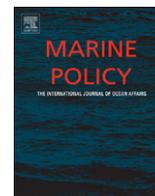




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## Sustainability of deep-sea fisheries

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## ABSTRACT

As coastal fisheries around the world have collapsed, industrial fishing has spread seaward and deeper in pursuit of the last economically attractive concentrations of fishable biomass. For a seafood-hungry world depending on the oceans' ecosystem services, it is crucial to know whether deep-sea fisheries can be sustainable.

The deep sea is by far the largest but least productive part of the oceans, although in very limited places fish biomass can be very high. Most deep-sea fishes have life histories giving them far less population resilience/productivity than shallow-water fishes, and could be fished sustainably only at very low catch rates if population resilience were the sole consideration. But like old-growth trees and great whales, their biomass makes them tempting targets while their low productivity creates strong economic incentive to liquidate their populations rather than exploiting them sustainably (Clark's Law). Many deep-sea fisheries use bottom trawls, which often have high impacts on nontarget fishes (e.g., sharks) and invertebrates (e.g., corals), and can often proceed only because they receive massive government subsidies. The combination of very low target population productivity, nonselective fishing gear, economics that favor population liquidation and a very weak regulatory regime makes deep-sea fisheries unsustainable with very few exceptions. Rather, deep-sea fisheries more closely resemble mining operations that serially eliminate fishable populations and move on.

Instead of mining fish from the least-suitable places on Earth, an ecologically and economically preferable strategy would be rebuilding and sustainably fishing resilient populations in the most suitable places, namely shallower and more productive marine ecosystems that are closer to markets.

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## 1. Introduction

Fishing has profoundly changed the distribution of fishes and fisheries worldwide, and is now occurring deep in the world's oceans far from fishing ports and consumers. These changes compel us to examine whether deep-sea fisheries can be sustainable.

It is difficult to appreciate how abundant marine life was in the past because people keep reducing expectations as we forget former conditions [1]. But the evidence is unmistakable. After reaching Labrador in 1508, Sebastian Cabot reported Atlantic cod (*Gadus morhua*, Gadidae) abundant enough to impede his ships' progress; two centuries later, Pierre de Charlevoix equated numbers of Grand Banks cod to grains of sand, calling cod fisheries "mines" more valuable than the mines of Peru and Mexico [2]. Many coastal ecosystems were phenomenally bountiful [3] until people impoverished them long ago [4]. Severe widespread depletion of large fishes in continental shelf

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waters [2] and in oceanic epipelagic ecosystems [5] was much more recent.

While increasing human population and affluence have raised global demand for fish, increasing scarcity of continental shelf and epipelagic oceanic fishes has driven industrial fishing farther from home ports and markets and to depths that were not even believed to host life until the 1870s. Global marine fisheries catches, as reported by fishing countries to the United Nations Food and Agriculture Organization (FAO), have stagnated at about 90 million metric tons since the late 1990s, and have declined since the late 1980s if the doubtful figures reported by China are excluded [6,7]. The large catch increase of the 1960s and 1970s was largely due the seaward and southward expansion of industrial (notably trawl) fisheries from waters along the coasts of developed countries of the Northern Hemisphere. When this expansion ended – in Antarctic waters – catches could increase only by fishing in deeper waters [8,9].

Scientists with expertise on fishes, fisheries and deep-sea biology question whether deep-sea fisheries can be sustainable [9–19]. A sound answer depends on but transcends ecology, taking ocean policy makers into the realms of economics and law.

Despite sharing an Ancient Greek root (*oikos*, meaning household), ecology and economics have diverged in their world views, often leading their practitioners to differing strategies for managing our collective household, the biosphere, including the 99% of its volume that is ocean. But there are fundamental similarities between ecology and economics. In fisheries it is commonplace to call populations “stocks,” alluding to their similarity to capital stocks in economics. Central to this paper is the analogy between (a) the biomass of fish stocks and the productivity they generate, with (b) capital stocks (principal) and the dividends (or interest) they generate. With deep-sea fisheries as our focus, this paper examines what the authors are calling Clark’s Law, the seminal connection between the ecological and economic determinants of sustainability as first explained in Clark [20,21]. Using comparable metrics and combining insights and the evidence from fisheries, ecology, economics and international ocean governance, this paper examines whether deep-sea fisheries can be sustainable. Governments and international governing organizations need to know this because maintaining biodiversity in the deep sea is crucial to biogeochemistry on a global scale, and hence to humankind [22,23].

## 2. Fishing deeper

Commercial fishing is occurring at increasing depths around the globe. Based on readily available catch data series and fish life history parameters, Morato et al. [24] showed that marine fisheries worldwide have operated at increased depths since the 1970s. In the high seas (i.e. beyond countries’ exclusive economic zones, EEZs), the increasing depth of fishing was more dramatic, some 250 m. They based this inference on the relative increase in the global catch of species (or higher taxa) known to occur in deeper waters, which have increased 7-fold since the mid-1960s [25]. As fisheries operated farther offshore and deeper, exploiting increasing portions of the ranges of marine species [26,27], they also exploited the deeper part of these species’ ranges. Accounting for this effect increases the mean depth of fisheries catches more than 4-fold.<sup>1</sup>

These studies show that fisheries are overexploiting both the last refuges for many fish species and species with less resilience [28,29], a point we examine in the following two sections.

## 3. Productivity of the deep sea

Once considered a vast cornucopia for a hungry world, the productivity of most of the open ocean is more akin to a watery desert. Ryther [30] was one of the first to quantify the scarcity of production to support large deep-sea fisheries. Using measurements of primary productivity and simple ecological rules about food chain trophic efficiency, he calculated that continental shelf fisheries in the western North Atlantic were unsustainable. Little attention was paid to his conclusion, however, and what had essentially become a fish-mining operation took 30 years to collapse. Shelf fisheries elsewhere also declined, so by 1999, 40% of the world’s major trawling grounds had shifted offshore [12,31].

Relatively little primary production per unit area occurs in most of the oceanic epipelagic zone, and its food energy may pass through several trophic levels as it sinks, with a rapid decline in biomass before reaching the benthos. This varies, however, with season and region, and recent work is increasing our understanding of flux of production from the surface to the seafloor [32]. Nonetheless, the combination of low epipelagic productivity and high rates of loss in the water column with increasing depth makes the vast majority of oceanic seafloor energy- and nutrient-scarce.

Much of the deep ocean is seemingly featureless (but, in places, species-rich) mud punctuated by isolated “oases” of high biomass supporting a diverse benthic and demersal fauna. Hydrothermal vents and cold seeps that rely on chemosynthetic primary production apparently have little or no interest for fisheries, but topographic features such as seamounts, mid-ocean ridges, banks, continental slopes and canyons can support commercially valuable species because these features modify the physical and biological dynamics in ways that enhance and retain food delivery [33,34]. Some commercially targeted species form dense breeding aggregations over deep-sea structures, further increasing biomass concentrations, allowing large catches over some seamounts.

