



Serial exploitation of global sea cucumber fisheries

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Abstract

In recent decades, invertebrate fisheries have expanded in catch and value worldwide. One increasingly harvested group is sea cucumbers (class Holothuroidea), which are highly valued in Asia and sold as trepang or bêche-de-mer. We compiled global landings, economic data, and country-specific assessment and management reports to synthesize global trends in sea cucumber fisheries, evaluate potential drivers, and test for local and global serial exploitation patterns. Although some sea cucumber fisheries have existed for centuries, catch trends of most individual fisheries followed boom-and-bust patterns since the 1950s, declining nearly as quickly as they expanded. New fisheries expanded five to six times faster in 1990 compared to 1960 and at an increasing distance from Asia, encompassing a global fishery by the 1990s. Global sea cucumber production was correlated to the Japanese yen at a leading lag. Regional assessments revealed that population declines from overfishing occurred in 81% of sea cucumber fisheries, average harvested body size declined in 35%, harvesters moved from near- to off-shore regions in 51% and from high- to low-value species in 76%. Thirty-eight per cent of sea cucumber fisheries remained unregulated, and illegal catches were of concern in half. Our results suggest that development patterns of sea cucumber fisheries are largely predictable, often unsustainable and frequently too rapid for effective management responses. We discuss potential ecosystem and human community consequences and urge for better monitoring and reporting of catch and abundance, proper scientific stock assessment and consideration of international trade regulations to ensure long-term and sustainable harvesting of sea cucumbers worldwide.

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Introduction

Over the past century, we have witnessed the decline of many traditional finfish fisheries as well as the expansion of existing and the establishment of new invertebrate fisheries (FAO 2009a). 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 because of their release from predation (e.g. Worm and Myers 2003; Heath 2005; Savenkoff *et al.* 2007; Baum and Worm 2009). Despite an overall global increase in invertebrate catches and target species (Anderson 2010), 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; Uthicke *et al.* 2009), 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).

Sea cucumber fisheries have expanded worldwide in catch and value over the past two to three decades (e.g. Conand and Byrne 1993; Conand 2004; FAO 2008). Sea cucumbers (class Holothuroidea) are elongated tubular or flattened soft-bodied marine benthic invertebrates, typically with leathery skin, ranging in length from a few millimetres to a metre (Bell 1892; Backhuys 1977; Lawrence 1987). Holothuroids encompass ~14000 known species (Pawson 2007) (although most fished species are within the order Aspidochirotrida) and occur in most benthic marine habitats worldwide, in temperate and tropical oceans, and from the intertidal zone to the deep sea (Hickman *et al.* 2006).

Indo-Pacific regions have harvested and traded sea cucumbers for over one thousand years, driven primarily by Chinese demand (Conand and Byrne 1993). Harvesters typically capture sea cucumbers by hand, spear, hook, or net while wading or diving

with snorkel or SCUBA (Self Contained Underwater Breathing Apparatus) gear. In some regions, and especially for less valuable species, sea cucumbers are trawled (Aumeeruddy and Payet 2004; Kumara *et al.* 2005; Choo 2008b). They are consumed both reconstituted from a dried form (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 in sea cucumber fisheries around the world (e.g. FAO 2004, 2008). However, sea cucumber populations are particularly vulnerable to overfishing for at least two primary reasons. First, harvesters can easily and effectively capture shallow water holothurians (Uthicke and Benzie 2000; Bruckner *et al.* 2003). 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; Uthicke *et al.* 2009), resulting in population collapse and inhibiting recovery (Uthicke and Benzie 2000; Bruckner 2005). Owing to these factors, overfishing has severely decreased the biomass of many sea cucumber populations (e.g. Skewes *et al.* 2000; Conand 2004; Lawrence *et al.* 2004). Thus far, even with harvesting closures, sea cucumber stocks seem slow to recover (D'Silva 2001; Uthicke *et al.* 2004; Ahmed and Lawrence 2007); and recovery can potentially be on the order of decades (Uthicke *et al.* 2004). Other broadcast spawning invertebrate populations that have been severely depleted, such as pearl oysters in the South Pacific, have not recovered even 50–100 years later (Dalzell *et al.* 1996).

Sea cucumbers are important ecologically as suspension feeders, detritivores and prey. 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; Massin 1982a; Moriarty 1982). Their function as suspension or 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). As suspension feeders, sea cucumbers regulate water quality by affecting carbonate content and the pH of the water (Massin 1982b). 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 1982b). For example, on coral reefs, healthy sea cucumber populations can bioturbate the entire upper five millimetres of sediment once a year ($4600 \text{ kg dry weight year}^{-1} 1000 \text{ m}^{-2}$), 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. Holothurians are also important prey in coral reef and temperate food webs (Birkeland *et al.* 1982; Birkeland 1989; Francour 1997) both in shallow and in deep water (Jones and Endean 1973; Massin 1982b), where they are consumed particularly by fishes, sea stars and crustaceans (Francour 1997).

In addition to the ecological importance of sea cucumbers, their fisheries are of great social and economic importance to many coastal communities. For example, just a few years after beginning in the Maldives, the sea cucumber fishery became the most highly valued fishery outside the tuna fishing season, representing 80% of the value of all non-fish marine products in 1988 (Joseph 2005). Sea cucumber fisheries form the main source of income for many coastal communities in the Solomon Islands (Nash and Ramofafia 2006) and for 4000–5000 families in Sri Lanka (Dissanayake *et al.* 2010). Perhaps most importantly, sea cucumber fisheries are economically decentralized. Whereas their total global value is low compared to other higher volume fisheries (Ferdouse 2004), economic benefits are obtained immediately at the village level (Kinch *et al.* 2008b). In contrast, other high-value fisheries, such as tuna fisheries, have higher initial costs and bring wealth to a more centralized group of people (Kinch *et al.* 2008b).

Despite the ecological and social importance of sea cucumber populations, the evaluation of their global status is challenging. There is generally a lack of abundance data; catch, import and export statistics are often incomplete; and the trade of sea cucumbers is complex (see Baine 2004; FAO 2004, 2008). Nonetheless, reports such as FAO (2004, 2008) and the SPC Beche-de-mer Information Bulletin (<http://www.spc.int/coastfish/en/publications/bulletins/beche-de-mer.html>) have assimilated much of

Table 1 Countries and regions included in different analyses and their sources.

Country	Sources	Landings		Localized status, depletion and management						
		Traj	Dist	Exp	Pop	Spat	Spp	Size	IUU	Lack reg
Australia	Uthicke and Benzie 2000; Uthicke 2004; Uthicke <i>et al.</i> 2004	'	'	NA	1	1	1	1	?	0
Canada – East	Hamel and Mercier 2008; Rowe <i>et al.</i> 2009	–	'	0	0	?	NA	?	?	0
Canada – West	Hand <i>et al.</i> 2008; Hamel and Mercier 2008	–	'	0	0	?	NA	1	?	0
Chile	Toral-Granda 2008b	–	'	?	?	?	?	?	?	1
Egypt	Lawrence <i>et al.</i> 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 2008b	'	'	1	1	1	1	1	1	1
Japan	Akamine 2004	–	'	0	0	?	?	?	?	0
Madagascar	Rasolofonirina <i>et al.</i> 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 2008b	'	'	1	1	?	NA	?	1	0
New Caledonia	Conand and Byrne 1993	'	'	1	1	1	1	?	?	1
Papua New Guinea	Kinch <i>et al.</i> 2008	'	'	1	1	1	1	1	1	0
Philippines	Schoppe 2000; Gamboa <i>et al.</i> 2004; Choo 2008a	'	'	1	1	1	1	1	1	1
Republic of Korea	Choo 2008b	'	'	?	?	?	?	?	?	?
Solomon Islands	Nash and Ramofafia 2006	'	'	1	1	1	1	1	?	0
Sri Lanka	Kumara <i>et al.</i> 2005; Dissanayake <i>et al.</i> 2010	–	'	1	1	1	1	?	1	1
Tanzania	Jiddawi and Ohman 2002; Mmbaga and Mgaya 2004	'	'	1	1	1	1	1	1	1
USA – Alaska	Hamel and Mercier 2008; Clark <i>et al.</i> 2009	–	'	0	0	?	NA	0	?	0
USA – California	Schroeter <i>et al.</i> 2001; Hamel and Mercier 2008	'	'	?	1	?	?	?	?	0
USA – Maine	Chenoweth and McGowan 1995; Hamel and Mercier 2008	–	'	?	?	?	NA	?	?	0
USA – Washington State	Bruckner 2005; Hamel and Mercier 2008	'	'	0	1	?	NA	?	1	0
Cambodia	del Mar Otero-Villanueva and Ut 2007	–	–	1	1	1	1	?	?	1
China	Chen 2004; Choo 2008b	–	–	1	1	?	NA	?	?	0
Ecuador – Galápagos	Hearn <i>et al.</i> 2005; Toral-Granda 2008a	–	–	1	1	1	1	?	1	0
Ecuador – Mainland	Toral-Granda 2008a	–	–	1	1	?	NA	?	1	1
Kenya	Samyn 2000	–	–	1	1	1	1	?	?	1
Peru	Toral-Granda 2008b	–	–	?	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 2008b	–	–	1	1	1	1	?	1	0
Torres Strait Islands	D'Silva 2001	–	–	1	1	?	?	?	?	0
Vietnam	del Mar Otero-Villanueva and Ut 2007; Choo 2008b	–	–	1	1	1	?	?	1	1
Yemen	Hasan 2009	–	–	1	1	?	1	?	1	?

