber catch is imported to Hong Kong where a majority is then re-exported to mainland China (Clarke 2004; Ferdouse 2004). We first verified this trend by examining the sea cucumber export and import values from the FAO Fisheries Commodities Production and Trade statistics[4] using a bump chart (Tufte 1990).

[4] http://www.fao.org/fishery/statistics/software/fishstat/en

Since the majority of sea cucumber is subsequently exported to China, and since China has a substantially larger economy than Hong Kong, we hypothesized that the rate of economic growth in China might drive global sea cucumber catch. To assess a trend in the Chinese economy, Chinese GDP data were obtained from the International Financial Statistics of the International Monetary Fund's World Bank World Development Indicators.[5] These data had been converted to a 2005 base year in US dollars to account for the change in the value of currency over time.

We tested the strength of the relationship between global sea cucumber catch and the rate of change of the log of Chinese GDP using ordinary least squares and robust regression (iterated re-weighted least squares with MM-estimation, herein referred to as "robust regression") (Huber 1981; Venables and Ripley 2002). We tested the correlation at lags of 0–6 years, with GDP leading catch. The log transformation of the GDP data was used to obtain normality of the regression residuals. Normality was not improved by log transforming the catch data; it was therefore left untransformed for clarity. Here and throughout this chapter, we estimated confidence intervals on our robust regression correlation coefficients using the adjusted bootstrap percentile (BC_a) method (Efron 1987; DiCiccio and Efron 1996; Venables and Ripley 2002).

There was moderate ($r = 0.55$ at lag $= 1$) and high ($r = 0.85$ at lag $= 1$) autocorrelation in the GDP and catch data respectively. Therefore, we adjusted the degrees of freedom in the least squares linear regression using the "modified Chelton method" (Pyper and Peterman 1998).

3.2.4 Rate of Development

Based on our results in the typical trajectory analysis and given that demand for sea cucumbers has been increasing (Baine 2004; Clarke 2004), we were interested in

[5] https://www.imf.org

whether sea cucumber fisheries had been developing more rapidly over time. More rapid development could be a consequence of increasing demand or value, and thus the need or pressure to fish harder. We evaluated whether the time from when individual fisheries started to when they achieved an overall peak or plateau in catch changed relative to when they started.

In a previous study (Chapter 2), we performed a related analysis across multiple invertebrate taxa. The problem in that study was that we were investigating all invertebrate taxa fished globally and were unable to check each individual fishery. Thus it was unclear whether a peak in catches reflected an overall peak in the fishery or just a localized peak in the catch series. Yet we did not want to compare localized peaks in recent fisheries with overall peaks in older fisheries, which itself would have generated the trend for which we were testing. Therefore, we decided whether a fishery had peaked by applying a conservative algorithm and assigning values to the unknown fisheries via sampling (Chapter 2). Here, we build upon that analysis by investigating one taxon in more detail. Instead of sampling possible values when trends were unclear, we verified that a perceived peak in catches reflected a true overall peak in the fishery (Table 3.1).

Time to peak catch was calculated as the time between the start of the fishery and the year of maximum catch using the same regions as in the typical trajectory analysis. We considered a fishery to have started when its loess smoothed catch surpassed 10% of its maximum loess smoothed catch. Since we were able to verify overall peaks in catch for the fisheries with the literature, we used them to determine our starting years. We also verified the starting year values with descriptions from the literature (Table 3.1). We adjusted the starting and peak years for the Mexican fishery to 1988 and 1991 respectively, the former an assumption based on the described start in the "late eighties" (Ibarra and Soberón 2002; Toral-Granda 2008*a*).

Since a rate using absolute volume (e.g. t/year) is mostly irrelevant for our purposes (see reasons outlined in Section 3.2.2), time to peak catch became our most direct proxy for rate of development. We tested the relationship between the log of time to peak and starting year using robust linear regression (Huber 1981; Venables and Ripley 2002).

3.2.5 Distance from Asia

Berkes et al. (2006) found that sea urchin fisheries developed increasingly far from their main market in Japan. They suggested this was a result of strong Japanese demand, roving buyers, and a lack of local and international regulations. Knowing that the majority of sea cucumber catch is exported to Hong Kong (and subsequently shipped to China) and that sea cucumber fisheries face many of the same pressures (Baine 2004; Clarke 2004; Ferdouse 2004), we hypothesized that there may be a relationship between the distance from the main importing nation, Hong Kong, and the years in which fisheries developed.

To the previously analyzed regions, we added four regions that surpassed our volume cutoffs but for which we could not verify peaks or plateaus in catch: west and east coasts of Canada, Maine (United States), and Chile. For these regions we used 10% of the maximum observed catch to determine a starting year.

We used great-circle distance to Hong Kong as a proxy for flight or shipping distance and hence transportation cost. As a point of departure, for each country or region, we used the city with the greatest population as a proxy for the main air-freight airport or shipping dock. To find these largest cities by population we used the 2006 dataset *world.cities*, which is part of the package *maps* (Becker et al. 2009) in the statistical package R (R Development Core Team 2009). Great-circle distances between cities were calculated using the function *rdist.earth* from the package *fields* (Furrer et al. 2009).

Our hypothesis began in 1950 (when FAO started recording catch). By this time Japan and Korea had long established sea cucumber fisheries that could not be considered new or emerging. However, in the 1950s, when the catch data start, they were the closest to Hong Kong and from there the expansion began. We therefore included Korea and Japan as starting in 1950.

We tested the relationship between the log of distance from Hong Kong and the year of fishery initiation with robust regression (Huber 1981; Venables and Ripley 2002). We log transformed the distance data to obtain a normal distribution of the residuals.

3.2.6 Sensitivity Analyses

We tested the robustness of our results in the typical trajectory analysis, change in time to peak, and spatial expansion from Asia to a set of alternative cut offs and scenarios. We repeated our typical trajectory and time to peak analyses including only fisheries that surpassed 200 t, 250 t, or 500 t for one, two, or three years. Since the United States and Canadian fisheries are given extra weight by splitting them into regions, we tried aggregating these catch series by country and assuming that neither had reached a peak in catch (i.e. including them only in the distance from Asia analysis).

3.2.7 Localized Status, Depletion, and Management

To evaluate other types of depletion that would have been hidden in our broad-scale global overview using aggregated catch, we reviewed recent reports of sea cucumber fisheries from around the world (Table 3.1) to assess whether there was any reporting of overexploitation, population decline, serial exploitation or lack of regulation.

In all cases we recorded whether these cases were confirmed present, confirmed absent, or unknown/not reported (Table 3.1). In our analysis, unknown or not reported instances were coded as absent. Our results are therefore conservative since many existing cases are likely unknown or not reported in the investigated literature.

We reviewed all recent available literature from FAO (2004), FAO (2008*b*), the SPC Beche-de-mer Information Bulletin, the primary literature, and available governmental documents. In addition to the regions evaluated in previous sections of this study, we report results for regions for which we could find confirmed presence or absence of least two of the investigated cases:

- *Overexploitation*: We identified evidence that the fishery was currently overexploited. Where biomass estimates were available, the harvesting level had to be above an estimated sustainable yield as of the last reported year. Where biomass estimates were unavailable, we relied upon assessment of the exploitation level in the literature.

- *Population decline*: We looked for descriptions or data noting either a decline in abundance, decline in catch per unit effort (CPUE), or local extirpation attributed to fishing in at least one major fishery in the region.

- *Spatial expansion*: We identified descriptions of the fishery moving or expanding spatially from easy to fish locations (often handpicking near-shore) to more difficult to fish locations (snorkelling, SCUBA gear from boats, or trawling further away from shore).

- *Species expansion*: In countries that had more than one commercial species available, we looked for descriptions or data indicating a transition from a fishery focused on high-value species to low-value species over time as high-value species became depleted.

- *Size depletion*: We looked for evidence or descriptions that there had been a general reduction in the size of sea cucumber species fished over time.

- *Illegal fishing*: We looked for instances where illegal, unreported, and unregulated (IUU) catches were considered a substantial impediment to the management and conservation of sea cucumber populations. Although IUU catches have likely occurred in all investigated fisheries, they are suspected of forming a substantial portion of the overall catch in some fisheries, even exceeding the reported legal catch (e.g. Choo 2008*b*).

- *Lack of regulation*: We noted fisheries that were considered not regulated as of the last available report. A ban on fishing was not considered regulated unless it was preceded by management or regulations. The inclusion of licenses with no regulatory means to control license numbers or effort in general was not in itself considered regulation.

3.3 Results

3.3.1 Catch Data

The Sea Around Us Project catch database reports sea cucumber landings for 37 countries. Of these, we included in our analysis 23 countries that surpassed 250 t for at least two years, and an additional four regions from the United States, two from Canada, and one from Australia (Figure 3.2). We found documentation of a peak in catch or projected plateau for 18 of the regions (Table 3.1), which were included in the typical trajectory and time to peak analyses (Figure 3.2B–S). The other four fisheries that may still be expanding in volume, plus Japan, were added for the distance from Asia analysis (Figure 3.2A, T–W). Finally, additional fisheries with lower catch volumes or unreported catch data that were included in the localized status, depletion, and management analyses are listed in Table 3.1.