Rowe et al. [35] calculated that a bottom fishery in 100 km<sup>2</sup> of the deep central Pacific would produce no more than 200 kg annually, a minuscule quantity compared to the 8000 t of orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) caught on average each year over the 30 years of that fishery [36]. Therefore, the success of large-scale deepwater fisheries depends upon regional- or local-scale production processes. This emphasizes, at very least, the need for site-specific information and a precautionary approach as the footprint of fisheries expands.

In the deep sea, despite the apparent higher levels of productivity over seamounts and similar features, species cannot support high levels of exploitation. Fishing on spawning aggregations has rapidly depleted even shallow-water fishes [12], and life history characteristics of deep-sea species magnify their vulnerability. Many deep-sea trawl fisheries show a serial pattern of “boom and bust,” as we show in later sections.

## 4. Life histories and population resilience of deep-sea fishes

Deep-sea fishes show remarkable adaptations to life in a cold, dark, low-productivity environment [37]. Depth and temperature directly affect fish growth rates, which tie to a range of life history characteristics that affect the maximum intrinsic population growth rate ( $r_{max}$ ) [38,39], including delayed maturity, high maximum age and low average productivity [24,40–44]. Low fish stock productivity, in turn, affects the capacity of those species to respond to fishing pressure and tightly restricts the maximum catch that a population can tolerate [45].

<sup>1</sup> T. Morato, R. Watson and D. Pauly, unpublished data.

Delayed maturity and low or episodic recruitment are common traits in many overexploited fish stocks worldwide [46–48]. Due to cold temperatures and high variance in food resources, most deep-sea fishes grow slowly, although species vary in allocation of their reproductive investment (large or small eggs, reproducing often or rarely), likely in response to the environmental variance experienced by their offspring. Many deep-sea species have larger eggs and hence lower fecundity than other teleosts of similar size [49]. Greater yolk reserves for the developing larva may be an adaptation to food limitation.

Although some deep-sea fishes are highly fecund, they seem to have characteristics of “periodic strategists” [41], namely long lifespans to accommodate extremely variable early survival. This strategy is often accompanied by high variance in recruitment success and spawning frequencies less than once per year [50,51], leading to resilience too low to compensate for high adult mortality.

At first it might seem that high fecundity leads to greater average population resilience, but empirical evaluation of many taxa indicate that more fecund fishes do not show higher recruitment or faster recovery rates than species with fewer offspring per year [45,46,52,53]. Life table analysis of two highly fecund North Atlantic grenadier species suggests very slow response to exploitation and potential for multi-decadal recovery times [29]. Two overfished stocks of very long-lived North Pacific rockfishes (genus *Sebastes*, Sebastidae) are currently on recovery plans that span several decades, in spite of fecundity estimates in the hundreds of thousands of larvae per female [54].

Are deep-sea fishes less resilient, on average, than those in shallow marine ecosystems? Resilience (and its opposite, intrinsic vulnerability) reflects the capacity of a species or population to tolerate impacts without irreversible change in its population structure [55,56], which are tightly linked to its life history. Because temperature and ecosystem productivity are related to species’ growth, one can generally predict a resilience “score” for any species based on limited biological information.

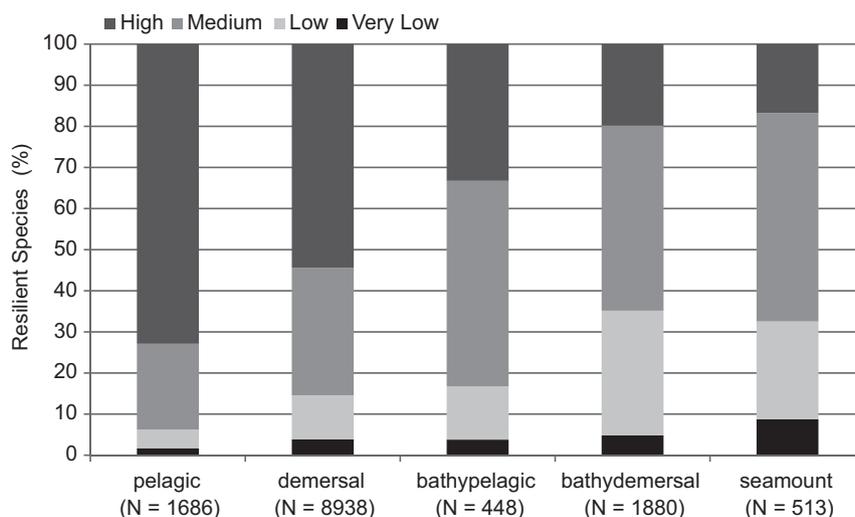
For species with either growth rate or fecundity estimates (or both) documented in FishBase, a much smaller proportion receive a “highly resilient” ranking (high growth rates, small body size and/or high fecundity per body mass) among bathypelagic, bathydemersal, and seamount species (Fig. 1), and a higher proportion of these are therefore “low” and “very low” resilience species. Seamounts cover a broad depth range and host some

species that may not qualify as true “deep-sea” fishes, yet even these include very few species having “highly resilient” characteristics. While these resilience ratings are based on preliminary estimates or characteristics for many species, they are generated through well-established empirical relationships observed in shallow-water species and suggest that deep-sea environments do constrain productivity in many deep-sea fishes.

Generally, a species’ resilience is directly linked to its intrinsic rate of population increase ( $r_{max}$ ), which is a function of the vital rates affecting births and deaths in the population [52,57]. Populations with lower  $r_{max}$  are less productive and will have slower recovery from fishing mortality [47]. While low-productivity stocks should be able to cope with very low fishing pressure, the maximum exploitation rate they can tolerate may fall below key economic rates, threatening the population. Intrinsic vulnerability to fishing is calculated from a fuzzy logic expert system that incorporates known relationships between life history and ecological characteristics of a species or population and their intrinsic vulnerability to fishing [55]. The index requires one or more of the following data: maximum body length, age at maturity, longevity, von Bertalanffy growth parameter  $K$ , natural mortality rate, fecundity and fish’s behavior in forming aggregations. Such information is available through online databases (e.g., FishBase). The intrinsic vulnerability index scales from 1 to 100, with 100 being most vulnerable to fishing.

Authors of this paper compiled and calculated various metrics of resilience and intrinsic vulnerability to fishing of a range of deep-sea fishes for which some biological information could be obtained. The list is restricted to species deeper than 200 m and which had either maximum age or growth data available in FishBase [56]. In this list, the authors excluded deep-sea fishes from the Mediterranean Sea because its temperature at depth is exceptionally warm ( $> 13^{\circ}\text{C}$ ), atypical for deep-sea habitats [58]. The authors also included examples of FAO’s [59] major deep-sea fishery species, which may sometimes occur in shallower waters ( $< 200$  m depth) but are well-represented in deep-sea fisheries (Table 1).