', included; –, not included; 0, absent; 1, present; ?, unknown or not mentioned, NA, not applicable; Traj, Trajectory and time to peak analyses; Dist, Distance from Asia analysis; Exp, Over-exploited; Pop, Population decline; Spat, Spatial expansion; Spp, Species expansion; Size, Size depletion; IUU, Illegal, Unregulated and Unreported fishing; Lack reg, Lack regulations.

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 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). However, we lack a quantitative analysis of the typical trajectory, potential drivers, and combined spatial and temporal dynamics of sea cucumber fisheries around the world.

In this paper, using a global catch database supplemented by regional fishery assessments, our objectives were to (i) quantitatively synthesize the current status and trends of sea cucumber fisheries worldwide, (ii) analyse their underlying drivers, (iii) test for patterns of serial exploitation and (iv) assess the management state of these fisheries to determine where improvements could be made. Our overall goal was to present data that could better inform the development of both global trade regulations and regional management strategies to ensure long-term and sustainable harvesting of sea cucumbers worldwide.

Methods

Catch data sources

Abundance data for sea cucumber populations are largely unavailable (see FAO 2004, 2008). Therefore, to form a globally consistent database for our analysis, we obtained catch data (reported landings in wet weight by country) for sea cucumber fisheries from the Sea Around Us Project (Watson *et al.* 2005). These data span from 1950 to 2006, are largely derived from the Food and Agriculture Organization's (FAO) catch database and are supplemented with regional and reconstructed datasets where possible (Zeller and Pauly 2007). Although, especially in the Indo-Pacific, some sea cucumber fisheries have been around for centuries, most fisheries have only started, resurged, or substantially expanded since the 1950s (see Table S1). Thus, our study considers this recent resurgence of sea cucumber fisheries around the globe.

Not all catches reported to FAO are reliable (e.g. Clarke 2004; Watson *et al.* 2005). We therefore compared these catch data against regional records wherever possible (Table 1). We aimed at getting the most reliable estimates for the characteristics of the catch trends including starting years, years of peak catch and general patterns of increase and decline. As there are a number of distinct relatively 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. Because Canada reports sea cucumber catches to FAO grouped as 'benthic invertebrates', we extracted catch data for British Columbia and the Atlantic provinces 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 (<http://www.maine.gov/dmr/commercialfishing/historicaldata.htm>). Catch data for Washington and California were obtained from the Pacific Fisheries Information Network (<http://pacfin.psmfc.org/>). Data for Australia were extracted from Uthicke (2004) and were originally obtained from the Queensland Fisheries Service. They represent the gutted weight of *Holothuria whitmaei* on the Great Barrier Reef throughout the recent revival of the fishery beginning in the mid-1980s. Sea cucumbers were previously heavily fished in the region in the late 1800s and early 1900s (Uthicke 2004).

We made two alterations to the data: (i) we removed initial years with less than one tonne of catch, because countries inconsistently reported initial catches (this affected Indonesia, Fiji, Philippines and the Maldives); and (ii) we removed years of anomalously high catch from Madagascar (1964, 1994–1997). These years of catch did not match the trajectory reported by Rasolofonirina *et al.* (2004) who studied the fishery in detail. Because many of the low-volume catches in the database are erratically reported and of short duration, we focused on the more substantial fisheries when investigating catch trends. We investigated fisheries that surpassed 250 t wet weight for more than one year (to account for outlying years).

Although all sea cucumber catches reported to FAO are supposed to be in wet weight, Choo (2008) questioned whether this was entirely the case in southeast Asian countries. Because wet weight can be 6–25 times heavier than dry weight (Skewes *et al.* 2004; Purcell *et al.* 2009), this would affect our 250 t-inclusion criteria. However, all southeast Asian countries with available catch data were included in our analysis with the exception of Cambodia. Cambodia reported 150 t in 1987 and last reported 3 t in 2003, and there is no reason to believe that these catches are in dry weight and thus off by an order of magnitude (del Mar Otero-Villanueva and Ut 2007). Beyond the inclusion criteria of 250 t, we based our analysis on catch trends scaled to their maximum catch; therefore, wet vs. dry weight would not impact our conclusions.

Typical trajectory of sea cucumber fisheries

Under an ideal fisheries management scenario, a fishery would develop as a gradual increase towards a plateau near a sustainable yield (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) and, at least for tropical sea cucumber fisheries, a sustainable yield may be less than 5% of virgin biomass removed annually (Uthicke 2004). Therefore, we tested whether individual sea cucumber fisheries followed a similar trajectory of rapid increase, short peak and subsequent decline. We note that declining catch trends in the investigated fisheries may reflect declines in abundance because of over-exploitation (among other factors), or declines in catches because of restrictive management and changes in effort, or a combination of these.

To enable calculation of a typical trajectory, we lagged the catch series so that each country's catch reached a maximum in the same year. 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 *et al.* 1992; R Development Core Team 2009) (smoothing span = 75% of the data) so that our estimates were robust to outliers. Here, we focused on fisheries that had peaked or reached a plateau and excluded fisheries that were still expanding as we did not know when they would peak or plateau in catch. We did not include Japan as it has a long established fishery that started well before the 1950s, declined in catch from the 1970s to the 1990s because of management decisions (Akamine 2004), and has recently begun expanding its catches (Fig. 1a).

Absolute catch was not comparable between all regions investigated for several reasons: (i) catch is frequently underreported in some regions (Clarke 2004; Choo 2008b); (ii) the harvestable area was not comparable; and (iii) the ecological productivity and virgin biomass were not comparable. We therefore investigated the relative trajectory of sea cucumber fisheries irrespective of absolute volume by dividing the catch within each country by its standard deviation (standardized catch). However, when showing our results, we transformed our model fits back to the original scale of wet weight in tonnes.

We used a generalized additive model (GAM) (Hastie and Tibshirani 1990; Wood 2006, 2008) with a gamma error distribution and a log link to determine the typical trajectory. The gamma distribution is an appropriate distribution for

continuous non-negative data (such as fisheries catch); it is frequently used in combination with a log link to model catch due to suspected multiplicative effects on catch volume (see Xiao *et al.* 2004). We incorporated first-order autoregressive serial correlation structure of the catch series in our model (Pinheiro and Bates 2000; Wood 2006).

We modelled catch for each year i and each country j according to a parametric term β_j and a common smooth function f applied to the years Y_{ij} relative to the year of peak catch for each country Y_{peak_j} :

$$\text{Standardized catch}_{ij} \sim \text{gamma}(\mu_{ij})$$

$$\log(\mu_{ij}) = \beta_j + f(Y_{ij} - Y_{peak_j}) + e_i,$$

where μ_{ij} represents the mean of the gamma distribution, and e_i represents the autoregressive function:

$$e_i = \phi e_{i-1} + \varepsilon_i$$

ε_i represents independent identically distributed random variables that follow a normal distribution with a mean of zero. ϕ represents the correlation between subsequent years. We fit a separate GAM of the same form but with its own smooth function to the Republic of Korea data. Having developed into a substantial fishery before 1950, it followed a slower developmental trajectory than the other countries. Its exclusion had little effect on the model because it represented only 1 of 16 countries, but fitting it separately gave a more realistic picture of its trajectory.

Drivers of sea cucumber fisheries

The majority of global sea cucumber catch is imported to Hong Kong where it is mainly then re-exported to mainland China (Clarke 2004; Ferdouse 2004). Singapore is the second biggest market, but its annual imports and re-exports are well below Hong Kong's (Jaquemet and Conand 1999). Singapore last reported sea cucumber imports in 1994 with 1213 t compared to 7281 t for Hong Kong. We verified this trend by examining sea cucumber export and import values from FAO (2009b).

When supplier demand drives production, new orders for goods can suggest impending economic changes (Lahiri and Moore 1991). This is partic-