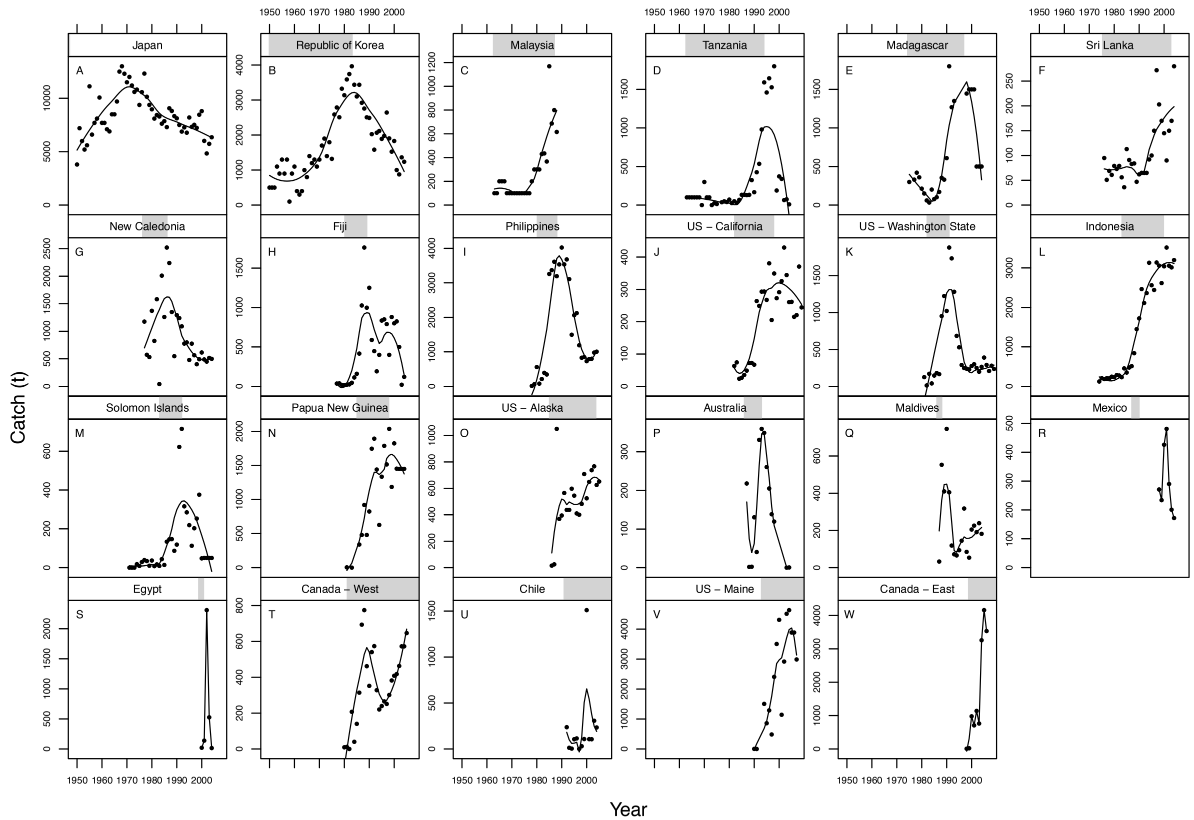

Figure 3.2: Sea cucumber catch trends as reported by the Sea Around Us Project and other sources (see Methods) for Japan (A), countries used in the typical trajectory and time to peak analysis (B–S), and countries or regions without a peak or plateau in catch that were added for the distance from Asia analysis (T–W). Lines represent the loess smoothing function that was used to derive the starting (10% of maximum) and peak years of catch. Grey bars in title regions indicate time from calculated start of fishery to year of peak catch. Countries are ordered by starting year within the two groups (A–S and T–W).

3.3.2 Typical Trajectory of Sea Cucumber Fisheries

The residuals to our additive models were more consistent with normality when assuming a Gaussian distribution to the data on an additive scale (Equations 3.1, 3.2, 3.3) than on a multiplicative scale (e.g. Equation 3.4). Additionally, our conclusions did not differ between the additive and multiplicative scale models. Therefore, we show and discuss only the results on the additive (not log-transformed) scale.

Our full, symmetric, and asymmetric additive models explained 58–60% of the null deviance in the models (Table 3.2; Figures 3.3A–C, 3.4). All models suggested a typical trajectory of a rapid incline, short peak and subsequent decline in catch, with a decline in catch that was approximately proportional to the incline. The full and asymmetric models indicated a slight rebound in catch approximately 10–15 years after a peak with minimal catch data available thereafter (Figures 3.3A, B). Assuming the incline and decline were symmetric (Figures 3.3C, 3.4) explained only slightly less of the null deviance (Table 3.2). The Generalized Cross Validation (GCV) scores suggested that, statistically, the asymmetric model was a better fit than the symmetric model (Table 3.2). This was confirmed by approximate hypothesis testing (F and Wald tests, $p < 0.001$); however, both models were reasonable approximations of the sea cucumber catch trajectories (Table 3.2). The asymmetric additive model explained only a slightly higher proportion of the null deviance (60% vs. 58%) and there was little evidence to suggest the full model over the symmetric model (Table 3.2). The better fit of the asymmetric model was driven largely by the Republic of Korea, Maldives, Fiji, and US – Washington State where the catch trends rebounded slightly while declining (e.g. Republic of Korea) or the rate of decline in catch plateaued (US – Washinton State) (Figure 3.4). Removal of any combination of these countries resulted in less evidence to support the asymmetric over the symmetric model (approximate F test, $p = 0.001$–0.455).

Table 3.2: Summary of additive models fit to sea cucumber catch. Shown are R^2 adjusted values, proportions of null deviance explained, Generalized Cross Validation (GCV) scores, and Akaike's information criterion (AIC) values.

Model	R^2 adj.	Deviance expl.	GCV	AIC
Full (Equation 3.1)	0.56	59%	0.112	302.4
Asymmetric (Equation 3.2)	0.58	60%	0.108	286.1
Symmetric (Equation 3.3)	0.56	58%	0.112	301.6

The regression tree (Figure 3.3D) confirmed aspects of the full additive model where the branch splits of the tree are indicated by vertical grey lines (Figure 3.3A). The regression tree indicated that the most important split in the data occurred 7.5 years before peak catch (Figure 3.3D). This is reflected by the smooth function for the additive model where the function divides between a negative and positive effect on catch (crosses 0) at -7.5 years (Figure 3.3A). The regression tree estimates catch before this split to be the lowest (-0.32 on an approximate -1 to 1 standardized scale) and this is reflected in the full additive model (Figure 3.3A). The next two branches of the tree split symmetrically at 3.5 years before and after the peak in catch. The highest estimated catch (0.57 on the standardized scale) occurred between 3.5 years before and after peak catch, which followed the full additive model, and was to be expected given how we lagged the data by maximum catch.

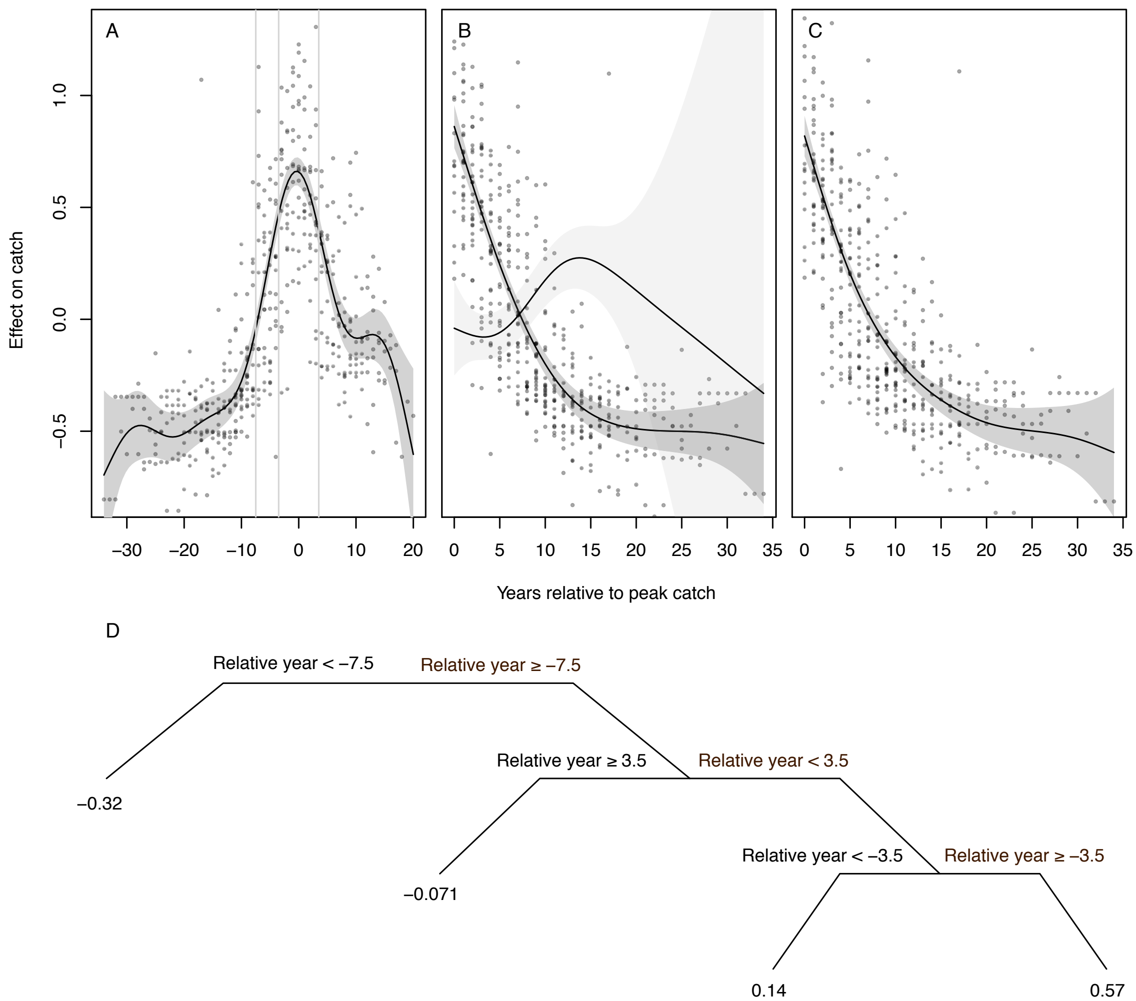

Figure 3.3: (A) Typical trajectory of global sea cucumber fisheries with catch trends lagged to peak in the same relative year (year 0) (Equation 3.1). (B) Asymmetric trajectory before and after peak in catch (i.e. absolute value of years relative to peak catch) (Equation 3.2). The line with the dark shaded region represents the smooth function applied to both the data before and after the peak; the line with the light shaded region represents the additional smooth function applied to the data after the peak. (C) Symmetric trajectory before and after peak in catch (Equation 3.3). Dots represent partial residuals of catch trends for individual countries and refer to the smooth functions with a dark shaded region. Black lines represent additive model smooth functions. Shaded regions represent approximate 95% Bayesian credible intervals. (D) Regression tree of scaled sea cucumber catch. Numbers at end of branches represent predicted volume of scaled catch (subtracted mean and divided by two standard deviations within each country), which varies approximately from −1 to 1. Vertical grey lines in A illustrate the branch divisions in D.