The data required for calculating  $r_{max}$  using conventional methods such as life table analysis [60] are not available for many deep-sea fishes. Therefore the authors used empirical relationships to estimate  $r_{max}$ . The authors assumed that  $r_{max}=2M$  [61], where  $M$  (the natural mortality rate) is estimated from Hoenig’s [62] empirical equation based on observed maximum age. If no



**Fig. 1.** Predicted resilience for fishes in different marine habitats from species entries in FishBase [56]. Resilience is defined by expected population doubling time and ability to compensate for a threshold level of biomass reduction within 10 years or 3 generations [147], based on observed values (rarely available for deep-sea fishes) or on empirical relationships between maximum productivity and age at maturity, lifespan, the von Bertalanffy age-length growth parameter  $K$ , and fecundity.

**Table 1**  
Life history, maximum population growth rate ( $r_{max}$ ) and intrinsic vulnerability index of 42 species of deep-sea fishes, those typically found deeper than 200 m and which had either maximum age or growth data available in FishBase [56]. The Table also includes examples of species exploited by deep-sea fisheries and commercially important non deep-sea fish that have available estimates of longevity or von Bertalanffy growth parameter  $K$  in FishBase [59]. Maximum body length ( $L_{max}$ ) is represented by total length.  $r_{max}$  is calculated from the approximations  $r_{max} \approx 2 \cdot M \approx 3 \cdot K$ . (R. Froese unpublished data; see text).  $M$  is estimated from Hoenig's [61] empirical equation based on observed maximum age. If no maximum age was known, we used the von Bertalanffy growth parameter  $K$  and followed Jensen's [55] suggested approximation with  $M=3/2K$ . Intrinsic vulnerability index is calculated using the method by [62].

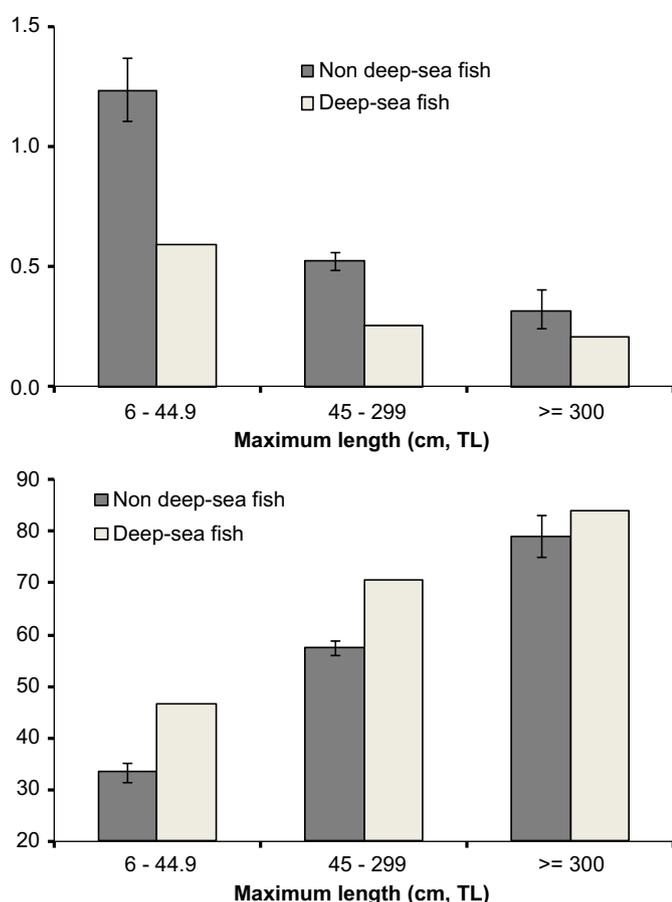
Family	Scientific name	Common name	$L_{max}$ (cm)	$r_{max}$ (year <sup>-1</sup> )	Max age (year)	Intrinsic vulnerability index
<b>Deep-sea fishes</b>						
Alepocephalidae	<i>Alepocephalus bairdii</i>	Baird's smooth-head	93	0.23	–	67
Alepocephalidae	<i>Alepocephalus rostratus</i>	Risso's smooth-head	47.4	0.24	–	58
Epigonidae	<i>Epigonus elegans</i>	–	16.4	1.09	8	24
Etmopteridae	<i>Etmopterus baxteri</i>	New Zealand lanternshark	68	0.16	57	71
Lophiidae	<i>Lophius budegassa</i>	Black-bellied angler	118	0.42	21	68
Macrouridae	<i>Coryphaenoides acrolepis</i>	Pacific grenadier	104	0.12	73	78
Macrouridae	<i>Coryphaenoides longifilis</i>	Longfin grenadier	110	0.59	15	57
Macrouridae	<i>Nezumia stegidolepis</i>	California grenadier	43	0.6	–	45
Neoscolopelidae	<i>Scopelogadus tristicus</i>	Pacific blackchin	21	1.38	–	23
Oreosomatidae	<i>Alloctytus niger</i>	Black oreo	47	0.06	153	69
Oreosomatidae	<i>Pseudocyttus maculatus</i>	Smooth oreo dory	68	0.09	100	73
Rajidae	<i>Bathyraja trachura</i>	Roughtail skate	91	0.44	20	61
Sebastidae	<i>Sebastes mentella</i>	Deepwater redfish	58	0.12	75	70
Sebastidae	<i>Sebastes altivelis</i>	Longspine thornyhead	39	0.20	45	60
Somniosidae	<i>Centrosetocheilus crepidater</i>	Longnose velvet dogfish	130	0.17	54	82
Somniosidae	<i>Proscymnodon plunketi</i>	Plunket shark	131	0.23	39	80
Trachipteridae	<i>Trachipterus arcticus</i>	Dealfish	303	0.21	–	84
<b>Deep-sea exploited fishes</b>						
Anoplopomatidae	<i>Anoplopoma fimbria</i>	Sablefish	120	0.08	114	82
Berycidae	<i>Beryx splendens</i>	Splendid alfonso	70	0.52	17	62
Centrolophidae	<i>Hyperoglyphe antarctica</i>	Bluenose warehou	140	0.15	60	85
Centrolophidae	<i>Hyperoglyphe perciformis</i>	Barrelfish	91	0.11	85	58
Channichthyidae	<i>Champsocephalus gunnari</i>	Mackerel icefish	66	0.45	–	56
Emmelichthyidae	<i>Plagiogeneion rubiginosum</i>	Rubyfish	60	0.88	10	41
Epigonidae	<i>Epigonus telescopus</i>	Black cardinal fish	75	0.09	100	74
Lotidae	<i>Molva dypterygia</i>	Blue ling	155	0.38	–	75
Macrouridae	<i>Coryphaenoides rupestris</i>	Roundnose grenadier	110	0.17	54	78
Macrouridae	<i>Macrourus berglax</i>	Roughhead grenadier	110	0.12	–	75
Nototheniidae	<i>Dissostichus eleginoides</i>	Patagonian toothfish	215	0.17	50	85
Nototheniidae	<i>Dissostichus mawsoni</i>	Antarctic toothfish	175	0.29	31	86
Oreosomatidae	<i>Alloctytus niger</i>	Black oreo	47	0.06	153	69
Oreosomatidae	<i>Pseudocyttus maculatus</i>	Smooth oreo dory	68	0.09	100	73
Pentaceroideae	<i>Pseudopentaceros richardsoni</i>	Pelagic armourhead	56	0.81	–	43
Pentaceroideae	<i>Pseudopentaceros wheeleri</i>	Slender armourhead	44	0.8	11	65
Pleuronectidae	<i>Reinhardtius hippoglossoides</i>	Greenland halibut	80	0.3	30	69
Polyprionidae	<i>Polyprion americanus</i>	Wreckfish	210	0.3	–	80
Polyprionidae	<i>Polyprion oxygeneios</i>	Hapuka	150	0.15	60	87
Sebastidae	<i>Sebastes fasciatus</i>	Acadian redfish	30	0.3	–	48
Sebastidae	<i>Sebastes marinus</i>	Ocean perch	100	0.15	60	77
Sebastidae	<i>Sebastes mentella</i>	Deepwater redfish	58	0.12	75	70
Sebastidae	<i>Sebastes proriger</i>	Redstripe rockfish	61	0.16	55	70
Serranidae	<i>Caprodon longimanus</i> <sup>1</sup>	Pink maomao	50	–	–	34
Trachichthyidae	<i>Hoplostethus atlanticus</i>	Orange roughy	75	0.06	149	73
Trichiuridae	<i>Aphanopus carbo</i>	Black scabbardfish	110	0.33	–	70
Trichiuridae	<i>Lepidopus caudatus</i>	Silver scabbardfish	210	0.9	–	58
<b>Non deep-sea fish examples</b>						
Clupeidae	<i>Clupea harengus harengus</i>	Atlantic herring	55	0.45	22	30
Engraulidae	<i>Engraulis ringens</i>	Peruvian anchoveta	24	3.00	3	39
Gadidae	<i>Gadus morhua</i>	Atlantic cod	200	0.40	25	68
Rajidae	<i>Raja clavata</i>	Thornback ray	120	0.80	12	53
Sciaenidae	<i>Larimichthys polyactis</i>	Small yellow croaker	40	1.70	7	30
Scombridae	<i>Scomber japonicus</i>	Chub mackerel	64	0.55	18	46
Serranidae	<i>Plectropomus leopardus</i>	Leopard coral grouper	146	0.38	26	46
Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead	430	0.29	35	82
Squalidae	<i>Squalus acanthias</i>	Spiny dogfish	160	0.14	75	87