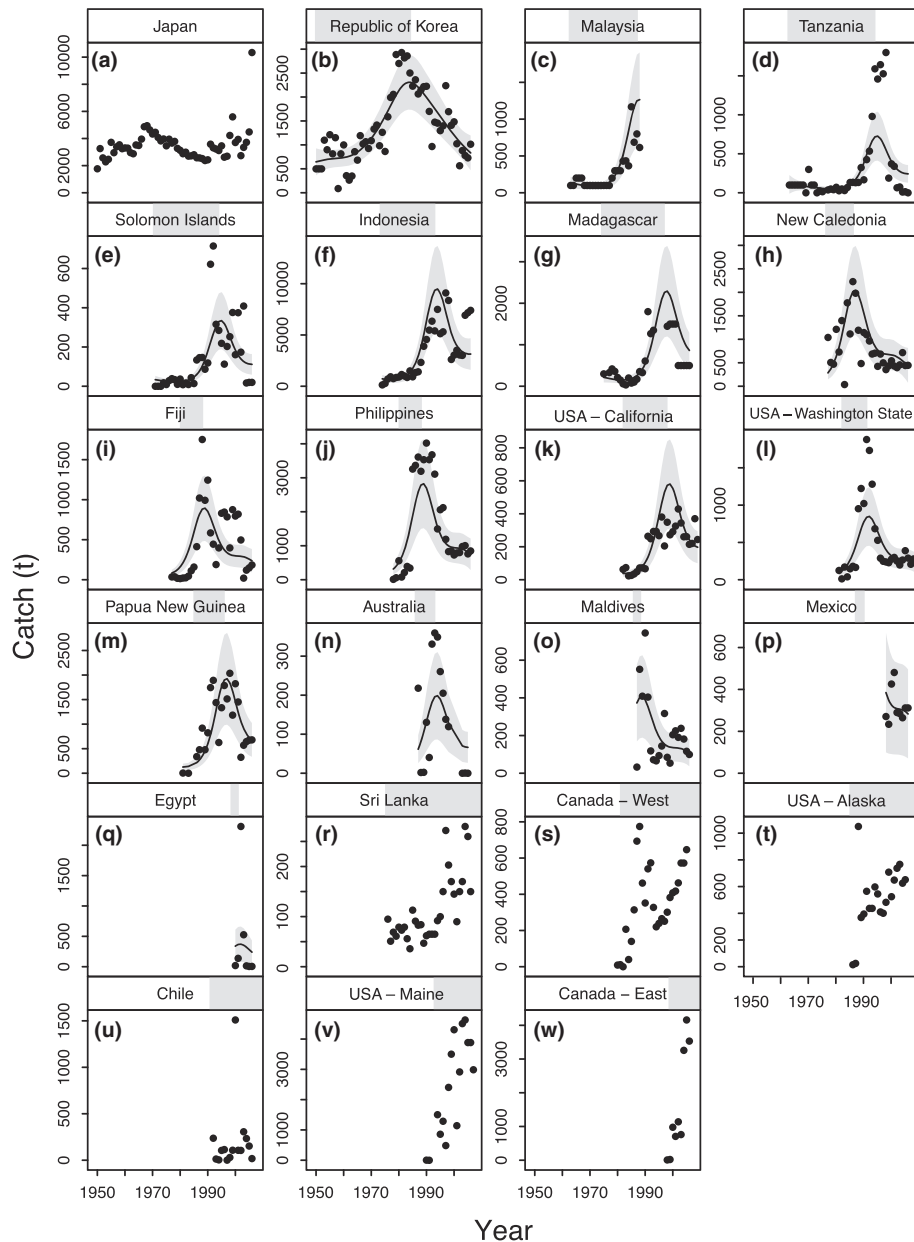


Figure 1 Sea cucumber catch trends as reported by the Sea Around Us Project and other sources (see Methods) for (a) Japan, (b–q) countries used in the time to peak analysis, and (r–w) countries or regions without a peak or plateau in catch that were added for the distance from Hong Kong analysis. Grey bars in title regions indicate time from calculated start of fishery (10% of peak catch) to year of peak catch (as determined by a loess function). Countries are ordered by starting year within the two groups (a–q and r–w). Lines represent predicted catch based on a single generalized additive model with country as a parametric term and a common smooth term. The Republic of Korea model was fitted separately. Shaded regions represent 95% credible intervals.

ularly true when demand fluctuates for high-value limited-volume goods because it encourages producers to wait for orders as opposed to anticipating demand (Lahiri and Moore 1991). Sea cucumbers are valuable, their value is mostly driven by

buyers in one region and they are transported over great distances (Clarke 2004). Therefore, we hypothesized that global sea cucumber production might correlate with the Asian economy at a leading lag.

Particularly since the Plaza Accord in 1985, an agreement to depreciate the United States dollar (USD) compared to the Japanese yen (JPY) and German mark, the USD/JPY exchange rate has been a primary factor describing the short-term macroeconomic performance of Asian countries (Kwan 1998). Further, unlike many other Asian currencies, the JPY has not been fixed to the USD throughout much of the investigated time period. Therefore, we used the value of the JPY in USD as a proxy for the relative strength of the Asian economy.

We defined global sea cucumber production as catches (1950–2006; sources as described above) combined with aquaculture production as reported by Chen (2004) from 2001–2002 and by FAO (2009b) from 2003–2008. China is the main aquaculture producer of sea cucumbers. Prior to 2001, they reported production mixed with ‘other aquatic products’, but Chen (2004) suspects this production was minimal.

We log transformed both time series to stabilize their variance and then took the annual first difference to achieve stationarity. With the knowledge that the Plaza Accord had a substantial effect on the USD/JPY relationship, and from visual inspection of the time series, we suspected the relationship between the two time series might have changed over time. We tested for correlation of the time series at lags of one and 2 years (with sea cucumber leading USD/JPY) before and after 1985. Correlation was strongest at a leading lag of one year before 1985 and 2 years after 1985. We shifted the data accordingly and proceeded to model this relationship using an additive model.

Rate of development

Given that demand for sea cucumbers has increased over time (Baine 2004; Clarke 2004), we tested whether newer fisheries reached peak catch or a long-term catch plateau more rapidly. This could indicate that demand created an increased pressure to fish or that less substantive stocks were increasingly exploited. We considered a fishery to have started when its loess-smoothed catch surpassed 10% of its maximum loess-smoothed catch. Here, we considered all new, resurging or expanding fisheries since 1950 because (i) prior catch data for historical fisheries is inconsistently available (and we may therefore

be missing peaks in the earlier catch data) and (ii) our hypothesis is based on the globalization of trade, which mainly developed during the second half of the 20th century. However, even fisheries that have been around for longer time periods often showed resurgence in recent years, which was used as the recent starting year (Table S1). We then tested the relationship between the time to peak and recent starting year using a generalized linear model (GLM) assuming a gamma error distribution and a log link.

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 as sea urchins (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 analysed regions, we added six regions that surpassed our volume cutoffs but for which we could not verify peaks or plateaus in catch (Fig. 1s–x). For these regions, we assigned starting years as 10% of maximum observed catch. We used great circle distance to Hong Kong as a proxy for flight or shipping distance and hence transportation cost. We acknowledge that distance is an imperfect metric of transportation cost; however, transportation cost has changed over time, and we were unable to obtain detailed historical records for all investigated countries. As a point of departure, we used the city with the greatest population as a proxy for the main air-freight airport or shipping dock. City population data were obtained from 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). We tested the relationship between the distance from Hong Kong and the recent start of the fishery since 1950 using a GLM with a gamma error distribution and a log link. We also tested whether the relationship changed when we used the earliest historical reported year of fishing (Table S1).

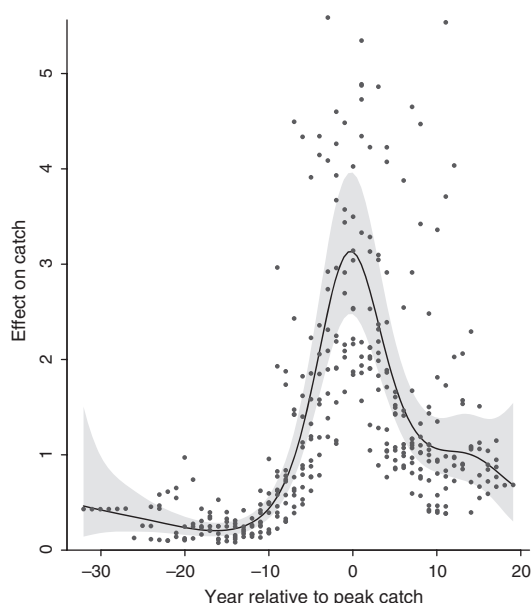


Figure 2 Typical trajectory of global sea cucumber fisheries with catch trends lagged to peak in the same relative year (year 0) from a generalized additive model. Dots represent partial residuals of catch trends for individual countries. The line represents the common fitted smooth function across countries, and the shaded region represents a 95% credible interval. The model was fitted using a gamma error distribution and log link and transformed back to the original scale for display. Some extreme values near the peak in catch are greater than the vertical scale and are not shown.

Sensitivity analyses

We tested the robustness of our results in the modelling of a typical catch trajectory, change in rate of development and spatial expansion from Asia to a set of alternative cut offs and scenarios. We repeated our analyses including only fisheries that surpassed 200 or 500 t wet weight for more than one year. Because the United States and Canadian fisheries were 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 modelling of distance from Asia).

Localized status, depletion and management

To evaluate other types of depletion that our global scale analysis using aggregated catch could have hidden, we reviewed recent reports of sea cucumber

fisheries from around the world (Table 1). We assessed whether there was any reporting of over-exploitation, 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 1). In our analysis, unknown or not reported instances were coded as absent. Therefore, our results likely underestimate the prevalence of these factors.

We reviewed all recent available literature from FAO (2004, 2008), 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 at least two of the investigated cases:

Over-exploitation

We identified evidence that the fishery was currently over-exploited. Where biomass estimates were available, the harvesting level had to be below an estimated maximum sustainable yield as of the last reported year. Most often such a reference point was unavailable or unreliable; therefore, we relied upon the assessment of the exploitation level in the literature.

Population decline

We searched for descriptions or data noting a substantial 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 2008a).

Lack of regulation

We noted fisheries that were considered unregulated as of the last available report. A ban on fishing was not considered regulation unless other management preceded it. The use of licenses with no regulatory means to control license numbers or effort was not in itself considered regulation.

Results

Catch data

Overall, global sea cucumber catch has increased over the past six decades from ~2300 t wet weight in 1950 to ~30500 t wet weight in 2006. The Sea Around Us Project catch database reports sea cucumber landings for 37 countries. Of these, we included in our analysis 19 countries that surpassed 250 t wet weight for at least 2 years, and an additional four regions from the United States, two from Canada and one from Australia (Fig. 1). We found documentation of a peak in catch or projected plateau for 16 of the regions, which were included when modelling the typical catch trajectory and assessing the rate of development (Table 1, Fig. 1b–q). The other six fisheries that may still be expanding in volume, plus Japan, were added for the distance from Asia analysis (Fig. 1a, r–w). Finally, additional fisheries with lower catch volumes or unreported catch data were included in the localized status, depletion and management analyses (Table 1).