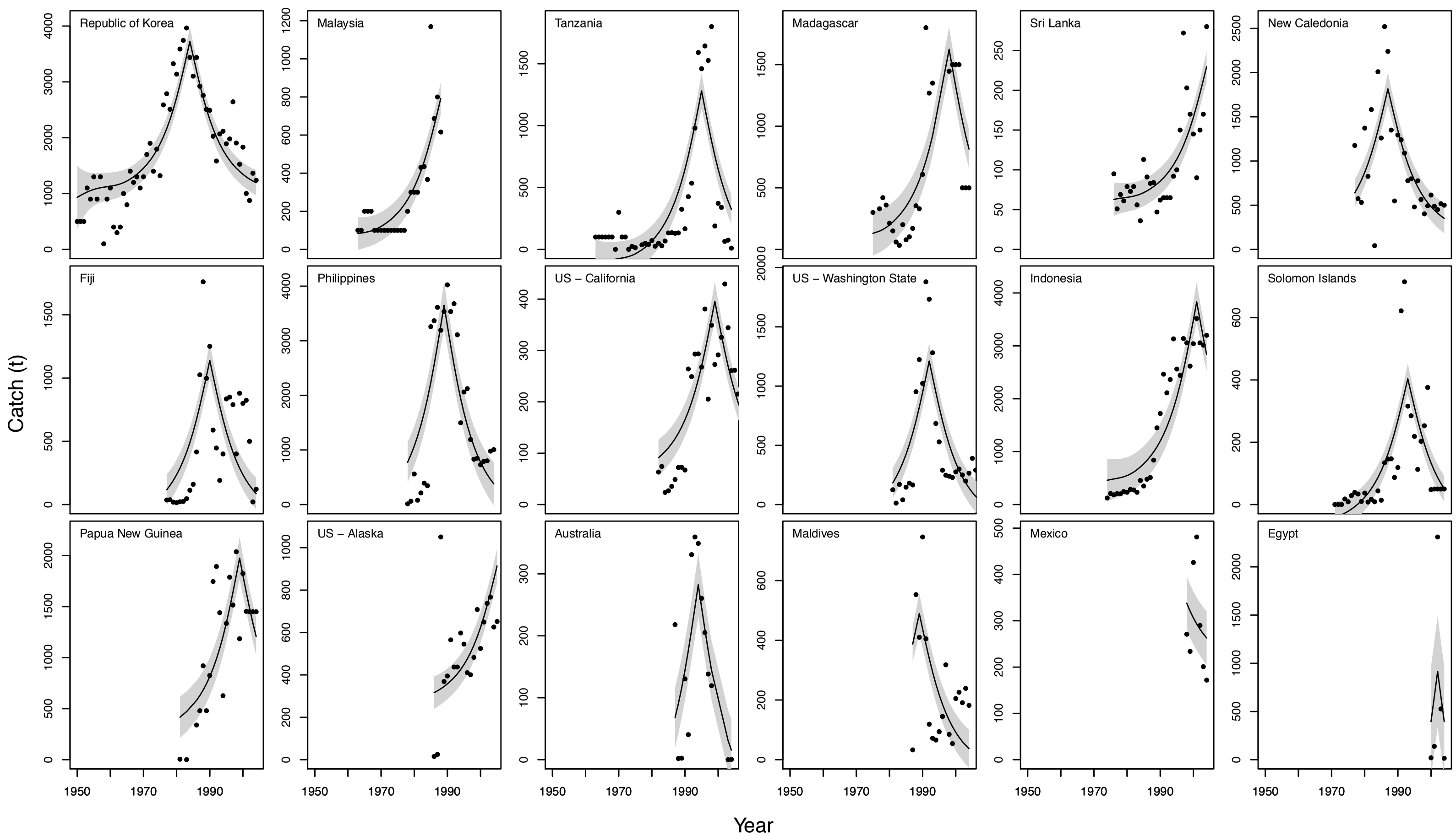

Figure 3.4: Symmetric additive model fits to sea cucumber catches by country. Lines represent additive model predictions based on a single additive model (with country as a parametric term) comparing scaled catch to absolute years before or after peak catch. Shaded regions represent two standard errors above and below the predicted values. Countries are ordered by ascending year of peak catch.

3.3.3 Drivers of Sea Cucumber Fisheries

In 2006, Hong Kong was responsible for 58% of global sea cucumber imports by volume (Figure 3.5). The majority of the remaining catch was imported by nearby Asian countries. Of the imports from 1950–2004, the time frame evaluated in this study, 64% were imported by Hong Kong (Chapter 2, Table 2.S-1). According to the FAO trade statistics, the largest exporter of sea cucumbers by volume was the Philippines (Figure 3.5). Overall, there were 2.3 times more imports reported than exports. Even just in Hong Kong, there were 1.3 times more imports reported than all global exports combined.

Global sea cucumber catch, including all reported catches in the Sea Around Us Project database, generally increased from 1950 to 1997 by five times in volume, and then fluctuated on the order of ∼12000 t in reported catches since (Figure 3.6A). The annual rate of change of the log of Chinese GDP fell sharply in the early 1960s and has generally been positive since reaching a maximum rate of change in the early 1990s (Figure 3.6B).

Correlating the two time series at various lags (so that GDP led catch), there was the greatest evidence of correlation at a two year lag: least squares regression accounting for autocorrelation, $r = 0.59$ (0.34, 0.84)[6]; robust regression, $r = 0.62$ (0.38, 0.85) (Figure 3.6C, D). Accounting for autocorrelation, the effective degrees of freedom decreased from a range of 44–50 to ∼13–14 over the various lags.

3.3.4 Rate of Development

Our time to peak analysis revealed that fisheries tended to reach their peak catch more rapidly over time: robust regression, r = -0.73 (-1.0, -0.4) (Figure 3.7A). Based

[6]Throughout this chapter, numbers in brackets indicate 95% confidence intervals.

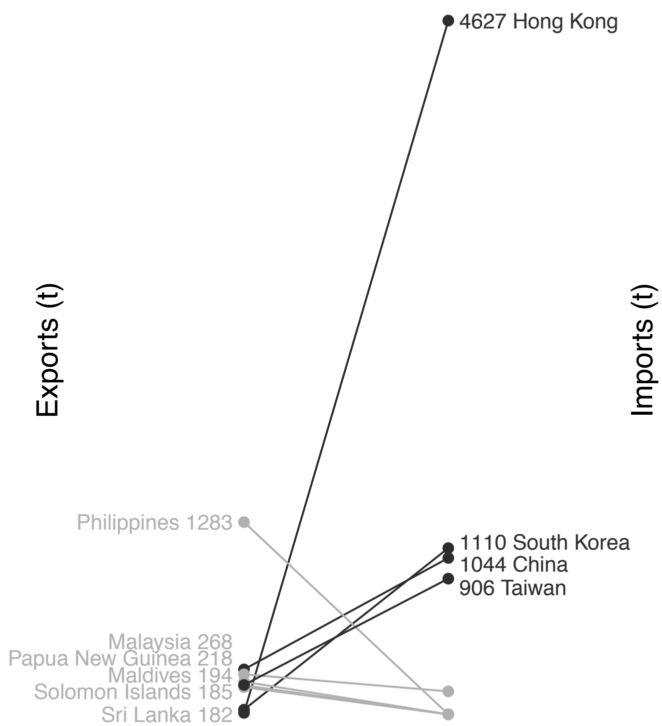

Figure 3.5: Bump chart of sea cucumber exports and imports by volume in 2006. Countries labeled on the left (grey text and lines) exported a greater volume than they imported. Countries labeled on the right (black text and lines) imported a greater volume than they export. Numbers beside country labels show export or import volume in tonnes. Only countries with greater than 150 t of imports or exports are shown.

on the regression, and assuming the errors are normally distributed on the exponential scale, the predicted time to peak catch decreased from 34 (19–61) years in 1960 to 6 (4–9) years in 1990.

3.3.5 Distance from Asia

Since 1950, sea cucumber fisheries tended to develop further and further away (exponentially) from their main Asian market: robust regression, $r = 0.56$ (0.28, 0.95) (Figure 3.7B). Sea cucumbers have been fished and traded in Japan since at least the 16th century (Akamine 2004). In the 1950s, most sea cucumber fisheries occurred in the Indo-Pacific yet by the 1990s sea cucumber fisheries spanned the globe (Figure 3.7C).