maximum age was known, the authors used the von Bertalanffy growth parameter  $K$  and followed Jensen's [63] suggested approximation with  $M=3/2K$ .

Table 1 generally suggests that very low resilience/productivity (i.e. high vulnerability) is typical of deep-sea fishes, including species that are commonly exploited by deep-sea fisheries.

The estimated  $r_{max}$  of the deep-sea species the authors studied has a mean value of less than  $0.37 \text{ year}^{-1}$ , with high intrinsic vulnerability (i.e., index  $> 60$ ). Similarly, species commonly exploited by deep-sea fisheries have low average  $r_{max}$  of  $0.314 \text{ year}^{-1}$ . Further, these have markedly lower  $r_{max}$  and higher intrinsic vulnerability index than non-deep-sea fishes (i.e., species generally found shallower than 200 m) of similar length (Fig. 2). This agrees with results from previous assessments that deep-sea demersal fishes, particularly those that aggregate around seamounts, are more vulnerable than other fishes [24,28]. Maximum body size alone may not be a good indicator of resilience or vulnerability to fishing because some of the highly vulnerable species are not large.

These metrics of resilience and intrinsic vulnerability, specifically  $r_{max}$ , can be compared to economic metrics to evaluate the sustainability of deep-sea fishing. In species where recruitment is more or less stable at population sizes above 50% of unexploited size, a reasonable assumption for many low-productivity species, the maximum intrinsic growth rate  $r_{max}=2M$ , where  $M$  is the natural mortality rate. This leads to a target fishing mortality rate for maximum sustainable yield (MSY) of  $F_{msy}=M$ . For species that have maximum ages of 30 years or greater,  $M$  is expected to be  $< 0.1$ ; thus, maximum fishing mortality rates under standard management models must also be  $< 0.1$ , a difficult target to meet in open-access fisheries. If a local stock or population is depleted ( $F \geq F_{msy}$ ) and does not receive significant recruitment from unexploited sources, the chances of local extinction are extremely high.



**Fig. 2.** The calculated (a)  $r_{max}$  and (b) intrinsic vulnerability index of non deep-sea (gray bars) and deep-sea (open bar) fishes. The error bars represent 95% confidence limits. Numbers of deep-sea fishes with available data to estimate  $r_{max}$  and intrinsic vulnerability index are too small to calculate meaningful confidence limits ( $N=42$  spp.) while the sample size for shallow water fishes is: 6–44.9 cm ( $N=215$  spp.), 45–299 cm ( $N=394$  spp.) and  $> = 300$  cm ( $N=29$  spp.).

Species with restricted geographic range and aggregation behavior are particularly vulnerable to overfishing [46,55,64]. Many deep-sea fishes that inhabit seamounts naturally aggregate for feeding and spawning. These species include orange roughy, splendid alfonsino (*Beryx splendens*), alfonsino (*Beryx decadactylus*, Berycidae), blue ling (*Molva dypterigia*, Lotidae) and slender armourhead (*Pseudopentaceros wheeleri*, Pentacerotidae). The level of population connectivity among seamounts is unknown for most species but recolonization rates may be very low or episodic [43]. This further reduces their resilience to fishing [24].

## 5. Principal vs. interest as a fishery concept

With a million dollars capital (=principal) in the bank, one can withdraw \$30,000 per year in perpetuity at a guaranteed 3% annual interest rate. Likewise, many stocks (equities) generate dividends, albeit more variably. Similarly, a fish biomass of one million kilograms that grows at an average rate of 3% per year will deliver, on average, 30,000 kg of fish per year in perpetuity. At a price of \$1/kg, that will provide gross revenues of \$30,000 per annum through time.