Typical trajectory of sea cucumber fisheries

The catch trajectories of individual sea cucumber fisheries followed a typical trajectory of rapid increase, short peak and subsequent decline because of over-exploitation or restrictive management. The GAM with a common smooth function across countries displayed a marked

consistent decline in catch after peaking, a trend similar in shape and magnitude to the initial expansion (Figs. 1, 2). The model explained 50% of the variance in the data (adjusted R^2). The correlation of catch between subsequent years across countries (ϕ) was estimated at 0.40. The separate Republic of Korea GAM was fit with a less-curved smooth function (estimated degrees of freedom of 4.1 vs. 6.8) with an adjusted R^2 of 0.74.

Drivers of sea cucumber fisheries

In 2006, Hong Kong was responsible for 58% of global sea cucumber imports by volume with the majority of the remaining catch imported by nearby Asian countries (Fig. 3). According to these FAO trade statistics, the largest exporter of sea cucumbers by volume was the Philippines (Fig. 3). 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.

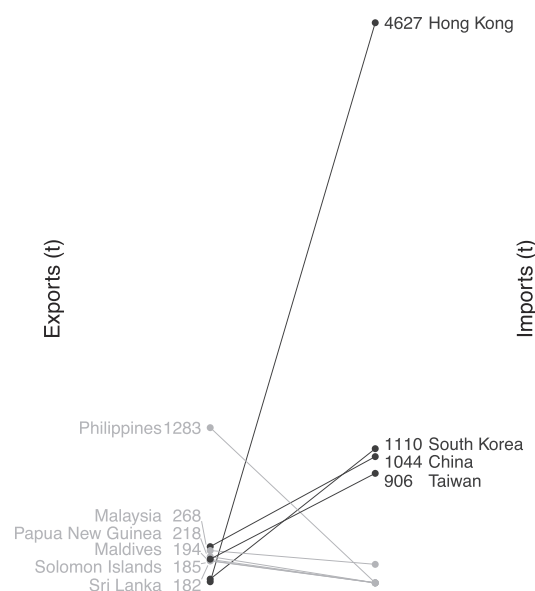


Figure 3 Bump chart of sea cucumber exports and imports by volume in 2006. Countries labelled on the left (grey text and lines) exported a greater volume than they imported. Countries labelled on the right (black text and lines) imported a greater volume than they exported. Numbers beside country labels show export or import volume in tonnes. Only countries with greater than 150 t of imports or exports are shown.

Both the value of the JPY in USD and global sea cucumber production increased sharply in the mid-1980s (Fig. 4a). They were most strongly correlated when sea cucumber production lead the yen by one year prior to the Plaza Accord in 1985 and by 2 years after (Fig. 4b). The shape of the additive model fit suggested there may be a closer association between the two time series at larger positive changes in global sea cucumber production (Fig. 4c). This means there was stronger evidence for large positive annual changes in sea cucumber production corresponding to large positive annual changes in the USD/JPY and less evidence for small positive or negative changes. The additive model explained 39% of the variation in the data (adjusted R^2 ; Fig. 4c).

Rate of development

Our data show that fisheries tended to reach peak catch more rapidly over time with an instantane-

ous rate of change in time to peak of -0.058 (95% CI (confidence interval): -0.076 to -0.040) (Fig. 5a). Based on the model, the predicted time to peak catch decreased from 34 years in 1960 (95% CI: 23–50 years) to 6 years in 1990 (95% CI: 5–8 years).

Distance from Asia

Since 1950, sea cucumber fisheries tended to develop increasingly far from their main Asian market with an instantaneous rate of change in distance of 0.037 (95% CI: 0.019 – 0.053) (Fig. 5b). The use of starting dates reflecting the earliest known fishing in each region extended the pattern over a longer period of time but did not substantially alter the shape or quality of the fit (Fig. S1, Table S1). Sea cucumbers have been fished and traded in the Indo-Pacific for over one thousand years (Conand and Byrne 1993). By the 1950s, most sea cucumber fisheries still occurred in the

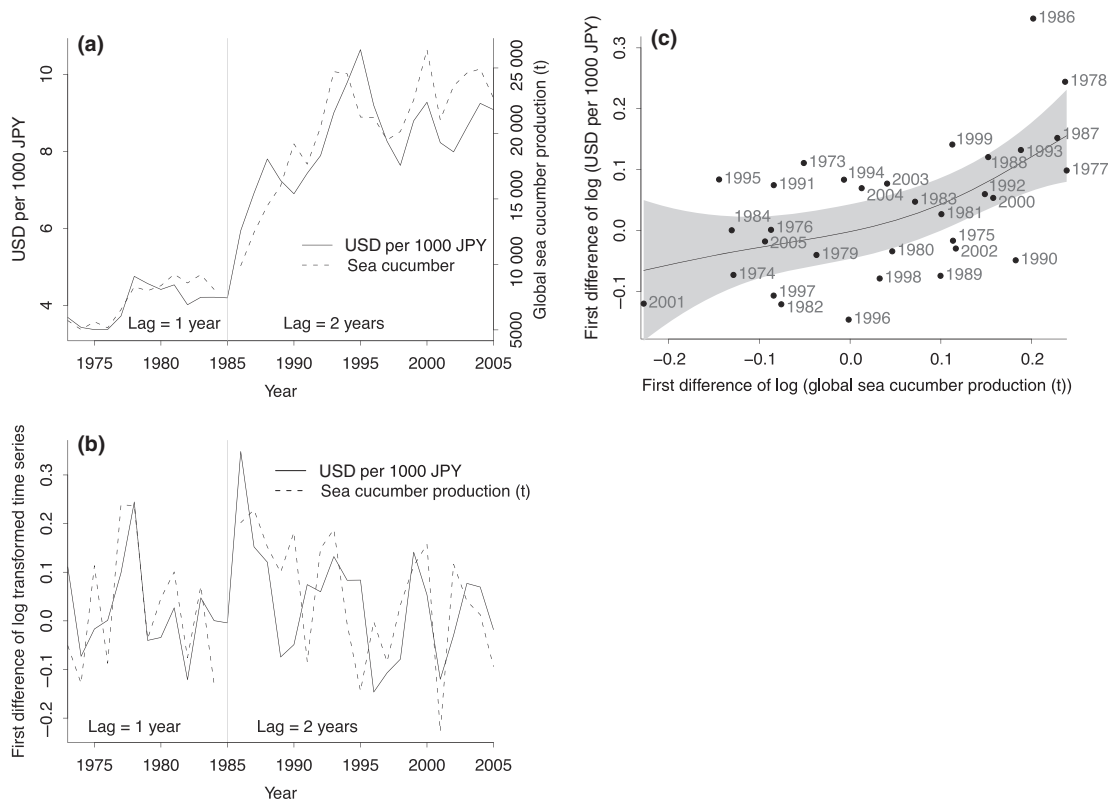


Figure 4 (a) The value of 1000 Japanese yen (JPY) in United States dollars (USD) and global sea cucumber production (capture and aquaculture fisheries combined in tonnes) over time. The sea cucumber production data was shifted forwards by one year before 1985 and 2 years after 1985 (the year of the Plaza Accord is represented by the vertical grey line). Years throughout all three panels refer to the years for the USD/1000 JPY series. (b) Annual first difference of the log transformed time series. (c) The two time series plotted against each other after lagging the data. Line and shaded region represents an additive model and 95% credible interval respectively.

Indo-Pacific, yet by the 1990s sea cucumber fisheries spanned the globe (Fig. 5c).

Sensitivity analyses

Our overall conclusions about the typical trajectory, rate of development 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.

Localized status, depletion and management

As of their last published reports (see Table 1), 69% of sea cucumber fisheries were noted as over-exploited and 81% as having declined in abundance because of overfishing (Fig. 6). Reports noted extinction or extirpation of at least one species in Egypt, Indonesia and Malaysia. See Table 1 for references for all examples in this section unless otherwise specified.