3.3.6 Sensitivity Analyses

Our overall conclusions about the typical trajectory, time to peak catch, and distance from the Asian market were robust to our choice of catch volume cutoff (see Methods) and the aggregating of United States regions and Canadian regions by country.

3.3.7 Localized Status, Depletion, and Management

As of their last published reports (see Table 3.1), 69% of sea cucumber fisheries were noted as being overexploited and 81% as having declined in abundance due to overfishing (Figure 3.8). Extinction or extirpation of at least one species was noted in Egypt, Indonesia, and Malaysia.[7]

[7] See Table 3.1 for references for all examples in Section 3.3.7 unless otherwise specified.

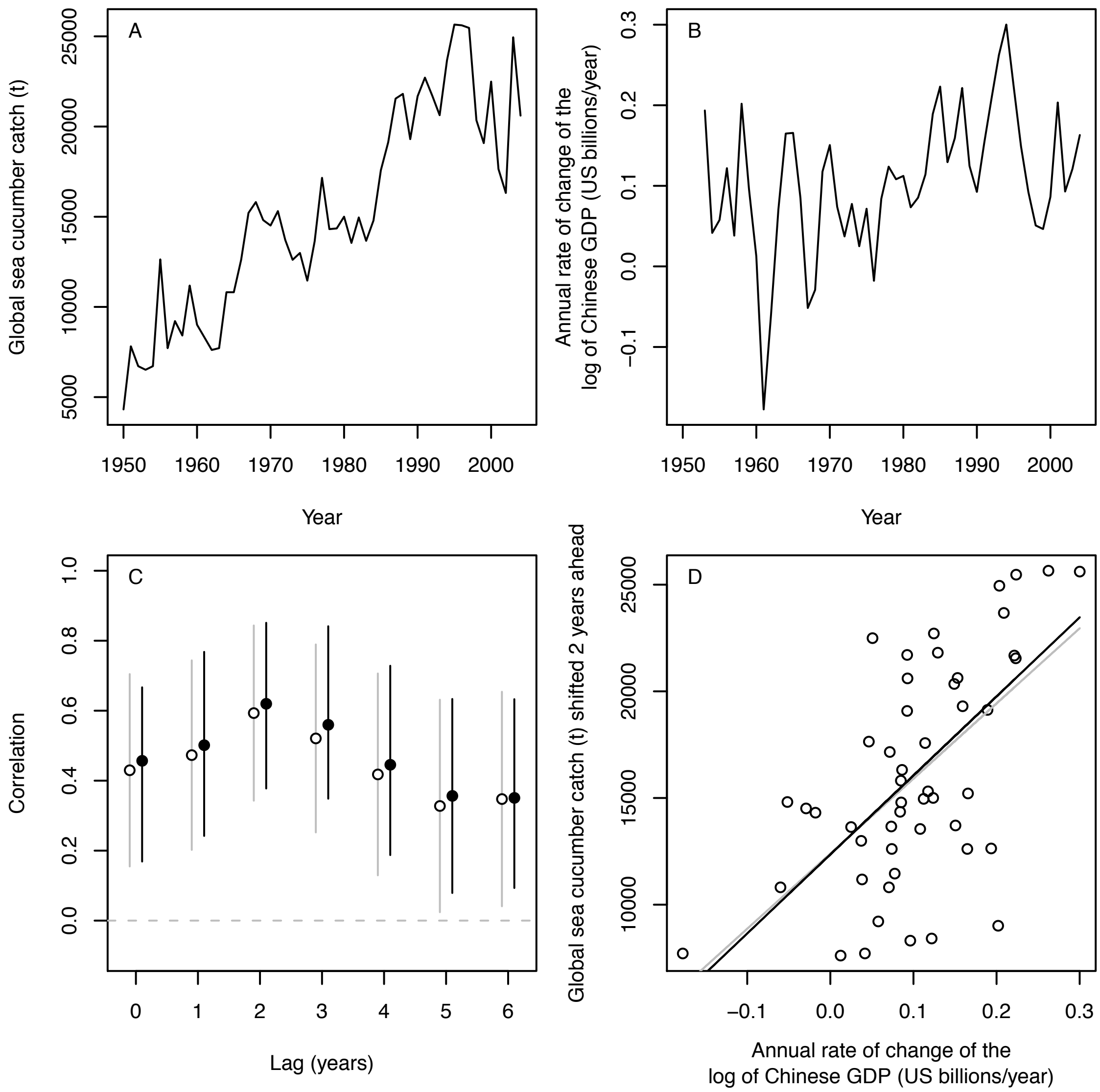

Figure 3.6: Trends of global sea cucumber catch volume (A) and the rate of change of Chinese GDP (B). (C) Correlation coefficients shifting catch at lags of 0–6 years with GDP leading catch. Open dots and grey lines represent correlation coefficients and 95% confidence intervals using ordinary least squares regression and adjusting the degrees of freedom to account for autocorrelation. Solid dots and lines represent correlation coefficients and bootstrapped 95% confidence intervals using robust regression but not accounting for autocorrelation. (D) Correlation of sea cucumber catch (lagged by two years) and rate of change of Chinese GDP. Dots represent individual years; black and grey lines represent robust and ordinary least squares regressions respectively with the correlation coefficients shown at the two year lag in C.

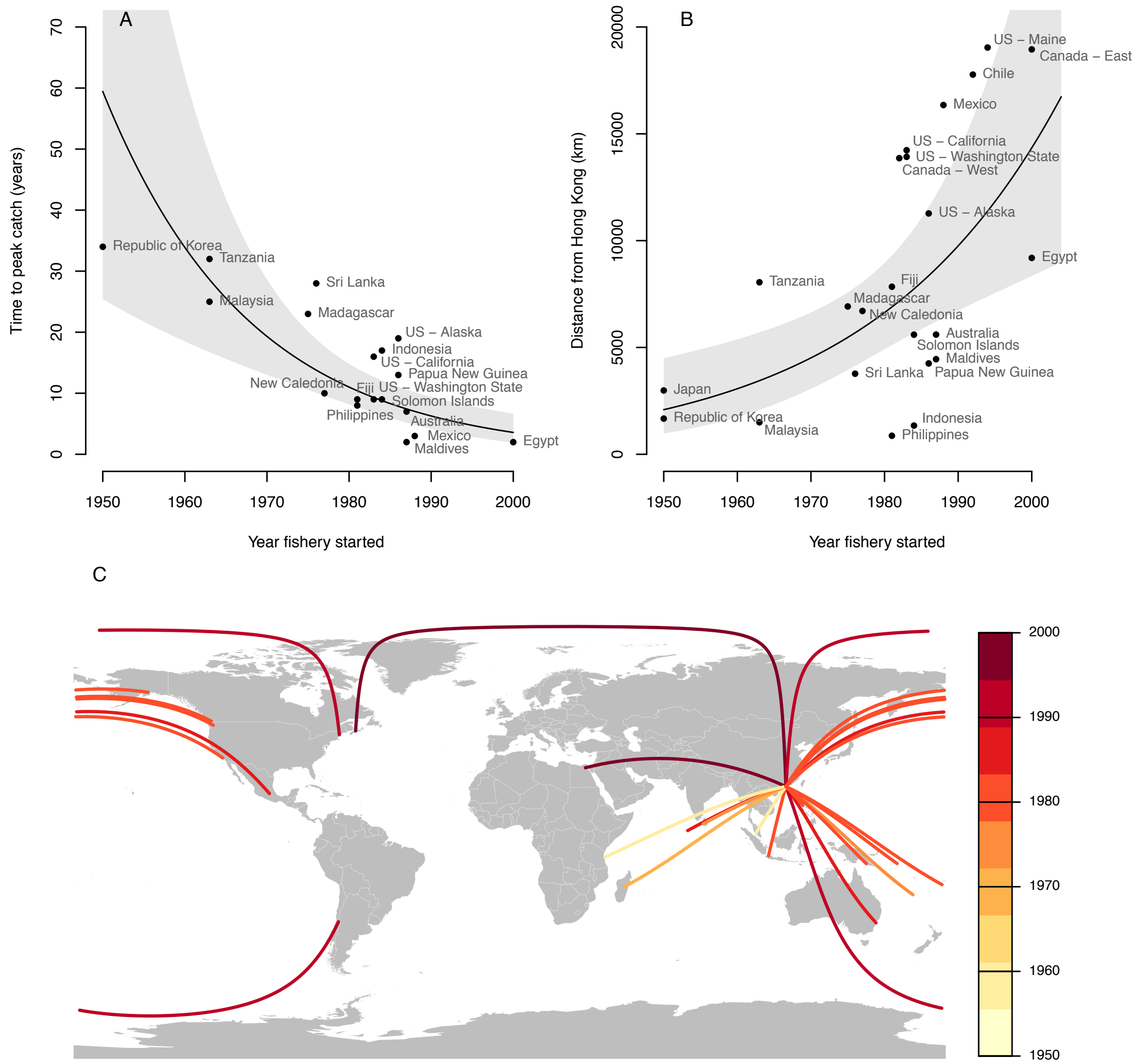

Figure 3.7: (A) Time for sea cucumber fisheries to reach a peak or long-term plateau in catch vs. the year they began (when catch surpassed 10% of its smoothed maximum). (B) Great circle distance between Hong Kong and the most populated cities of countries or regions fishing sea cucumbers vs. the year that the fisheries began. Lines in A and B represent robust regressions fit on log-transformed response data and shaded regions indicate two standard errors above and below the fit; r = -0.73 (-1.0, -0.4) and r = 0.56 (0.28, 0.95) respectively. (C) Map of global sea cucumber catch as exported to Hong Kong. Lines indicate great circle arc between the cities with the largest population in each country or region and Hong Kong. Colour reflects the starting year of the fishery.