The foregoing illustrates how the economic concepts of capital and interest are closely related to the biological concepts of population (stock) biomass and annual growth rate of fish. Assuming that there is neither net population compensation nor depensation – the null hypothesis unless there is adequately supported reasoning or metanalysis to indicate otherwise – depleting fishery resources “eats up” our fish capital, thereby reducing the interest (=usable productivity) it generates and undermining its capacity to benefit present and future generations [65].

Sustainability, therefore, is living off the interest that capital generates (=the surplus production that a fish stock generates). Withdrawing too much capital from a bank account and depleting fish stocks only decrease the interest (revenue) the stock will generate in the future.

## 6. Productivity and interest rates determine prospects for sustainability

The problems of overfishing can be split into two, the first being about open access and competitiveness, the second being that, even under sole ownership, the ocean can be emptied of fishes whose intrinsic growth rate is lower than the discount rate (=prevailing market rate).

It has long been known in economic theory [66–69] that open access to a natural resource usually leads to overexploitation because no single individual has an incentive for conservation (the first problem). This is the so-called tragedy of the commons [67]: The fish that I throw back into the sea will just be caught by someone else. However, Clark [20,21] showed that even a private sole owner who is the only one to fish may still have an economic incentive to drive the stock to extinction (the second problem) because, once a fishery is no longer a subsistence activity, but an industry, it must compete with other uses for capital. To take the analogy of the previous section, if the rate of return in other competing industries is 5%, then the rate of return in the fishing industry has to be 5%, even if it means eating into the fish capital, eventually withdrawing it down to zero.

To be specific, suppose the growth rate  $F(x)$  of the fish stock is given in terms of the stock  $x$  by a simple logistic equation

$$F(x) = rx[1 - x/K]$$

where  $r$  is the intrinsic growth rate of the resource and  $K$  is its carrying capacity. Now let  $i$  be the expected rate of return from the fishery. Colin Clark showed that if  $i > r$ , that is, if money grows faster

in the bank than fish in the sea, it is economically preferable, even for a sole owner, to liquidate the fish stocks and convert them into capital, thereby driving the fish stock to extinction. For deep-sea fishes, where productivity is very low, the effect is very pronounced.

## 7. Sustainability and spatial patterns of deep-sea fishing

Around the world, including in the deep sea, many fisheries are unmanaged or minimally managed. But for ones that are managed, the most commonly used methodology – stock assessment – does not incorporate spatial patterning of fish and fisheries. Diversity of life histories among populations of a species can be a major factor favoring non-declining catches [70]. Whether unmanaged or managed, failure to account for spatial heterogeneity of fishes is likely a major reason for the growing incidence of fishery collapses around the world [71], which the authors summarize for the deep sea in sections to follow.

The assumption that targeted fish species move around randomly, so that fishing pressure in any one place within the boundary of a fishery has the same impact as in any other, urgently needs to be revised, particularly in the deep sea. A model that better explains the serial depletion we see around the world comes from Berkes et al. [68]: A fishing operation locates a profitable resource patch, fishes it to unprofitability, then moves on, repeating this sequence until there are no more profitable patches to exploit, at which point the fishery is commercially (probably ecologically, and conceivably biologically) extinct. Fishing does not deplete fish populations uniformly throughout a fishery's spatial footprint. Rather, it is a patch-dynamic, mosaic process that takes "bites" out of marine ecosystems. If these bites deplete fish faster than they can regenerate, pushing them below the threshold of profitability, then the bites coalesce until there are no more patches of fish to be taken profitably.

This model has particular resonance in the deep sea. One reason is that deep-sea fishing vessels are generally larger, and therefore take bigger bites in any given fishing location, where new technologies allow people to locate and fish for biomass concentrations in areas that were until very recently hidden, inaccessible or too expensive to fish. The other is that deep-sea fish are so slow to recover from increased mortality.

Indeed, serial depletion is almost inevitable because – as Clark [20] observed in whales, which, like deep-sea fishes are slow-growing – it is economically rational behavior to reduce each stock to unprofitability until no more can be taken, then reinvest the capital (now in the form of money) to obtain higher return on investment. And when catch statistics are aggregated over large areas, this serial depletion in a mosaic spatial pattern is obscured and difficult to detect, with each as-yet unexploited patch giving the false impression of sustainability as it is found, depleted and abandoned by fishermen who move on, repeating the process.

The "roving bandits" Berkes et al. [68] describe are therefore the spatial causal driver for Clark's Law in the deep sea. By creating the illusion of sustainable catches while serially depleting patches in the fish stock mosaic, deep-sea fishing more closely resembles a Ponzi scheme than a sustainable activity. This bodes poorly for both deep-sea fishes and the future of their fisheries. The following sections provide spatially explicit longitudinal examples of deep-sea fisheries that shed light on this process.

## 8. Evidence for sustainability in deep-sea fisheries

### 8.1. Elasmobranchs

Deep-sea elasmobranch fishes are targeted directly, primarily for shark liver-oil, and are bycatch in fisheries targeting teleosts

and crustaceans. The low productivity of deep-sea elasmobranchs, many of which are poorly known taxonomically and whose population status is data-deficient, is a growing concern. Their inability to sustain fishing pressure has led experts to conclude that deep-sea elasmobranchs in general (not only larger species) are very vulnerable to overexploitation [64,72,73]. Several papers document the very low fishing mortality levels needed to over-exploit deep-sea sharks [9,74,75]. Depth gives them no refuge; deep-sea fisheries have already reached the maximum depths attainable by elasmobranchs [76].

Demographic data compiled by the IUCN Shark Specialist Group found suitable information for only 13 species (2.2%) of deep-sea chondrichthyans [73].  $r_{max}$  for these deep-sea species falls at the lower end of the productivity scale for elasmobranchs, making these among the lowest observed for any species. Population doubling times suggest recovery following exploitation will take decades to centuries. Moreover, there is a significant decline in the resilience of species with increasing maximum depth [73]. Whereas elasmobranchs are inherently vulnerable to overexploitation, deeper-dwelling ones are most vulnerable of all.

Harrison's dogfish (*Centrophorus harrissoni*, Centrophoridae) illustrates this. An endemic dogfish from Australia, it declined more than 99% from 1976–77 to 1996–1997 in waters of New South Wales, according to fishery-independent trawl surveys [74]. This species occupies a relatively narrow band of the continental slope, and like other *Centrophorus* species, is believed to be among the most biologically vulnerable of all sharks, with low fecundity (1–2 pups every 1–2 years), high longevity (in some cases at least 46 years) and probable late age at maturity [77]. IUCN now lists Harrison's dogfish as critically endangered. Unlike many other sharks, its decline was noted by research surveys. This highlights a common pattern around the world: Multi-species fisheries can threaten sharks [78] much faster than regulators act to mitigate their decline.