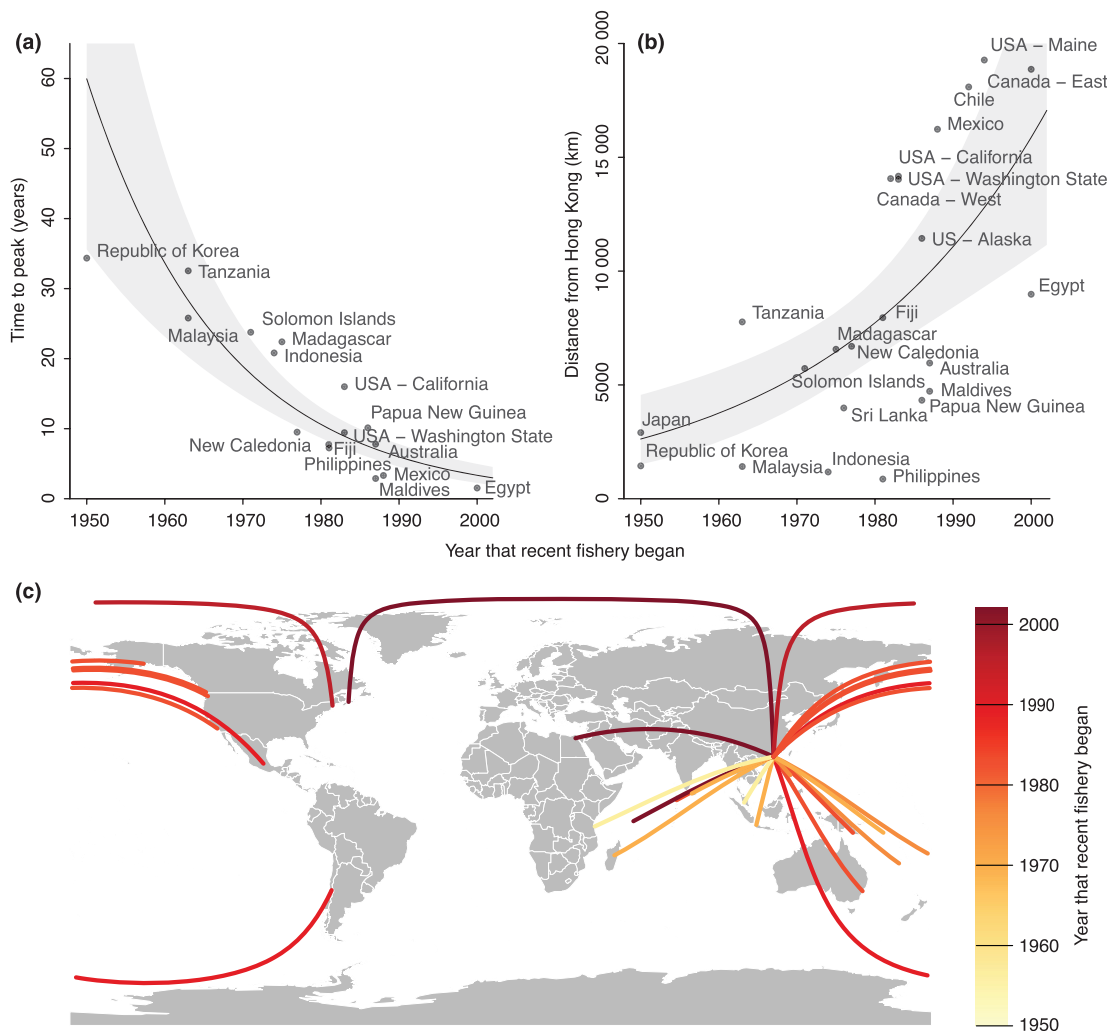


Figure 5 (a) Time for sea cucumber fisheries to reach a peak or long-term plateau in catch vs. the year when a recent (<50 years) fishery began. (b) Great circle distance between Hong Kong and the most populated cities of countries or regions fishing sea cucumbers vs. the year when a recent fishery began. Lines in a and b represent generalized linear model fits, and shaded regions indicate 95% confidence intervals. (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 recent fishery (see Fig. S1 for historical starting years).

Serial exploitation was reported in three forms. 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 low-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: *H. whitmaei* and *H. fuscogilva*) to harvesting high volumes of low-value species (e.g. 'edible' or 'burnt hotdog': *H. edulis* and 'patola': *H. leucospilota*) as the high-value species became depleted. Third, a reduction in the typical size of sea cucumbers harvested was noted in 35% of the fisheries. For example, on the Great Barrier Reef, the average weight of *H. whitmaei* in harvested zones was ~20% lower than in unfished zones (Uthicke and Benzie 2000). In the Galápagos, the mean fished size of *Isostichopus fuscus* decreased from 24.5 to 22.5 cm from 1999 to 2002 (Shepherd *et al.* 2004).

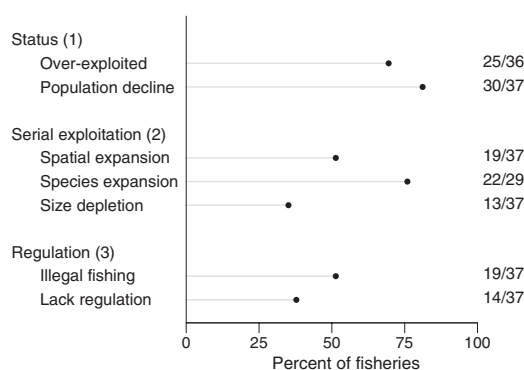


Figure 6 Frequency that local issues related to sea cucumber fisheries were documented in the literature. Issues evaluated were (from top to bottom) (1) status: evidence of current over-exploitation and a decline in abundance or biomass of the population; (2) serial exploitation: evidence of spatial fisheries expansion, expansion from high-value to low-value species and size depletion; and (3) regulation: evidence of illegal fishing and a lack of regulation. The number of occurrences compared to the number of fisheries in which that issue was relevant is indicated on the right.

IUU catches were considered a substantial impediment to the 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 British Columbia (Canada) fishery, initially followed a boom-and-bust pattern but tighter regulations on quotas, rotational harvesting and adaptive management have allowed stocks to recover (Hand *et al.* 2008).

Discussion

We provide the first quantitative synthesis of the spatial and temporal patterns of sea cucumber fisheries worldwide. Overall, global catch and production (including aquaculture) of sea cucumber fisheries has increased 13- and 16-fold over the past two to three decades. However, many individual sea cucumber fisheries followed a typical trajectory with a rapid increase, short peak, and in most cases a substantial downward trend, thereby suggesting a boom-and-bust pattern. We found that global sea cucumber production is tightly linked to the Asian economy, yet since 1950, sea cucumber fisheries developed increasingly far away from their main market in Hong Kong and developed faster over time. On a local or regional scale, there was consistent evidence of serial exploitation, especially a spatial expansion from near- to off-shore areas and species expansion from high- to low-value species for a majority of the investigated fisheries and also a decrease in size for about one-third. Finally, the majority of sea cucumber fisheries are not regulated, and in over two-thirds of fisheries, local records indicate current concerns about over-exploitation 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.

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 (2008b), sea cucumber catches tend to be low in volume compared to other fisheries, and so national governments often pay them little attention. For example, Malaysia stopped recording catches after the fishery started to decline in 1993 (Choo 2008b). Second, Choo (2008b) noted that some southeast Asian catches were severely underestimated and questioned whether some 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 2008b). Global reported imports are more than double reported exports (Fig. 3). Fortunately, there is less incentive to misreport imports of sea cucumber into Hong Kong, making these values more reliable, although still imperfect indicators of fishery trends (Clarke 2004). Based on import data from Hong Kong, Toral-Granda (2008b) determined that there were substantial IUU catches from Latin America. Baine (2004) reviewed international trade of sea cucumbers and found discrepancies in reported sea cucumber catch compared to exports 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 Fig. 3 despite a substantial continuing fishery (see Fig. 1 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 2008b). 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 2008b).

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 (Figs. 1, 6), consistent and publicly accessible data to evaluate their status would be highly valuable. At the very least, it would aid transparency and analysis if developed countries, such as Canada, reported sea cucumber catch internationally disaggregated from other benthic invertebrates. 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 databases to either wet or dry volume.

Typical trajectory and rate of development

Ideally, a developing fishery would gradually build in volume and fishing capacity towards a plateau near a consistent and sustainable catch level (Hilborn and Sibert 1988). Our analysis of typical catch trajectory (Fig. 1) combined with our analysis of local issues of depletion (Fig. 6) suggests that sea cucumber fisheries tend to over-shoot an ideal capacity and decline substantially thereafter. In fact, our results suggest they may frequently be crashing nearly as quickly as they are expanding. Importantly, our analysis of local reports supports the hypothesis that in many cases peaks in catch are a result of resource depletion and not management-induced reductions. However, there are notable exemptions such as Japan where the decline in catch from the 1970s to 1990s was a 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 Introduction).

The sea cucumber fisheries investigated were also reaching this peak in catch faster over time (Fig. 5a). 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 of the fishery, caused stocks to collapse by 2003 (Lawrence *et al.* 2004).

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 (Fig. 6). 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.

Global market drivers

Sea cucumbers have a long history of international trade. 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 has occurred uninterrupted since at least 1681 (Choo 2008b). Our results suggest that the global volume of sea cucumber fisheries may be connected to the Chinese economy (Figs. 3, 4). Moreover, the distance from Asia of the countries fishing for sea cucumbers may be linked to when the fisheries started (Fig. 5b, c and Fig. S1). 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 (Chen 2004; Clarke 2004). Yet the once strong Chinese wild harvests of sea cucumbers have all but disappeared in many regions (Choo 2008b). 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 (Figs. 1, 6), the demand for sea cucumbers in Asia continues to rapidly increase (Chen 2004; Clarke 2004; Ferdouse 2004).

Although China is the main consumer of sea cucumbers, Hong Kong controls most of the trade of high-value species as a result of 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.* 2008a) 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 to 2004, increasing 3–5-fold from just 1990–2004 (Chen 2004) and rivalling the price of shark fin (Clarke 2004) at over \$400 USD per kg (Chen

2004). This has important implications for the conservation and management of sea cucumbers as 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 (Fig. 6) 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).

Serial exploitation

We found evidence of both small- and large-scale serial exploitation. On a global scale, since at least 1950, sea cucumber fisheries have expanded exponentially from their point of origin in Asia to now encompass the globe (Fig. 5b, c and Fig. S1). On a local scale, by assembling reports on individual regions, we found that about half of the countries also showed 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 (Fig. 6). From our review of the literature, we are unaware of other unexploited fisheries or fisheries that could be substantially expanded. However, there likely exist sea cucumber populations in deeper waters and lower value species that have not yet been fully exploited.

We have tested for patterns of serially expanding exploitation rather than serial depletion. Serial depletion implies that the decline of one fishery drives the development of the next, whereas we have tested for patterns of sequential addition with or without depletion. We suspect the observed patterns of serial exploitation are a combined function of decreasing cost of transportation and increasing ease of communication owing to globalization (e.g. Thorpe and Bennett 2001; Berkes *et al.* 2006) as well as increased demand for sea cucumbers (e.g. Clarke 2004; Ferdouse 2004) and the decline of many historically large sea cucumber fisheries (Figs. 1, 6).