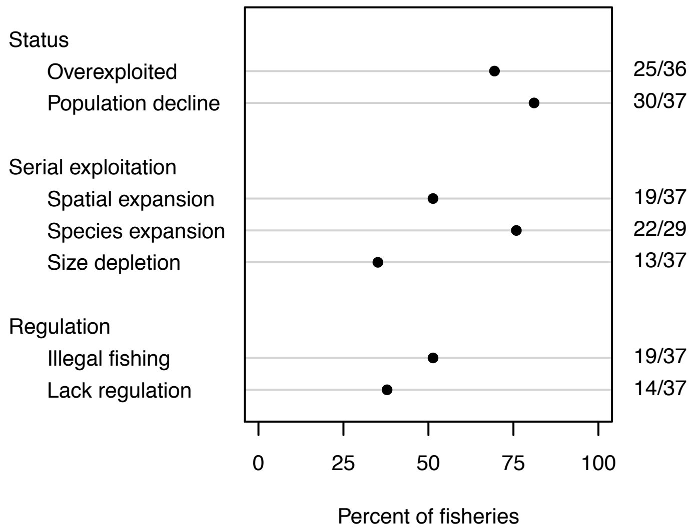

Figure 3.8: Cleveland dot plot of frequency that local issues related to sea cucumber fisheries were documented in the literature. Issues evaluated were (from top to bottom) status: evidence of current overexploitation, a decline in abundance or biomass of the population; serial exploitation: evidence of spatial fisheries expansion, expansion from high-value to low-value species, and size depletion; regulation: evidence of illegal fishing and a lack of management. The number of occurrences compared to the number of fisheries in which that issue was relevant are indicated on the right.

Serial exploitation was found in three different ways. First, spatial expansion was described for 51% of the fisheries. Commonly, in the tropical fisheries (for example, the Maldives, Philippines, and Sri Lanka), harvesting started as hand gathering near shore. As stocks became depleted fishers moved further offshore using snorkelling, SCUBA diving, and sometimes dragging gear.

Second, expansion from high- to lower-value species was noted in 76% of those fisheries with more than one species available to harvest commercially. For example in Malaysia and Madagascar, harvesting transitioned from fisheries focused on harvesting low volumes of high-value species (e.g. sandfish: *Holothuria scabra* and black and white teatfish: *Holothuria nobilis* and *Holothuria fuscogilva*) to harvesting high volumes of low-value species (e.g. “edible” or “burnt hotdog”: *Holothuria edulis* and "patola": *Holothuria leucospilota*) as the high-value species became depleted. Third, a reduction in the typical size of sea cucumbers harvested was noted in 35% of regions. For example, on the Great Barrier Reef the average weight of sea cucumbers in harvested zones was $\sim$ 20% lower than in unfished zones (Uthicke and Benzie 2000). In the Galápagos, the mean fished size decreased from 24.5 to 22.5 cm from only 1999 to 2002 (Shepherd et al. 2004).

IUU catches were considered a substantial impediment to management or conservation of sea cucumber populations in 51% of fisheries. In regions such as Indonesia and the Philippines, illegal or unreported fishing is thought to greatly exceed the catches from legal fishing. Reported catch is estimated to be only 25% of actual catch in Indonesia (Tuwo 2004).

Regulations (as described in the Methods) were absent in 38% of fisheries. Countries such as Egypt transitioned directly from an open fishery to a complete ban on fishing. Others, such as Sri Lanka, have licenses but no restrictions on license numbers, regulation of quotas, or catch limits. In contrast, some fisheries, such as the one in British Columbia (Canada) initially followed a boom-and-bust pattern but tighter regulations on quotas, rotational harvesting, and adaptive management allowed stocks to recover (Hand et al. 2008).

3.4 Discussion

Here we provide the first quantitative synthesis of the spatial and temporal patterns of sea cucumber fisheries worldwide. Overall, global catch and value of sea cucumber fisheries has strongly increased over the past 2-3 decades. Yet, we found that many individual sea cucumber fisheries followed a typical trajectory with a rapid increase, short peak and in most cases a substantial downward trend after peaking suggesting a boom-and-bust pattern. Also, since 1950, sea cucumber fisheries have developed exponentially further away from their main market in Hong Kong and have developed faster over time. When we reviewed fisheries on a local scale we identified consistent evidence of patterns of serial exploitation. In particular, we found evidence for the expansion over space and from high- to low-value species for a majority of fisheries but also a decrease in size for about a third of the fisheries investigated. Finally, the majority of sea cucumber fisheries are not regulated, and in over two-thirds of cases, local records indicate current concerns about overexploitation and population declines. Because sea cucumbers are of high ecological and increasing social and economic importance, our results highlight the urgent need for better monitoring, assessment and regulation of their fisheries.

3.4.1 Data Quality

Throughout our analysis we encountered problems with the quality, quantity, availability, and consistency of data related to sea cucumber fisheries. Reasons for these inaccuracies are manifold. First, as noted by Choo (2008*a*), sea cucumber catches often tend to be low in volume compared to other fisheries and so national governments often pay little attention. For example, Malaysia stopped recording catches after the fishery started to decline in 1993 (Choo 2008*a*).

Second, some countries report catches in wet weight and some in dry weight (Conand 2004) but there is uncertainty about which countries do which. For example, Choo (2008*a*) noted that southeast Asian catches were severely underestimated, and questioned whether some or all of their catches may be reported in dry weight instead of wet weight.

Third, there is often great pressure to under-report catches and exports, typically for tax evasion purposes (Clarke 2004; Choo 2008*a*). Global reported imports are more than double reported exports (Figure 3.5). Fortunately, there is less incentive to misreport imports of sea cucumber into Hong Kong, making these imports more reliable, although still imperfect indicators of fishery trends (Clarke 2004). Based on import data from Hong Kong, Toral-Granda (2008*a*) determined that there were substantial IUU catches from Latin America. Baine (2004) reviewed international trade of sea cucumbers and found reports of discrepancies in sea cucumber catch reports compared to export statistics for many countries, citing Indonesia, Papua New Guinea, Mozambique, and the Solomon Islands as examples. We note that Indonesia has not reported sea cucumber exports since 1989 in the FAO data shown in Figure 3.5 despite the fact that the fishery has continued in substantial quantity (see Figure 3.2 and Tuwo 2004)

Fourth, countries often report sea cucumber catch and exports under combined categories. For example, China reported sea cucumbers as “other” until 2001 (Choo 2008*a*). Canada reports sea cucumbers as “benthic invertebrates” to FAO (Hamel and Mercier 2008). Malaysia combines dried and salted sea cucumber exports into one category, making it difficult to determine trends in their volume (Baine 2004). Further, sea cucumbers traded in other industries, such as the cosmetic and aquarium trade, are often not recorded (Choo 2008*a*).

Without even basic catch data, let alone consistently reported fisheries independent data, assessing the status of sea cucumber fisheries around the world is challenging. Because of their increasing value and propensity to follow boom-and-bust patterns (Figures 3.3, 3.8), consistent and publicly accessible data to evaluate their status would be of great value. At the very least, it would aid transparency and analysis if developed countries, e.g. Canada, did not aggregate to such a high level when reporting benthic invertebrate catch. Further, it would aid analysis if published conversion factors (Skewes et al. 2004; Purcell et al. 2009) were used to standardize sea cucumber catch in the FAO and Sea Around Us Project catch databases to either wet or dry volume.

3.4.2 Typical Trajectory and Time to Peak

Ideally, a developing fishery would gradually build in volume and fishing capacity to a level near MSY and then be maintained at a consistent catch level (Hilborn and Sibert 1988). Our typical trajectory analysis (Figures 3.3, 3.4) combined with our analysis of local issues of depletion (Figure 3.8) suggest that sea cucumber fisheries tend to overshoot an ideal capacity and decline substantially thereafter. In fact, our results suggest they may be crashing nearly as quickly as they are expanding (Figures 3.3C, 3.4). Importantly, our analysis of local issues supports the idea that in many cases peaks in catch tend to be a result of resource depletion and not management induced reductions in catch; however, there are notable exemptions such as Japan where the decline in catch is the result of restrictive management (Akamine 2004). The typical trajectory we observed may be indicative of fisheries that are allowed to expand without restrictions until the resource itself limits the fishery. If the fishery continues, it does so at a substantially reduced biomass with the resulting loss of social and economic benefits and ecosystem services (see Section 3.1 Introduction).

The sea cucumber fisheries investigated were also reaching this peak in catch faster over time (Figure 3.7A). One of the most recent fisheries, the sea cucumber fishery in Egypt, began in 1998 and by 2000 had increased so substantially that the Red Sea Governorate banned the fishery in its jurisdiction (Lawrence et al. 2004). Illegal fishing continued and, combined with a brief re-opening, stocks collapsed by 2003 (Lawrence et al. 2004). Besides our own analyses in Chapter 2, we are unaware of other studies that have explicitly tested for this pattern.

The observed decrease in time to peak is likely a combined result of increasing demand and the exploitation of smaller fisheries as more substantial fisheries have declined. An alternative hypothesis would be that management is bringing the fisheries' expansion under control more rapidly; however, a review of the literature by country does not support this hypothesis as most declines in fisheries are associated with population declines (Figure 3.8). If this trend of more rapid expansion continues, it will be vital for management to act even more quickly to bring fisheries expansion under control before resource depletion does so itself.