The leafscale gulper shark (*Centrophorus squamosus*) is targeted for its liver oil, often as part of multi-species demersal fisheries. It matures late, has only 5–8 pups per year and lives to be 70 years old [79]. In the North Atlantic, landings peaked in 1986 and have declined steadily since then. Further confounding matters are reporting problems: Landings of this species are often aggregated with a closely related species, and over large areas.

Little differentiates these two sharks from other deep-sea elasmobranchs except for the availability of catch and demographic data. It is likely that other deep-sea elasmobranchs show similar patterns.

### 8.2. Orange roughy

Orange roughy is a deepwater demersal species with an almost global distribution. It inhabits continental slopes and seamounts from 500–1500 m depths. It is slow-growing and reaches ages exceeding 100 years. Natural mortality in adults is low (estimated at  $0.045 \text{ year}^{-1}$  off New Zealand), they mature late (at about 30 years), their fecundity is low relative to most teleost species, and adults do not spawn every year. These characteristics make orange roughy much less productive than most shallower-living commercially fished species.

Fishing for orange roughy started in New Zealand waters in the late 1970s. Subsequently other fisheries developed off south-eastern Australia in the late 1980s, in the North Atlantic in 1989, off Namibia in 1995, off Chile in 1998 and in the southwest Indian Ocean (SWIO) in 1999 [80].

New Zealand catches rose steadily through the 1980s as new populations were discovered, and when the Australian fishery found spawning fish off St Helens Seamount, global catches skyrocketed to over 100,000 t (Fig. 3). Numerous new fisheries followed in the 1990s and early 2000s, the largest occurring

off Namibia and SWIO. The New Zealand fishery has dominated global catches, and is the only one that has persisted over time with total catches of more than a few thousand tonnes. Much of this comes from a restricted area of the Chatham Rise east of the main New Zealand islands [81]. Stocks in most other fishing grounds around New Zealand have declined substantially [82], and mirror the global pattern on a smaller spatial scale. Serial depletion has occurred in some of the seamount-based fisheries, and a number of areas are now closed (Fig. 4).

The Australian fishery was very large between 1989 and 1993 when catch rates of spawning fish on St. Helens Seamount were high, but the stocks were rapidly depleted and quotas were progressively reduced [83]. The St. Helens fishery is now closed completely and Australia declared orange roughy a “threatened species” in 2006. A similar situation occurred off Namibia and Chile [84–86], where, despite extensive research and precautionary management objectives, catches could not be sustained, and fisheries are now very small or orange roughy are just bycatch. Similarly, in SWIO, large catches were taken for a short time, with uncontrolled increase in effort in the early 2000s with no management on the high seas, then a sharp drop in catches and catch rates [87].

Sissenwine and Mace [18] noted two patterns in these catch histories. In the first, small stocks were fished down rapidly before effective management could be implemented. In the second, with larger stocks, research initially overestimated stock size, often coupled with non-conservative management practises and “fishing-down” phases, which led to excessive depletion. Francis and Clark [82] and Clark [88] have further examined sustainability issues with orange roughy, and attributed over-exploitation to a combination of biological characteristics and habitat/fishery factors whereby their aggregation behavior makes them vulnerable to rapid depletion, and research-management limitations that mean often too little is learnt too late. Economic considerations have also been important, as the market value for orange roughy has historically been high, creating an economic incentive for fishers to target the species [89].

Orange roughy stocks in New Zealand and Australia have generally continued to decline even when catch has been reduced to levels thought to be sustainable. Stock assessments are often highly uncertain, partly because biological knowledge is lacking to make the population models ecologically realistic. Several New Zealand stock assessments have suggested that there may have been several decades of below-average recruitment for some orange roughy populations [82]. Lack of knowledge of recruitment is one of the main concerns about the sustainability of these fisheries [11,90].

### 8.3. Slender (pelagic) armourhead

There are three species of armourhead: slender (*Pseudopentaceros wheeleri*), pelagic (*P. richardsoni*) and longfin (*P. pectoralis*). *P. wheeleri*, then commonly (if erroneously) called “pelagic” armourhead, was the target of large fisheries in the North Pacific. Slender armourhead are relatively short-lived (11 years) and fast-growing compared to orange roughy. They spend several years as

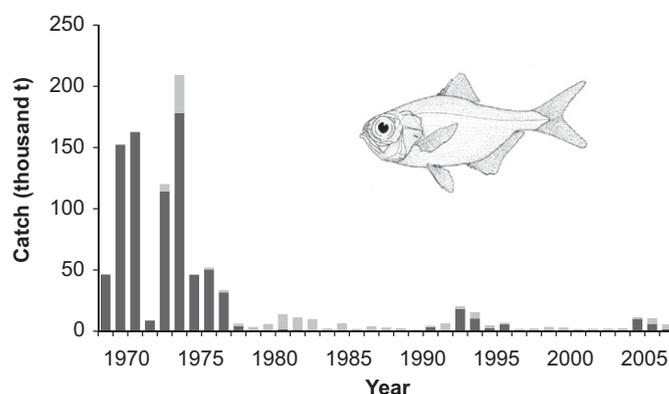


Fig. 4. Catches of slender armourhead (dark gray) and alfonsino (light gray) from Emperor and Hawaiian seamounts [80,133,148]. Splendid alfonsino image: wikipedia.org.

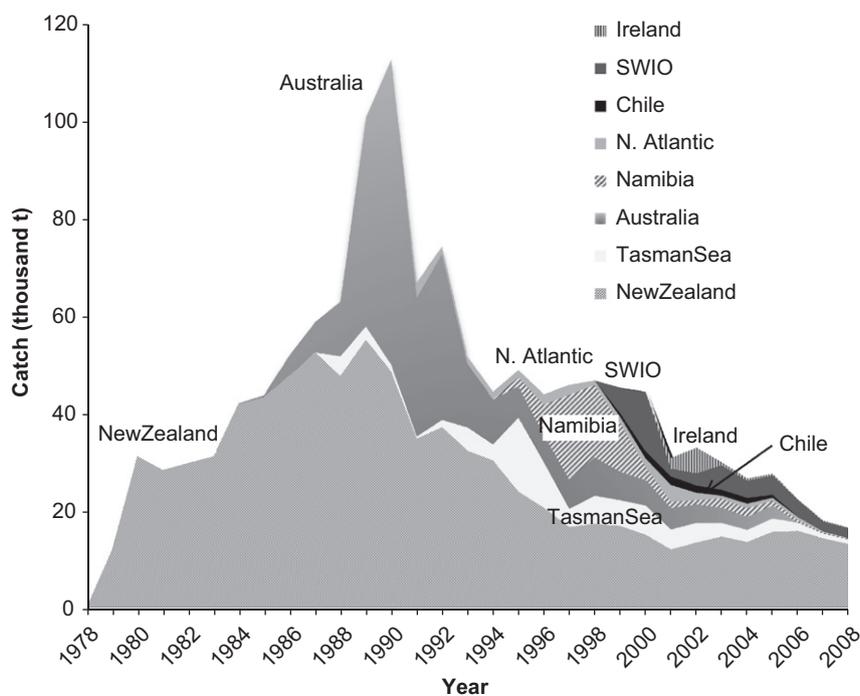


Fig. 3. Estimated catches of orange roughy in the major global fishing areas from 1978 to 2008. (Various data sources, authors unpublished records, FAO Statistics, ICES reports, NZ Plenary reports).

pelagic fish migrating over large areas of the North Pacific before becoming demersal and aggregating on seamounts to spawn during the last years of their lives [91].