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. Sethi *et al.* (2010) showed a pattern of the serial addition of lower value 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 because of over-exploitation, 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 Stockhausen 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), and western (Hand *et al.* 2008) and eastern Canada (Rowe *et al.* 2009). Further, it has also been recommended as an indicator for the health of Pacific Island sea cucumber fisheries by the Australian Government (Friedman *et al.* 2008).

Ecosystem and human community effects

Sea cucumbers play many important roles in marine ecosystems, including as consumers, biotur-

batators, water quality regulators and prey (see Introduction). Our results show that sea cucumber fisheries typically have catch trends that decline nearly as quickly as they expand (Fig. 1), are reaching peaks in catch increasingly rapidly (Fig. 5a), are expanding spatially, typically fish through species and often affect the size structure of the population (Fig. 6). Reductions in biomass from sea cucumber fisheries can be substantial. For example, in the Torres Strait (Northern Australia), Skewes *et al.* (2000) estimated that adult sea cucumber (*Holothuria scabra*) biomass declined to 100 t from a virgin biomass of 1600 t and did not show signs of recovery until 2009 (Skewes *et al.* 2010). In Egypt (Lawrence *et al.* 2004), Indonesia (Choo 2008b) 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 Introduction). However, the rapid expansion in recent years (Fig. 5) and local issues of depletion, IUU catches and lack of regulation (Fig. 6) 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.* 2008a). This is especially severe for countries that depend highly on sea cucumber fisheries and have few 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 continue to be just one of many alternative income options (e.g. United States) or may become more important because of the over-exploitation 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 has 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).

Management solutions

Sea cucumber fisheries are inherently difficult to manage. Holothurians are difficult to size, difficult to age, and their weight differs by season and location (e.g. Hand *et al.* 2008). This leads to a lack of knowledge about biological parameters such as larval time, recruitment and minimum density needed for successful reproduction. Further, many sea cucumber fisheries occur in regions where strong governance is lacking, and regulations are often lacking completely (Fig. 6). 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 3-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 Fig. 2, 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 (Fig. 1) recovered. Although still with problematic corruption and declining abundance, the implementation 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. First, because of 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). Second, 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. These declines were undetectable by CPUE.

Despite effective management in some regions, the majority of sea cucumber fisheries do not enjoy the same success (Fig. 6). 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 to the local situation to be effective (Worm *et al.* 2009). IUU catches were a substantial problem in 51% of the investigated fisheries (Fig. 6). Therefore, attempts to implement quotas may not be a successful strategy for many of these regions, especially without stronger governance (Smith *et al.* 2010).

In the 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). Currently, one species (*Isostichopus fuscus*) is listed on CITES Appendix III by Ecuador to enlist the cooperation of other nations in controlling its export. Appendix II listing would require exporting nations to certify that their sea cucumber exports would not be detrimental to the survival of the species. Alternatively, import tariffs can benefit the long-term conservation of renewable resources and usually 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 manage 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 and patterns of serial spatial, species and size 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 and proper scientific stock and ecosystem impact assessment to ensure more sustainable harvesting of sea cucumbers.

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References

- Abraham, T.J., Nagarajan, J. and Shanmugam, S.A. (2002) Antimicrobial substances of potential biomedical importance from holothurian species. *Indian Journal of Marine Sciences* **31**, 161–164.
- Ahmed, M.I. and Lawrence, A.J. (2007) The status of commercial sea cucumbers from Egypt's northern Red Sea Coast. *SPC Beche de Mer Information Bulletin* **26**, 14–18.
- Akamine, J. (2004) The status of the sea cucumber fisheries and trade in Japan: past and present. In: *Advances in Sea Cucumber Aquaculture and Management*. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 39–47.
- Allee, W.C. (1938) *The Social life of Animals*. W.W. Norton & Company, New York, NY, USA.
- Al-Rashdi, K.M. and Claereboudt, M.R. (2010) Evidence of rapid overfishing of sea cucumbers in the Sultanate of Oman. *SPC Beche-de-mer Information Bulletin* **30**, 10–13.
- Anderson, S.C. (2010) *Trends, drivers, and ecosystem effects of expanding global invertebrate fisheries*. MSc thesis, Dalhousie University, 134 pages.
- Anderson, S.C., Lotze, H.K. and Shackell, N.L. (2008) Evaluating the knowledge base for expanding low-trophic-level fisheries in Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2553–2571.
- Andrew, N.L., Agatsuma, Y., Ballesteros, E. *et al.* (2002) Status and management of world sea urchin fisheries. *Oceanography and Marine Biology: An Annual Review* **40**, 343–425.
- Aumeeruddy, R. and Conand, C. (2008) Seychelles: a hotspot of sea cucumber fisheries in Africa and the Indian Ocean region. In: *Sea Cucumbers: A Global Review of Fisheries and trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 195–209.
- Aumeeruddy, R. and Payet, R. (2004) Management of the Seychelles sea cucumber fishery: status and prospects. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 239–246.
- Backhuys, W. (1977) *Handbook of the Echinoderms of the British Isles*. Uitgever, Rotterdam, Netherlands. Reprint of 1927 edition published by Oxford University Press, Oxford.
- Baine, M. (2004) From the sea to the market place: an examination of the issues, problems and opportunities in unravelling the complexities of sea cucumber fisheries and trade. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 119–131.
- Baine, M. and Sze, C.P. (1999) Sea cucumber fisheries in Malaysia, towards a conservation strategy. *SPC Beche-de-mer Information Bulletin* **12**, 6–10.
- Baum, J.K. and Worm, B. (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* **78**, 699–714.
- Becker, R.A., Wilks, A.R., Brownrigg, R. and Minka, T.P. (2009) *maps: Draw Geographical Maps*. R package version 2.1-0.
- Bell, F.J. (1892) *Catalogue of the British Echinoderms in the British Museum (Natural History)*. Order of the Trustees, London.
- Bell, J., Purcell, S.W. and Nash, W. (2008) Restoring small-scale fisheries for tropical sea cucumbers. *Ocean & Coastal Management* **51**, 589–593.
- Berkes, F., Hughes, T.P., Steneck, R.S. *et al.* (2006) Globalization, roving bandits, and marine resources. *Science* **311**, 1557–1558.

- Birkeland, C. (1989) The influence of echinoderms on coral-reef communities. In: *Echinoderm Studies 3, volume 3* (eds M. Jangoux and J.M. Lawrence). A.A. Balkema, Rotterdam, Netherlands, pp. 1–79.
- Birkeland, C., Dayton, P.K. and Engstrom, N.A. (1982) A stable system of predation on a holothurian by four asteroids and their top predator. *Australian Museum Memoir* **16**, 175–189.
- Brander, J.A. and Taylor, M.S. (1998) Open access renewable resources: trade and trade policy in a two-country model. *Journal of International Economics* **44**, 181–209.
- Bremner, J. and Perez, J. (2002) A case study of human migration and the sea cucumber crisis in the Galapagos Islands. *Ambio* **31**, 306–310.
- Bruckner, A. (2004) Technical workshop on the conservation of sea cucumbers in the families Holothuridae and Stichopodidae, Kuala Lumpur (Malaysia), 1–3 March 2004. Workshop proceedings 6.13, Convention on International Trade in Endangered Species of Wild Fauna and Flora.
- Bruckner, A.W. (2005) The recent status of sea cucumber fisheries in the continental United States of America. *SPC Beche-de-mer Information Bulletin* **22**, 39–46.
- Bruckner, A.W. (2006) The proceedings of the CITES workshop on the conservation of sea cucumbers in the families Holothuridae and Stichopodidae. Technical Memorandum NMFS OPR 34, NOAA.
- Bruckner, A.W., Johnson, K. and Field, J. (2003) Conservation strategies for sea cucumbers: Can a CITES Appendix II listing promote sustainable international trade? *SPC Beche-de-mer Information Bulletin* **18**, 24–33.
- Chen, J. (2003) Overview of sea cucumber farming and sea ranching practices in China. *SPC Beche-de-mer Information Bulletin* **18**, 18–23.
- Chen, J. (2004) Present status and prospects of sea cucumber industry in China. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 25–37.
- Chenoweth, S. and McGowan, J. (1995) *Sea Cucumbers in Maine: Fishery and Biology*. DMR Research Reference Documents 95/1, Maine Department of Marine Resources, Maine, USA.
- Choo, P.S. (2004) Fisheries, trade and utilization of sea cucumbers in Malaysia. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 57–68.
- Choo, P. (2008a) The Philippines: a hotspot of sea cucumber fisheries in Asia. In: *Sea Cucumbers: A Global Review of Fisheries and Trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 119–140.
- Choo, P. (2008b) Population status, fisheries and trade of sea cucumbers in Asia. In: *Sea Cucumbers: A Global Review of Fisheries and Trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 81–118.
- Clark, J.E., Pritchett, M. and Hebert, K. (2009) *Status of Sea Cucumber Stocks in Southeast Alaska and Evaluation of the Stock Assessment Program*. Fishery Data Series 09-12, Alaska Department of Fish and Game, Anchorage, Alaska.
- Clarke, S. (2004) Understanding pressures on fishery resources through trade statistics: a pilot study of four products in the Chinese dried seafood market. *Fish and Fisheries* **5**, 53–74.
- Cleveland, W.S., Grosse, E. and Shyu, W.M. (1992) Local regression models. In: *Statistical Models in S* (eds J.M. Chambers and T.J. Hastie). Chapter 8, Wadsworth & Brooks/Cole, Pacific Grove, California, pp. 309–376.
- Conand, C. (2004) Present status of world sea cucumber resources and utilisation: an international overview. In: *Advances in Sea Cucumber Aquaculture and Management*, FAO Fisheries Technical Paper 463 (eds A. Lovatelli, C. Conand, S.W. Purcell, S. Uthicke, J.F. Hamel and A. Mercier). Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 13–23.
- Conand, C. and Byrne, M. (1993) A review of recent developments in the world sea cucumber fisheries. *US National Marine Fisheries Service Marine Fisheries Review* **55**, 1–13.
- Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**, 405–410.
- Dalzell, P., Adams, T. and Polunin, N. (1996) Coastal fisheries in the Pacific islands. *Oceanography and Marine Biology: An Annual Review* **34**, 395–531.
- Dissanayake, D., Athukorala, S. and Amarasiri, C. (2010) Present status of the sea cucumber fishery in Sri Lanka. *SPC Beche-de-mer Information Bulletin* **30**, 14–20.
- D'Silva, D. (2001) The Torres Strait bêche-de-mer (sea cucumber) fishery. *SPC Beche-de-mer Information Bulletin* **15**, 2–4.
- FAO (2004) *Advances in Sea Cucumber Aquaculture and Management*. Technical Report 463, Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO (2008) *Sea Cucumbers: A Global Review of Fisheries and Trade*. Technical Report 516, Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO (2009a) *The State of World Fisheries and Aquaculture 2008*. Technical report, Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO (2009b) Fisheries commodities production and trade: Fisheries and Agriculture Organization of the United Nations. Electronic database. <http://www.fao.org/fishery/statistics/software/fishstat/en> (last accessed October 2010).
- Ferdouse, F. (2004) World markets and trade flows of sea cucumber/bêche-de-mer. In: *Advances in Sea Cucumber Aquaculture and Management*. Food and Agriculture