3.4.3 Global Market Drivers

Sea cucumbers have a long history of being harvested and traded internationally. For example, sea cucumbers have been a major export commodity from Japan for at least 350 years (Akamine 2004) and harvesting in some Chinese islands had gone uninterrupted since at least 1681 (Choo 2008*a*).

Our results suggest that the global volume of sea cucumber fisheries may be connected to the Chinese economy (Figures 3.6, 3.5). Moreover, the distance from Asia of the countries fishing for sea cucumbers may have driven when their fisheries began (Figure 3.7B, C). Today, almost 90% of sea cucumbers harvested globally are ultimately consumed in southeast Asia and the Far East (Ferdouse 2004). Consumption of sea cucumbers within Hong Kong (Clarke 2004) and western countries (Ferdouse 2004) appears to be declining while at the same time consumption is increasing in mainland China (Clarke 2004; Chen 2004). Yet, the once strong Chinese wild harvests of sea cucumbers have all but disappeared in many regions (Choo 2008*a*). Despite the rise in sea cucumber farming in China (Chen 2003), wild caught product is still in high demand, and, combined with the growing economy of China, and the decline of many sea cucumber fisheries globally (Figures 3.4, 3.8), the demand for sea cucumbers in Asia continues to rapidly increase (Clarke 2004; Chen 2004; Ferdouse 2004).

Although China is the main consumer of sea cucumbers, Hong Kong controls most of the trade of high-value species due to processing capacity and lack of import duties (Clarke 2004; Ferdouse 2004) with typically only lower value species being directly exported to China (Ferdouse 2004). Importantly, the price of sea cucumbers is elastic (Kinch et al. 2008*a*) with the value increasing as the resource becomes scarcer. For example, as the Chinese wild fisheries declined and Japan scaled back the volume of their fisheries, the value of *Apostichopus japonicus* increased 170 fold from 1960–2004, increasing 3–5 fold from just 1990-2004 (Chen 2004) and now rivaling the price of shark fin (Clarke 2004) at over $400 USD/kg. This has important implications for the conservation and management of sea cucumbers since their demand is likely to only further increase as they become scarcer.

Not all sea cucumber species are sold at a high price. Ferdouse (2004) notes that the range of purchasing powers possessed by Asian consumers provides demand for a range of sea cucumber species. This opens the door to harvesting of a variety of species, fishing through the species-value chain (Figure 3.8), and to fisheries such as those in Maine (United States) and eastern Canada where a low-value species (*Cucumaria frondosa*) is harvested in large quantities using trawl gear to make the fishery profitable (Therkildsen and Petersen 2006).

3.4.4 Serial Exploitation

We found evidence of both small and large scale serial exploitation. On a global scale, over the past 55 years, sea cucumber fisheries have expanded exponentially from their point of origin in Asia to now encompass the globe (Figure 3.7B, C). On a local scale, by assembling reports on individual regions, we found that about half of the countries have also shown patterns of serial exploitation over space, about three-quarters showed patterns of serial exploitation of decreasing value of the species fished, and about one-third showed a serial exploitation of decreasing individual size (Figure 3.8).

Similar patterns have been detected for other species. For example, patterns of spatial serial exploitation have been detected for abalone fisheries in California (Karpov et al. 2000), oysters in North America and eastern Australia (Kirby 2004), crab species in Alaska (Orensanz et al. 1998), and sea urchins (Andrew et al. 2002; Berkes et al. 2006) and tuna (Myers and Worm 2003) globally. By species, Pauly et al. (1998) and Essington et al. (2006) showed a pattern of the serial addition of lower value and lower trophic level species to global fisheries. Examples of declines in fished body size are numerous. For example, Hutchings (2005) and Shackell et al. (2009) found declines in body size of predatory fishes in the Northwest Atlantic due to overexploitation and Ward and Myers (2005) detected declines in pelagic fish size in the tropical ocean. For invertebrates, fishing induced body size changes have been noted for many populations including intertidal gastropods in California (Roy et al. 2003), blue crabs in Chesapeake Bay (Lipcius and Stockhousen 2002), and cephalopods in Australia (Hibberd and Pecl 2007).

Our findings suggest that, for sea cucumbers and potentially other high-value marine invertebrates, patterns of serial exploitation by location, species, and size are common and therefore may be predictable. Such knowledge could be used to better inform and preemptively regulate the expansion of current and future fisheries on local or global scales. For example, restrictions on the use of more powerful fishing technologies that allow fishers to travel further offshore and collect in greater volumes (e.g. SCUBA, trawling) could be considered from the early stages of management.

Species not yet targeted could be included in regulation to prevent a cascade of population depletions moving down the value chain. Lessons learned from commercially valuable species could be used to predict the rise in exploitation of subsequent, lower-value species and offer the necessary protection to ensure their long-term viability. Although difficult to measure (e.g. Hand et al. 2008), quantitative or anecdotal indications of decline in body size could be considered in assessing the status of sea cucumber fisheries. Size structure has already been used as a management tool in regions such as Alaska (Clark et al. 2009), western (Hand et al. 2008) and eastern Canada (Rowe et al. 2009). Further, the Australian government recommends it as a management tool for Pacific Island sea cucumber fisheries (Friedman et al. 2008).

3.4.5 Ecosystem and Human Community Effects

Sea cucumbers form many important roles in marine ecosystems as consumers, bioturbators, water quality regulators, and prey (see Section 3.1 Introduction). Our results show that sea cucumber fisheries typically have catch that declines as quickly as it expands (Figures 3.3, 3.4), are reaching peaks in catch increasingly rapidly (Figure 3.7A), are expanding spatially, typically fish through species, and often affect the size structure of the population (Figure 3.8). Reductions in biomass from sea cucumber fisheries can be consequential. For example, in the Torres Strait, adult sea cucumber biomass was estimated to have been reduced to 100 t from a virgin biomass of l600 t (Skewes et al. 2000). In Egypt (Lawrence et al. 2004), Indonesia (Choo 2008*a*), and Malaysia (Choo 2004), populations have declined to levels of extirpation. Given the fishery patterns we have shown in this study, the large reductions in biomass, the Allee effect experienced by sea cucumber populations at low densities (Uthicke and Benzie 2000; Bruckner 2005), and therefore the slow recoveries observed (D'Silva 2001; Uthicke et al. 2004; Ahmed and Lawrence 2007), these trends may represent a substantial loss of ecosystem services.

Sea cucumber fisheries have provided income, and in some regions food, for many coastal communities for decades if not centuries or millennia (see Section 3.1 Introduction). However, the rapid expansion in recent years (Figure 3.7) and local issues of depletion, IUU catches, and lack of regulation (Figure 3.8) threaten the long-term viability of these fisheries. The resulting social and economic consequences of declining sea cucumber fisheries for coastal villages could be substantial (Kinch et al. 2008*a*). This is especially severe for countries that highly depend on sea cucumber fisheries and have not many alternative income sources, such as the Solomon Islands (Nash and Ramofafia 2006), Sri Lanka (Dissanayake et al. 2010), and the Maldives (Joseph 2005). In other regions, sea cucumber fisheries may rather be just one of many alternative income options (e.g. United States) or became important because of the overexploitation or restrictive management of more traditional fisheries (e.g. eastern Canada; Anderson et al. 2008).

In addition to the loss of income and food, the decline or extirpation of sea cucumber populations entails the loss of potentially undiscovered bioactive compounds that could benefit healthcare worldwide (Petzelt 2005; Lawrence et al. 2009). A wealth of potentially medicinal compounds have been isolated from holothurian species including antitumour, antiviral, anticoagulant, and antimicrobial compounds (Kelly 2005). For example, Haug et al. (2002) found high levels of antibacterial activity in the eggs of *Cucumaria frondosa* and suggested the potential for new antibiotics. Abraham et al. (2002) found antimicrobial substances in a range of holothurian species off the coast of India. Perhaps most importantly, Lawrence et al. (2009) found significant intraspecific variation between populations of the same species among different habitats suggesting greater value for future bioprospecting. Even if severely depleted populations recover, these populations may lack the genetic diversity and therefore potential bioprospecting uses (Lawrence et al. 2009).

3.4.6 Management Solutions

Sea cucumber fisheries are inherently difficult to manage. They are difficult to size, difficult to age, and their weight differs by season and location (e.g. Hand et al. 2008). Further, many sea cucumber fisheries occur in regions where strong governance is lacking, and regulations are often lacking completely (Figure 3.8).

Nonetheless, some sea cucumber fisheries have been successfully managed. Via a fisheries law, rights systems, permits, and fishery co-operatives, Japan has succeeded in drawing back overfishing and restocking depleted areas (Akamine 2004). The holothurian fishery in southeast Alaska (United States) is carefully controlled. Harvest levels are set based on the lower 90% bound of a biomass estimate, areas are fished on a three year rotation schedule, and separate areas are left closed as controls (Clark et al. 2009). The fishery in British Columbia, Canada initially followed the typical boom-and-bust pattern shown in Figures 3.3 and 3.4, but management stepped in, reduced quotas, added license restrictions, and implemented adaptive management (Hand et al. 2008). As a result, CPUE (Hand et al. 2008) and catches (Figure 3.2) recovered. Although still with problematic corruption and declining abundance, the implantation of a co-management regime in the Galápagos has increased the effectiveness of license and quota control and reduced conflict between management and fishers (Shepherd et al. 2004).