In 1967, Soviet trawlers discovered large aggregations on seamounts in the southern Emperor Seamount Chain [80,92]. The Soviet fleet caught up to 130,000 t a year in the early stages of the fishery [80]. Most catches were taken on four seamounts at depths between 300 and 600 m. Effort in the early years was very high, with 18,000 Soviet trawler-days between 1969 and 1975 [92]. Stock size initially was estimated at between 240,000 and 350,000 t [93]. Large Japanese trawlers joined the fishery in 1969, and combined catches of the two fleets peaked at about 180,000 t in 1973, before dropping rapidly. Japanese catch per unit effort decreased from a peak of 54 t h<sup>-1</sup> in 1972 to less than 1 t h<sup>-1</sup> from 1978. They switched to targeting alfonsino on the seamounts, although, by 1982, both fisheries had become small [91]. Nonetheless, some Japanese fishing continued for alfonsino during the 1980s–90s, with annual catches typically 1000 to 6000 t. Catches of armourhead were generally small, but in 1992 and 1993 and again in 2004 larger catches over 10,000 t were taken.

Hence, although the armourhead stock was heavily overfished during the 1960–1980s, it has recovered somewhat, with apparent pulses of recruitment contributing to the improved catches. However, the stock has not recovered to anywhere near its earlier size.

#### 8.4. Grenadiers

There are almost 400 species of grenadiers [94] but only a handful in the genera *Coryphaenoides*, *Macrourus* and *Albatrossia* are of adequate size, habit and occurrence to qualify as the target of a fishery. The many species of *Coryphaenoides* occur from the upper slope to abyssal plain depths in all oceans. The four species of *Macrourus* occur on the slope in high latitudes of the North Atlantic and Southern Oceans. The single species of *Albatrossia* (the giant grenadier, *A. pectoralis*) occurs on slopes across the North Pacific.

Roundnose grenadier (*Coryphaenoides rupestris*) and rough-head grenadier (*Macrourus berglax*) have been fished to near-exhaustion in the Northwest Atlantic [94]. The *C. rupestris* fishery began in 1965 shortly after the former Soviet Union found commercially fishable populations, peaked at 83,964 t in 1971, crashed and never recovered until it ceased under moratorium in 1992. The fishery began off northern Labrador and swept through the range and local populations were depleted, concluding off southern New England. In 2008, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) placed *C. rupestris* on its list of endangered species. The fishery moved to the Northeast Atlantic but appears to have peaked there in 2004 at 30,000 t. As *C. rupestris* landings diminished, the focus shifted to *M. berglax*. Never as large a fishery, it peaked at near 9000 t in 2000 in the Northwest Atlantic. Stock assessments show that the population has declined 88%. Bycatch of *Macrourus* throughout the Southern Ocean is not inconsiderable and a targeted fishery is very possible.

Some fishery scientists believe there could be a viable fishery in the Northwest Pacific for the lightly exploited giant grenadier and popeye grenadier (*C. cinereus*) [94]. These are undoubtedly abundant on the upper slopes across the region, but there are no historical data and what little demographic information exists is inadequate to determine how populations might respond to exploitation. Because of the particular bioenergetic characteristics of grenadiers, models derived for shallow-water species cannot be used even if appropriate data were available. Initial overfishing can have very long-term effects, as has been shown for *C. rupestris* and *M. berglax*, and studies based on these two species show that recovery time, even with a modest level of fishing, can be on the order of centuries [29].

#### 8.5. Black scabbardfish

In some cases, deep-sea fishes have been targeted for more than a century, mainly around oceanic islands with steep slopes [95]. These fisheries are typically labor-intensive and use handlines or longlines from small boats. The Madeira traditional deepwater fishery is one of the more longstanding examples. It probably started in the early 1800s when local fisherman targeting squalid sharks between 600 and 800 m depth for oil to light their homes accidentally caught black scabbardfish (*Aphanopus carbo*, Trichiuridae) [96,97]. Its quality and flavor quickly made this fish the “trustworthy friend for poor local communities” [96] and an important fishery for Madeira Island.

This fishery changed little until 1982, when monofilament drifting longlines replaced hemp lines and hooks per line increased [98]. This gear change, along with better equipped boats, helped local fisherman searching for new fishing grounds to increase catches from about 1000 t in 1982 to 3000 t in 1992 [98]. Black scabbardfish are now fished between 800 and 1200 m on slopes of islands and seamounts [97].

This species may show fast growth for a deep-sea fish, maturing at about 3 to 4 years and with longevity of 12–24 years [99,100], which could help to explain its apparent sustainability. Another reason is that the fishery used hook and line gear [101].

In the past, the complexity of Madeira’s seafloor prevented bottom trawling. Now that trawlers can fish on steep slopes, the Portuguese government and regional authorities have prohibited use of trawls in both Madeira and the Azores. This became an EC regulation (EC Reg. 1568/2005) under the new Common Fisheries Policy to foster conservation of sensitive deep-sea habitats and species [102].

Black scabbardfish fisheries are still artisanal in Portugal but are much more industrialized elsewhere (e.g., French deepwater freezer trawler fisheries in northern European waters) [103], where CPUE shows a population decline [104]. For this reason, the international Council for the Exploration of the Sea (ICES) has asked for significant reductions in fishing effort. Present landings in northern Europe are probably maintained by serial exploitation of new fishing grounds. But in waters between the Azores and the Canary Islands, artisanal longline black scabbardfish fisheries seem to have stable catches and biomass, and may remain so if fishing effort does not increase [104].