- Organization of the United Nations, Rome, Italy, pp. 101–116.
- Francour, P. (1997) Predation on holothurians: a literature review. *Invertebrate Biology* **116**, 52–60.
- Friedman, K., Purcell, S., Bell, J. and Hair, C. (2008) *Sea Cucumber Fisheries: A Manager's Toolbox*. Technical report, Australian Centre for International Agricultural Research, Australian Government.
- Gamboa, R., Gomez, A.L. and Nievaes, M.F. (2004) The status of sea cucumber fishery and mariculture in the Philippines. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 69–78.
- Hamel, J.F.H. and Mercier, A. (2008) Population status, fisheries and trade of sea cucumbers in temperate areas of the Northern Hemisphere. In: *Sea Cucumbers: A Global Review of Fisheries and Trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 257–291.
- Hand, C.M., Hajas, W., Duprey, N., Lothead, J., Deault, J. and Caldwell, J. (2008) *An Evaluation of Fishery and Research data Collected During the Phase 1 sea Cucumber Fishery in British Columbia, 1998 to 2007*. Canadian Science Advisory Secretariat Research Document 065, Fisheries and Oceans Canada, Nanaimo, BC, Canada.
- Harrold, C. and Pearse, J.S. (1989) The ecological role of echinoderms in kelp forests. In: *Echinoderm Studies 2* (eds M. Jangoux and J.M. Lawrence). A.A. Balkema, Rotterdam, Netherlands, pp. 137–233.
- Hasan, M.H. (2008) Fisheries status and management plan for Saudi Arabian sea cucumbers. *SPC Beche-de-mer Information Bulletin* **28**, 14–21.
- Hasan, M.H. (2009) Stock assessment of holothuroid populations in the Red Sea waters of Saudi Arabia. *SPC Beche-de-mer Information Bulletin* **29**, 31–37.
- Hastie, T.J. and Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman and Hall, New York.
- Haug, T., Kjuul, A.K., Styrvold, O.B., Sandsdalen, E., Olsen, O.M. and Stensvag, K. (2002) Antibacterial activity in *Strongylocentrotus droebachiensis* (Echinoidea), *Cucumaria frondosa* (Holothuroidea), and *Asterias rubens* (Asteroidea). *Journal of Invertebrate Pathology* **81**, 94–102.
- Hearn, A., Martinez, P., Toral-Granda, M., Murillo, J. and Polovina, J. (2005) Population dynamics of the exploited sea cucumber *Isostichopus fuscus* in the western Galápagos Islands, Ecuador. *Fisheries Oceanography* **14**, 377–385.
- Heath, M. (2005) Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science* **62**, 847–868.
- Hibberd, T. and Pecl, G. (2007) Effects of commercial fishing on the population structure of spawning southern calamary (*Sepioteuthis australis*). *Reviews in Fish Biology and Fisheries* **17**, 207–221.
- Hickman, C.P., Roberts, L.S., Larson, A., l'Anson, H. and Eisenhour, D.J. (2006) *Integrated Principles of Zoology*, 13th edn. McGraw-Hill, New York, NY, USA.
- Hilborn, R.W. and Sibert, J. (1988) Adaptive management of developing fisheries. *Marine Policy* **12**, 112–121.
- Hutchings, J.A. (2005) Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 824–832.
- Ibarra, A.A. and Soberón, G.R. (2002) Economic reasons, ecological actions and social consequences in the Mexican sea cucumber fishery. *SPC Beche-de-mer Information Bulletin* **17**, 33–36.
- Jiddawi, N. and Ohman, M. (2002) Marine fisheries in Tanzania. *Ambio* **31**, 518–527.
- Jones, O.A. and Endean, R. (1973) The biology and ecology of tropical holothurians, vol. ii, biology i. In: *Biology and Geology of Coral Reefs* (eds O.A. Jones and R. Endean). Academic Press, New York, pp. 325–367.
- Joseph, L. (2005) *Review of the Beche de mer (Sea Cucumber) Fishery in the Maldives*. Technical Report 79, Food and Agriculture Organization of the United Nations, Madras, India.
- Karpov, K.A., Haaker, P.L., Taniguchi, I.K. and Rogers-Bennett, L. (2000) Serial depletion and the collapse of the California abalone (*Haliotis* spp.) fishery. In: *Workshop on Rebuilding Abalone Stocks in British Columbia* (ed A. Campbell), Vol. **130**. Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, Canada, pp. 11–24.
- Kelly, M.S. (2005) Echinoderms: their culture and bioactive compounds. In: *Echinodermata: Progress in Molecular and Subcellular Biology*. Subseries: Marine Molecular Biotechnology (ed V. Matranga). Springer-Verlag, Berlin Heidelberg, pp. 139–165.
- Kinch, J., Purcell, S.W., Uthicke, S. and Friedman, K. (2008a) Papua New Guinea: a hotspot of sea cucumber fisheries in the Western Central Pacific. In: *Sea Cucumbers: A Global Review of Fisheries and Trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 57–57.
- Kinch, J., Purcell, S.W., Uthicke, S. and Friedman, K. (2008b) Population status, fisheries and trade of sea cucumbers in the Western Central Pacific. In: *Sea Cucumbers: A Global Review of Fisheries and Trade*. Fisheries and Aquaculture Technical Paper 516. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 7–55.
- Kirby, M.X. (2004) Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 13096–13099.
- Konstantinova, I. (2004) Aquaculture in the Russian Far East. *International Market Research Reports (IMRR)*. Vladivostok, Russia.