Marine reserves have often been part of a successful sea cucumber management regime (e.g. Hand et al. 2008; Clark et al. 2009). Although reserves may not always have a direct effect on the abundance and size structure of holothurian populations (Lincoln-Smith et al. 2006), they serve two other important purposes: (1) Due their sessile nature and broadcast spawning, holothurians are suspected of experiencing an Allee effect making restocking efforts particularly necessary at low population densities (Uthicke et al. 2004; Bell et al. 2008). If of sufficient size (> 19–40 ha), reserves can act as nucleus breeding populations (Purcell and Kirby 2006). (2) Reserves are particularly important for sea cucumber fisheries as a monitoring tool (Uthicke and Benzie 2000; Schroeter et al. 2001). For example, in California (United States), Schroeter et al. (2001) detected fishing mortality induced stock declines of 33–83% by comparing seven fished sites with two non-fished sites that were undetectable by CPUE.

Despite effective management in some regions, the majority of sea cucumber fisheries do not enjoy the same success (Figure 3.8). Further, unlike the above mentioned examples, many sea cucumber fisheries exist in isolated coastal communities where the residents depend on the fishery for income (e.g. Joseph 2005; Nash and Ramofafia 2006; Dissanayake et al. 2010). Management needs to be tailored to the size of the fishery and local situation to be effective (Worm et al. 2009). IUU catches were a substantial problem in 51% of the investigated fisheries (Figure 3.8). Therefore, attempts to implement quotas may not be successful strategies for many of these regions, especially without stronger governance (Smith et al. 2010).

In light of the lack of strong local governance, international regulations that control trade (such as CITES Appendix II) may be one of the best hopes for the conservation of highly valued sea cucumber populations (Bruckner et al. 2003; Bruckner 2004; 2006). Alternatively, import tariffs can benefit the long-term conservation of renewable resources and almost always benefit the exporting country (Brander and Taylor 1998). Unfortunately, the process by which international regulations are developed is often too slow to react to the global expansion of high-value invertebrate fisheries to effect meaningful conservation (Berkes et al. 2006).

Where sufficient governance exists, the results of our study suggest two important steps to managing existing and future holothurian fisheries. First, the expansion rate of new fisheries had best be reduced to a level where management has time to react to early warning signs of resource depletion. Second, lacking changes in regulation, the catch trajectory (Figures 3.3, 3.4) and patterns of spatial (Figure 3.7B, C), species (Figure 3.8), and size (Figure 3.8) serial expansion or depletion are largely predictable. Knowledge of the impending sequence of events can therefore be preemptively incorporated into the management of new and existing high-value marine fisheries. Overall, our study highlights the urgent need for better monitoring and reporting of catch and abundance data for sea cucumbers and proper scientific stock and ecosystem-impact assessment to ensure a more sustainable harvesting of current and development of future fisheries.

Chapter 4

Discussion

In this thesis, I provided the first quantitative evaluation of the status, ecosystem effects, and drivers of increasingly valuable marine invertebrate fisheries on a global scale. I did so both in a cross-taxa framework considering all major invertebrate fisheries worldwide (Chapter 2) and in greater detail for one taxa, sea cucumbers (Chapter 3). My findings highlight the rapid increase in invertebrate fisheries by volume, value, diversity of taxa fished, and number of countries participating. They also document the increasing overexploitation of some invertebrate populations, as well as a spatial expansion and temporal acceleration of fisheries development. Further, I aimed to place the volume of catches and gear used to harvest invertebrates into the context of their effects on marine ecosystems. For sea cucumber fisheries, my results provide the first global quantitative analysis of a typical trajectory and trends in expansion over space and time. These trends can be linked to growing market demand in Asia. I confirm these trends and uncover further local issues of serial exploitation, population depletion, and management by systematically reviewing the available regional literature for all major sea cucumber fisheries. I highlight the importance of a sustainable development of these fisheries to coastal communities around the world that depend on them for income and nutrition, as well as the conservation of sea cucumbers which provide important ecosystem functions and services.

In this general discussion, I will highlight the overall contributions of my work to our knowledge of invertebrate fisheries in terms of: (1) methodological contributions to the analysis of the status, temporal and spatial trends in fisheries; (2) the effects of scale with respect to the spatial and taxonomic aggregation of catches; (3) management implications; and (4) ecosystem consequences. Thereby, I will draw comparisons across Chapters 2 and 3. I will conclude with a general outlook on the possible next steps and urgent issues to be studied regarding invertebrate fisheries.

4.1 Methodological Contributions

The assessment of fisheries status is inherently challenging (Hilborn and Walters 1992). However, this is even more challenging for most invertebrate fisheries, where fisheries independent data is largely unavailable (Caddy 1986; Perry et al. 1999; Smith and Sainte-Marie 2004; Anderson et al. 2008) and landings data for high-value species is fraught with incentives to misreport (Clarke 2004; Ferdouse 2004). However, for the majority of invertebrate fisheries, landings are the only available data source to use for analysis. Thus, it was necessary to work with the uncertainty and variability surrounding landings data, especially on a global scale. Further complicating matters was the varying (and often short) time span of available data. Consequently, I developed new methods for analyzing trends, which are highlighted in the following.

A central problem to approximating population status from fisheries catch trends is that catch can be affected by many factors besides trends in population abundance (Harley et al. 2001; Hilborn and Walters 1992). Fisheries catches can vary due to true fluctuations in population abundance, changes in management policies, changes in fishermen's interest and therefore effort in a given fishery, changes in gear used, or reporting inaccuracies — either from fisher to local regulatory body (see "Illegal fishing" in Figure 3.8) or from local regulatory body to national or international body (e.g. FAO) (Clarke 2004; Ferdouse 2004). Thus, although catch trends may partly reflect true underlying population signals, conclusions need to be reasonably robust to the variability in catches induced by other factors.

In this thesis I dealt with this variability in catch trends in three primary ways. First, I used methods that were robust to outliers thereby requiring a strong weight of evidence before detecting a signal, for example, loess smoothers (Cleveland 1979; Cleveland et al. 1992), additive models (Hastie and Tibshirani 1990; Wood 2004), and robust regression (Huber 1981; Venables and Ripley 2002). Second, I tested the sensitivity of my results to changes in cutoffs, data aggregation, and smoothing functions. Third, where possible I verified observed trends in catches with local reports describing trends in the fisheries. Whereas this is an important step for any analysis, it is especially so with catch data.

A possible alternative to the robust methods described and applied in this thesis would be state space models, which may be particularly suited to analyze catch data (Freeman and Kirkwood 1995). They provide a formal framework to estimate uncertainty due to process variability (here the true underlying population variability) and measurement error (e.g. reporting inaccuracies, changes in effort, and changes in gear). Although more challenging to implement, state space models could be applied to many of the problems discussed in this thesis, and may provide an important direction and framework for future analyses.

A second central problem I repeatedly addressed in this thesis was the evaluation of multiple sets of short time series data (longitudinal data) in which observations were truncated (censored) at the beginning, end, or both. If not accounted for, the structure of this data could have introduced biases to analyses investigating changes over time. I encountered this problem with both the fishery status analysis

(Chapter 2) and time to peak analyses (Chapter 2 and 3). Here, older fisheries had longer data series often showing several local peaks in catches in addition to an overall peak. In contrast, newer fisheries often showed only one or few peak(s) and it was unclear if they represented an overall peak in the catch series. In Chapter 2, when assessing fishery status, I addressed the increasing censoring of newer fisheries by developing robust methods that dynamically assessed status. There I used the first major peak in a fishery as it developed to treat all catch series equally (see Section 2.3.5). When assessing time to peak across taxa, I addressed the censoring by implementing a sampling routine to draw censored values from a pool of potential values (see Section 2.3.8). In Chapter 3, I dealt with the same problem by verifying individual catch trends with descriptions of fishery trends in the literature until so few censored cases remained that they did not affect the overall outcome of the analysis. Although challenging, it is imperative that this bias be accounted for to conduct valid inference.

To my knowledge, their exists no formal statistical methodology to deal with this type of censored data without either (1) making an assumption about the underlying trend, itself the objective of my inference, or (2) sampling possible values from a probability distribution. Where such a distribution is unclear, as in Section 2.3.8, values can be sampled from previously observed possible values. Censored data can be formally accounted for with survival analysis by using, for example, a Cox proportional hazards model (Cox 1972), which I tried in this thesis. However, this type of model cannot be used when the underlying survival probability is suspected of changing over time and is the statistic of interest. The approaches demonstrated here could be applied in any field where there is an analysis of time to an event that is suspected of changing.

4.2 The Effects of Scale

Throughout Chapters 2 and 3, the level of taxonomic and spatial aggregation of catches affected the conclusions. When examining country by country catch trends (e.g. Figures 2.S-4, 3.2), the picture looked remarkably different than catch series aggregated by taxa across countries (e.g. Figures 2.2, 3.6). Also, when I investigated sea cucumber fisheries in greater detail (Chapter 3), patterns of faster fishery development time from the 1960s to 1990s were strongly evident that were not clear in the cross-taxa analysis where I had to make conservative assumptions about the time to peak of potentially censored fisheries (Chapter 2). Further, even catch statistics aggregated on a large regional scale can hide underlying local patterns of serial exploitation (Chapter 3, Figure 3.8).

As of yet, it is unclear whether the more pronounced patterns identified for sea cucumbers by examining them at a finer scale in Chapter 3 are unique to that taxa. I tried investigating other taxa in more detail as well; for example, squid fisheries suggested similar patterns. However, squid fisheries are driven by multiple main markets and import statistics of sufficient temporal length to make defensible conclusions were unavailable (Section 2.3.7). Other invertebrate taxa also lacked sufficiently detailed data or had a more complex market structure that would need a different analytical approach. It is plausible, although so far difficult to confirm, that the patterns observed for sea cucumber fisheries may apply to many high-value invertebrate fisheries that have expanded over the last half century. The time frame is important, since recent fisheries have developed in an age when rapid and comparatively inexpensive international transport has been available (Berkes et al. 2006).