- Kumara, P.B.T.P., Cumarathunga, P.R.T. and Linden, O. (2005) *Present Status of the Sea Cucumber Fishery in Southern Sri Lanka: A resource Depleted Industry*. SPC Beche-de-mer Information Bulletin 22, 24–29.
- Kwan, C.H. (1998) *The Yen, the Yuan, and the Asian Currency Crisis*. Technical report Asia/Pacific Research Center, Stanford University, Stanford, California, United States.
- Lahiri, K. and Moore, G.H. (Eds) (1991) *Leading Economic Indicators: New Approaches and Forecasting Records*. Cambridge University Press, Cambridge, UK.
- Lawrence, J. (1987) *A Functional Biology of Echinoderms*. Croom Helm, London & Sydney.
- Lawrence, A., Ahmed, M., Hanafy, M., Gabr, H., Ibrahim, A. and Gab-Alla, A.F. (2004) Status of the sea cucumber fishery in the Red Sea – the Egyptian experience. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 79–90.
- Lawrence, A.J., Afifi, R., Ahmed, A.M., Khalifa, S. and Paget, A.T. (2009) Bioactivity as an options value of sea cucumbers in the Egyptian Red Sea. *Conservation Biology* 24, 217–225.
- Lincoln-Smith, M., Pitt, K., Bell, J. and Mapstone, B. (2006) Using impact assessment methods to determine the effects of a marine reserve on abundances and sizes of valuable tropical invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 1251–1266.
- Lipcius, R.N. and Stockhausen, W.T. (2002) Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Marine Ecology Progress Series* 226, 45–61.
- del Mar Otero-Villanueva, M. and Ut, V.N. (2007) Sea cucumber fisheries around Phu Quoc Archipelago: a cross-border issue between South Vietnam and Cambodia. *SPC Beche-de-mer Information Bulletin* 25, 32–36.
- Massin, C. (1982a) Food and feeding mechanisms: Holothuroidea. In: *Echinoderm Nutrition* (eds M. Jangoux and J. Lawrence). A.A. Balkema, Rotterdam, Netherlands, pp. 43–55.
- Massin, C. (1982b) Effects of feeding on the environment: Holothuroidea. In: *Echinoderm Nutrition* (eds M. Jangoux and J. Lawrence). A.A. Balkema, Rotterdam, Netherlands, pp. 494–497.
- Mmbaga, T.K. and Mgay, Y.D. (2004) Sea cucumber fishery in Tanzania: identifying the gaps in resource inventory and management. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 193–203.
- Moriarty, D.J.W. (1982) Feeding of *Holothuria atra* and *Stichopus chloronotus* on bacteria, organic carbon and organic nitrogen in sediments of the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 33, 255–263.
- Myers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Nash, W. and Ramofafia, C. (2006) Recent developments with the sea cucumber fishery in Solomon Islands. *SPC Beche-de-mer Information Bulletin* 23, 3–4.
- Orensanz, J., Armstrong, J., Armstrong, D. and Hilborn, R.W. (1998) Crustacean resources are vulnerable to serial depletion – the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. *Reviews in Fish Biology and Fisheries* 8, 117–176.
- Pauly, D., Christensen, V., Guenette, S. et al. (2002) Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Pawson, D.L. (2007) Phylum echinodermata. In: *Linnaeus Tercentenary: Progress in Invertebrate Taxonomy, volume 1668 of Zootaxa* (eds Z.Q. Zhang and W. Shear). Magnolia Press, Auckland, New Zealand, pp. 749–764.
- Petzelt, C. (2005) Are echinoderms of interest to biotechnology? In: *Echinodermata: Progress in Molecular and Subcellular Biology. Subseries: Marine Molecular Biotechnology* (ed V. Matranga). Springer-Verlag, Berlin Heidelberg, pp. 1–6.
- Pinheiro, J.C. and Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York.
- Purcell, S.W. and Kirby, D.S. (2006) Restocking the sea cucumber *Holothuria scabra*: Sizing no-take zones through individual-based movement modelling. *Fisheries Research* 80, 53–61.
- Purcell, S.W., Gossuin, H. and Agudo, N.S. (2009) Changes in weight and length of sea cucumbers during conversion to processed beche-de-mer: Filling gaps for some exploited tropical species. *SPC Beche-de-mer Information Bulletin* 29, 3–6.
- R Development Core Team (2009) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org> (last accessed October 2010). ISBN 3-900051-07-0.
- Rasolofonirina, R., Mara, E. and Jangoux, M. (2004) Sea cucumber fishery and mariculture in Madagascar, a case study of Toliara, southwest Madagascar. In: *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper 463. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 133–149.
- Rowe, S., Comeau, P., Singh, R. et al. (2009) *Assessment of the Exploratory Fishery for Sea Cucumber (Cucumaria frondosa) in Southwest New Brunswick*. Canadian Science Advisory Secretariat Research Document 005. Fisheries and Oceans Canada, Dartmouth, NS, Canada.
- Roy, K., Collins, A., Becker, B., Begovic, E. and Engle, J. (2003) Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters* 6, 205–211.

- Samyn, Y. (2000) Conservation of aspidochirotid holothurians in the littoral waters of Kenya. *SPC Beche-de-mer Information Bulletin* **12**, 12–17.
- Savenkoff, C., Swain, D., Hanson, J. *et al.* (2007) Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). *Ecological Modelling* **204**, 115–128.
- Schoppe, S. (2000) Sea cucumber fishery in the Philippines. *SPC Beche-de-mer Information Bulletin* **13**, 10–12.
- Schroeter, S., Reed, D., Kushner, D., Estes, J. and Ono, D. (2001) The use of marine reserves in evaluating the dive fishery for the warty sea cucumber (*Parastichopus parvimensis*) in California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1773–1781.
- Sethi, S.A., Branch, T.A. and Watson, R. (2010) Global fishery development patterns are driven by profit but not trophic level. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 12163–12167.
- Shackell, N.L., Frank, K.T., Fisher, J.A.D., Petrie, B. and Leggett, W.C. (2009) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **277**, 1353–1360.
- Shepherd, S., Martinez, P., Toral-Granda, M. and Edgar, G. (2004) The Galapagos sea cucumber fishery: management improves as stocks decline. *Environmental Conservation* **31**, 102–110.
- Skewes, T., Dennis, D. and Burrridge, C. (2000) *Survey of Holothuria scabra (sandfish) on Warrior Reef, Torres Strait. 2000*. CSIRO Division of Marine Research, Cleveland, Queensland.
- Skewes, T., Smith, L., Dennis, D., Rawlinson, N., Donovan, A. and Ellis, N. (2004) Conversion ratios for commercial beche-de-mer species in Torres Strait. Torres Strait Research Program Final Report R02/1195, Australian Fisheries Management Authority.
- Skewes, T., Murphy, N., McLeod, I., Dovers, E., Burrridge, C. and Rochester, W. (2010) *Torres Strait Hand Collectables 2009 Survey: Sea Cucumber*. CSIRO Division of Marine Research, Cleveland, Queensland.
- Sloan, N.A. (1984) Echinoderm fisheries of the world: a review. In: *Proceedings of the Fifth International Echinoderm Conference* (eds B.F. Keegan and B.D.S. O'Connor). A.A. Balkema, Rotterdam, Netherlands, pp. 109–124.
- Smith, M.D., Roheim, C.A., Crowder, L.B., Halpern, B.S. *et al.* (2010) Sustainability and global seafood. *Science* **327**, 784–786.
- Therkildsen, N. and Petersen, C. (2006) A review of the emerging fishery for the sea cucumber *Cucumaria frondosa*: biology, policy, and future prospects. *SPC Beche-de-mer Information Bulletin* **23**, 16–25.
- Thorpe, A. and Bennett, E. (2001) Globalization and sustainability of world fisheries: a view from Latin America. *Marine Resource Economics* **16**, 143–1647.
- Toral-Granda, V. (2008a) Galapagos Islands: a hotspot of sea cucumber fisheries in Latin America and the Caribbean. In: *Sea Cucumbers: A Global Review of Fisheries and Trade. Fisheries and Aquaculture Technical Paper 516*. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 231–253.
- Toral-Granda, V. (2008b) Population status, fisheries and trade of sea cucumbers in Latin America and the Caribbean. In: *Sea Cucumbers: A Global Review of Fisheries and Trade. Fisheries and Aquaculture Technical Paper 516*. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 213–229.
- Tuwu, A. (2004) Status of sea cucumber fisheries and farming in Indonesia. In: *Advances in Sea Cucumber Aquaculture and Management. FAO Fisheries Technical Paper 463*. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 49–55.
- Uthicke, S. (1999) Sediment bioturbation and impact of feeding activity of *Holothuria (Halodeima) atra* and *Stichopus chloronotus*, two sediment feeding holothurians, at Lizard Island, Great Barrier Reef. *Bulletin of Marine Science* **64**, 129–141.
- Uthicke, S. (2001) Nutrient regeneration by abundant coral reef holothurians. *Journal of Experimental Marine Biology and Ecology* **265**, 153–170.
- Uthicke, S. (2004) Overfishing of holothurians: lessons from the Great Barrier Reef. In: *Advances in Sea Cucumber Aquaculture and Management* (eds A. Lovatelli, C. Conand, S.W. Purcell, S. Uthicke, J.F. Hamel and A. Mercier). Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 163–171.
- Uthicke, S. and Benzie, J. (2000) Effect of beche-de-mer fishing on densities and size structure of *Holothuria nobilis* (Echinodermata: Holothuroidea) populations on the Great Barrier Reef. *Coral Reefs* **19**, 271–276.
- Uthicke, S. and Conand, C. (2005) Local examples of beche-de-mer overfishing: an initial summary and request for information. *Beche-de-mer Information Bulletin* **21**, 9–14.
- Uthicke, S., Welch, D. and Benzie, J. (2004) Slow growth and lack of recovery in overfished holothurians on the Great Barrier Reef: evidence from DNA fingerprints and repeated large-scale surveys. *Conservation Biology* **18**, 1395–1404.
- Uthicke, S., Schaffelke, B. and Byrne, M. (2009) A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms *Ecological Monographs* **79**, 3–24.
- Velimirov, B., Field, J.G., Griffith, C.L. and Zoutendyk, P. (1977) The ecology of kelp bed communities in the Benguela upwelling system: analysis of biomass and spatial distribution. *Helgolander Wissenschaftliche Meeresuntersuchungen* **30**, 495–518.
- Ward, P. and Myers, R.A. (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* **86**, 835–847.

- Watson, R., Alder, J., Kitchingman, A. and Pauly, D. (2005) Catching some needed attention. *Marine Policy* **29**, 281–284.
- Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall, New York.
- Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **70**, 1467–9868.
- Worm, B. and Myers, R.A. (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**, 162–173.
- Worm, B., Hilborn, R., Baum, J.K. *et al.* (2009) Rebuilding global fisheries. *Science* **325**, 578–585.
- Xiao, Y., Punt, A., Millar, R. and Quinn II, T.Q. (2004) Models in fisheries research: GLMs, GAMS and GLMMs. *Fisheries Research* **70**, 137–139.
- Yingst, J.Y. (1976) The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. *Journal of Experimental Marine Biology and Ecology* **23**, 55–69.
- Zeller, D. and Pauly, D. (Eds) (2007) *Reconstruction of marine fisheries catches for key countries and regions (1950–2005)*. Fisheries Centre Research Reports. Vol. 15 Issue 2.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Alternative analysis of the distance from Hong Kong for sea cucumber fisheries using historical starting dates.

Table S1. Documentation of the historical (Hist.) and/or recent (Rec.) starting years of global sea cucumber fisheries used in Fig. S1 and Fig. 1.

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