4.3 Management Implications

Many invertebrate species that are of interest to fisheries tend to be sessile or slow-moving benthic organisms that are relatively easy to fish out of large spatial areas (Botsford et al. 2004; Orensanz et al. 2004; Smith and Sainte-Marie 2004). Also, several species are broadcast spawners (e.g. sea cucumbers, sea urchins, abalone) that require a sufficient population density to persist lest they suffer an Allee effect (see Chapter 3 Introduction; Quinn et al. 1993; Hobday et al. 2001; Smith and Sainte-Marie 2004). As well, some species, such as sea cucumbers (Uthicke et al. 2004), abalone (Hobday et al. 2001), and some clams (Orensanz et al. 2004) have slow life histories that reduce the capacity for rapid population replenishment. Given these factors that increase vulnerability to overfishing, their high economic value (FAO 2009*a*), and the patterns of declines discussed in this thesis, it is possible that invertebrates are as, if not more, susceptible to overharvesting than finfish species. Therefore, the consideration of management strategies such as rotational harvesting (Caddy and Seijo 1998; Myers et al. 2000) and reserving portions of the population as unfished (e.g. Schroeter et al. 2001) are of utmost importance. Unfortunately, the sessile nature of many invertebrates lends them both to ease of protection within marine reserves but also perhaps to slow repopulation and recruitment from these reserves without additional restocking efforts (Purcell and Kirby 2006; Bell et al. 2008). Regardless, their relative immobility greatly increases the efficacy of using reserves as baselines to assess the effects of harvesting on surrounding populations (Schroeter et al. 2001).

Aside from their vulnerability to fishing, many invertebrates are in need of better monitoring, stock assessment, and fisheries regulation (Chapter 3; Anderson et al. 2008). Throughout this thesis I encountered problems with the lack of abundance data, reporting inaccuracies, and IUU catches. Further, a frequent sentiment was the lack of awareness of, and regulations to stop, the overexploition of invertebrate populations. Whereas this may be related to their previously low value and catch volume, in recent decades this has rapidly changed (Chapter 2) and concomitantly needs to be addressed with adequate management; ideally, before pervasive declines in abundance occur. Unfortunately, many invertebrate fisheries have already experienced strong population declines such as abalone in the southern United States and Mexico (Tegner et al. 1996; Hobday et al. 2001), oyster populations in Chesapeake Bay (Rothschild et al. 1994), ornamental invertebrate fisheries in Florida (Rhyne et al. 2009) and many sea cucumber fisheries around the world (Table 3.1). In contrast, in Chapter 2 I highlight examples of successful invertebrate fisheries management, namely Chilean artisanal gastropod (Castilla and Fernandez 1998), and New Zealand (Breen and Kendrick 1997) and western Australian (Phillips et al. 2007) rock lobster fisheries. In Chapter 3 I note successfully managed sea cucumber fisheries on the west coast of Canada (Hand et al. 2008), Alaska (Clark et al. 2009), and Japan (Akamine 2004). Other examples exist too, such as fisheries for sea urchins on the west coast of Canada (Perry et al. 2002), northern prawns in Australia (Hilborn et al. 2005; Dichmont et al. 2006), and abalone in Tasmania (Prince et al. 1998; Hilborn et al. 2005). These examples suggest that many of the same principles that apply to successful management of finfish fisheries can be applied to invertebrate fisheries (Hilborn et al. 2005; Worm et al. 2009). These strategies include property rights and incentives to harvesters that encourage conservation (Hilborn et al. 2005), trade regulations (Brander and Taylor 1998), protected areas (Quinn et al. 1993), a precautionary approach that collects necessary scientific information in phases (Perry et al. 1999), as well as effort restrictions, gear control, and appropriate quotas (Stefansson and Rosenberg 2005). Additionally, strong governance institutions operating at levels from the local to international scale are imperative to prevent the sequential exploitation of high-value newly emerging invertebrate fisheries (e.g. sea urchins, Berkes et al. 2006; and sea cucumbers, Chapter 3).

4.4 Ecosystem Consequences

There is increasing evidence that the removal of top oceanic predators can affect several lower trophic levels of marine food webs, sometimes leading to trophic cascades (e.g. Myers et al. 2007; Heithaus et al. 2008; Baum and Worm 2009). In reverse, it is plausible that the removal of the base of the food web could have cascading effects up the food web. Foremost, reducing prey abundance will limit the amount of energy available to higher trophic levels (Pope et al. 1994; Jennings et al. 2002). Reducing prey abundance will therefore likely have strong effects on the abundance as well as the recovery of currently depleted higher trophic levels. The direct effects of fishing prey on their predators are less established; however, there are examples of direct negative effects of overfishing blue mussels and cockles on eider ducks in the Danish Wadden Sea (Meltofte et al. 1994; Lotze 2005). Not only could this apply to bird-invertebrate or fish-invertebrate interactions, but also to invertebrate-invertebrate trophic relationships where depleting one population could affect another. For example, lobster (Lawrence 1987, and references within) are known to predate on sea urchins, but empirical evidence of the direct effect of removing prey on predator abundance is scarce. This represents an interesting area for future research.

In addition to acting as the base of marine food webs, many invertebrates provide critical ecosystem services. In this thesis I highlighted both the overall removal of biomass across taxa of species that provide important services including habitat, detritus consumption, and algal grazing; and a specific example, of bivalves, where I approximated the loss of filtration capacity globally on a daily basis (Chapter 2). In Chapter 3, I reviewed the ecological role that sea cucumbers play in coral reefs, temperate food webs, and kelp forests as water filterers, deposit feeders, and bioturbators. Local examples indicate that the overexploitation of sea cucumbers has already resulted in a measurable loss of such services (Bruckner et al. 2003). On a local and international level, the ecosystem services provided by invertebrates need to be studied in more detail and considered in management plans for invertebrate fisheries if we are to ensure a sustainable resource use and intact marine ecosystems in the future.

4.5 Outlook

This thesis has contributed to our understanding of global invertebrate fisheries dynamics, their drivers, and ecosystem consequences. Further, it has demonstrated novel and robust approaches to assessing these dynamics. In this section, I will outline three possible future extensions to this work.

First, the techniques and approaches of this thesis could be applied to other marine species. The robust and dynamic fishery-status assessment method (Section 2.3.5) could be applied to finfish and the results compared to previous methodologies as well as to invertebrates. With sufficiently long and reliable import data, the approaches to quantitatively assess large-scale spatial expansion of fisheries (Sections 2.3.7, 3.2.5) could be applied to other high-value taxonomic groups with more complex market structures. The fishery-by-fishery literature review conducted for sea cucumbers (Table 3.1) could be applied to other species to allow a more accurate analysis of boom-and-bust patterns over time without as many censored fisheries to sample time to peak for (as done in Section 2.3.8), and syntheses of local issues not evident from catch data aggregated on larger scales (Section 3.2.7).

Second, stock-recruit relationships for invertebrates are frequently unknown (Caddy 2004) but would be an important piece to the puzzle in managing their fisheries and predicting their stock status. When available they are typically highly uncertain, for example, for bay scallops in North Carolina (Peterson and Summerson 1992), crustaceans in Western Australia (Caputi et al. 1998), tropical shrimps (Garcia 1996), and abalone (McShane 1995). Even for the most intensely studied fish populations, stock-recruit relationships are challenging to identify without combining data across many populations (Myers et al. 1995; Myers and Mertz 1998). For invertebrates, I see two areas for future research: the systematic aggregation of existing stock-recruit data to allow meta-analytic inference,[1] and the application of carefully designed experimental studies by population to enhance the available data pool from which to draw (Wahle 2003).

Third, life-history characteristics such as slow growth (Uthicke et al. 2004), broadcast spawning and low population density (Quinn et al. 1993; Hobday et al. 2001), and large body size (Jablonski 1994) are suspected of decreasing the resilience of some invertebrate populations to overexploitation. However, for marine invertebrates, a systematic assessment of the relationship between life-history traits and frequency of overexploitation, rate of repopulation, or population status is lacking. Such analyses have been conducted for many other taxonomic groups, for example, for marine fishes (Denney et al. 2002; Reynolds et al. 2005*a*), marine and freshwater fishes (Olden et al. 2007), freshwater fishes (Reynolds et al. 2005*b*), birds (Bennett and Owens

[1] Work ongoing at: http://www.marinebiodiversity.ca/RAMlegacy/srdb/updated-srdb/srdb-resources

1997; Norris and Harper 2004), and terrestrial mammals (Cardillo et al. 2005; 2008; Davidson et al. 2009). But, comparatively little is available for marine invertebrates (see Dulvy et al. 2003 for a review). Logistic regression, potentially in a multimodel framework (Burnham and Anderson 2002), and regression trees represent powerful approaches on which to build predictive models that can be used to assess risk status for other species that we lack life-history data for (Davidson et al. 2009; Anderson et al. Unsubmitted manuscript). Such models would be particularly useful for marine invertebrates where knowledge of life-history traits is often lacking.

4.6 Conclusions

In conclusion, this thesis highlights the ecological and economic importance of marine invertebrates, their increasing contribution to marine fisheries, and their patterns of expansion and depletion both over space and time partly driven by world markets. The findings repeatedly suggest the need for more rigorous monitoring and reporting and for the opportunity to use successfully managed fisheries (both invertebrate and finfish) to better inform the management of new, emerging fisheries. These steps are critical if we are to ensure the long-term resilience of invertebrate populations, ocean ecosystems, and human well-being.

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