#### 8.6. Other bony fishes

A number of other deep-sea teleosts are targets of major commercial fisheries in various parts of the world. These include alfonsinos (*B. splendens* and *B. decadactylus*, Berycidae), oreos (in particular smooth oreo dory (*Pseudocyttus maculatus*) and black oreo (*Alloctytus niger*, Oreosomatidae), toothfishes (Patagonian toothfish, *Dissostichus eleginoides* and Antarctic toothfish, *D. mawsoni*, Nototheniidae), sablefish (*Anoplopoma fimbria*, Anoplopomatidae), blue ling (*Molva dypterygia*), cusk (*Brosme brosme*, Lotidae) and wolffishes (*Anarhichas* spp., Anarhichadidae). Oreos are long-lived and slow-growing like orange roughy, but the other species are more like typical shallow-dwelling species.

Catch histories of these fisheries show differing trends, but the current catch levels of all are markedly lower than historical maxima (Table 2). Decreases in catch result from a combination of overfishing, a trend in some areas towards longlining rather than trawling (e.g. trawling became more limited under the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) for *D. eleginoides*, and was prohibited from the beginning for *D. mawsoni* in the Ross Sea), and improved management through catch reductions.

**Table 2**  
Recent (2007) reported catch by species relative to the historical maximum [146].

Species	Maximum reported catch (t)	Year of maximum catch	2007 reported catch (t)	2007 catch as percentage of maximum catch
Toothfishes	44,200	1995	24,700	56
Alfonsinos	14,200	2003	6900	49
Oreos	46,600	1981	17,800	38
Sablefish	64,900	1972	27,100	42
Blue ling	36,800	1980	8200	22
Wolffishes	26,000	1979	2000	8
Cusk	55,600	1980	26,900	48

While catch levels overall can appear relatively stable, a number of species have undergone such regional declines that their fisheries have collapsed. Alfonsino fisheries off the Azores and Corner Rise seamounts in the 1970s by the former Soviet Union lasted only a few years, and a spawning location for blue ling in the North Atlantic yielded 8000 t in one year before ceasing as catches dropped rapidly [80]. In the western North Atlantic, the three species of wolffish, and cusk, have reported declines in stock size of over 90% within the time period of three generations, and 38% of deep-sea bottom fish species in that area could be “at-risk” based on the extent of population declines in surveys [29].

Yet off New Zealand, oreo fisheries have had relatively stable landings for an extended period, and current stock status for both major commercial species is estimated to be around 50% of unfished levels [36]. Hence, fisheries can be sustained where life history characteristics are known and appropriate management is applied to limit catches and/or effort levels.

### 8.7. Deep-sea corals

Precious corals are caught in some deep-sea fishing operations. They have been sought for use as adornments for millennia in Mediterranean countries. Today, black, pink/red and gold corals (Antipathidae, Corallidae and Zoanthidae) are collected for the jewelry trade in the Mediterranean, India, Japan, Pacific Islands, Hawaii and the Caribbean. In the Pacific Island region, collecting is generally done selectively using scuba or submersibles, and the precious coral “beds” are protected from overfishing [105,106], though lack of profitability has halted this fishery in recent years.

Deep-sea corals are also landed in large quantities as unwanted bycatch in other fisheries [107–109]. For example, between 1990 and 2002, Alaskan fisheries, primarily in the Aleutian Islands, landed approximately 4186 t of corals and sponges, with ~90% removed by bottom trawling [110]. In British Columbia, between 1996 and 2002, at least 15 hauls took over 4 t apiece. Orange roughly trawling on the South Tasman Rise seamounts (adjacent to the Australia EEZ) landed 1.6 t of coral per hour during the first year of the fishery (1997–1998). Indeed, in the first year they took over 1100 t of corals, a coral bycatch about 25% of the orange roughly catch [107]. Coral bycatch is highest when trawling moves into a previously unfished area, then rapidly declines. From a conservation perspective, therefore, reduced coral bycatch is not necessarily a good sign.

Although short-term effects of bottom trawling are now widely known [111–113], there have been limited studies on long-term impacts [114]. Estimated recovery rates depend on the life history of a particular organism, and range from one to five times their generation time [115]. Deep-sea corals are slow-growing and can be extremely long-lived [116], more than 4000 years for some colonies [117,118], which makes them exceedingly vulnerable to overexploitation. The benthos on seamounts closed to fishing have shown no signs of appreciable recovery from the impacts of bottom trawling even after 10 years of closure [119].

For these deep-sea biogenic habitats, recovery is therefore likely to take centuries or more [120].

In recent years, Australia, New Zealand, USA, Norway, UK and Portugal have established large trawl closures to protect seafloor ecosystems. There are also efforts to limit bottom trawling on the high seas, including closures in the North and South Atlantic [108,121].

## 9. Biomass, productivity, their economic analogs and sustainability

Some resources are nonrenewable: When people exploit them, they don’t regenerate. As humans deplete nonrenewable capital stocks, our survival and prosperity therefore depend increasingly on renewable ones. But some renewable resources have such low resilience that our consumption essentially makes them nonrenewable, at least over time scales of human lifetimes. The lower their productivity or resilience, the more important it is for people to exercise self-restraint because resource biomass and productivity drive economics that, in turn, are crucial to the prospects for sustainability.

One can gage prospects for sustainable use of renewable resources with a simple  $2 \times 2$  table (Table 3). Its two dimensions are related because a fish stock’s biomass generates production of new biomass, just as capital generates interest or dividends. But biomass and productivity are also critically different. Species and ecosystems occur in all four quadrants, and their position in these quadrants determines economic incentives for human behaviors that, in turn, determine prospects for sustainability.

Location, depth, biomass concentration (which all feed into the cost of fishing) and per unit value all affect whether a population is profitable or unprofitable to exploit, which largely determines whether people *want* to extract a resource. As Sethi et al. succinctly summarize, “Taxa with higher potential profit are targeted first, followed by progressively less economically attractive alternatives [122].” Although deep-sea fishes are more expensive to exploit, those having sufficiently high biomass concentrations make tempting targets.

In the deep sea there are some areas where biomass density, hence potential catch per unit effort, is high. These generally occur where currents advect food, usually zooplankton, from larger areas. Such transported production is filtered by seamount invertebrates (e.g., corals) or captured by fishes such as orange roughly, which hover near seamount crests. But these situations are unusual in the deep sea; most high-biomass areas and fisheries have occurred shallower, on continental shelves and in epipelagic upwelling zones, where high productivity feeds the high yields of resources that would be sustainable if only our fisheries were well-managed.

Whether a population can be sustainably fished is determined by Clark’s Law. It can be interpreted, for all practical purposes, to mean that people can only sustainably take living resources that exceed a productivity threshold, the percentage of annual biomass increment that exceeds prevailing annual interest rates. An insufficiently productive fish stock cannot, in practice, be exploited

**Table 3**  
Suitability for commercial fisheries as a function of fish stock biomass and productivity (=resilience).

	Productivity	
	Low	High
Biomass		
Low	Unprofitable	Unprofitable
High	Unsustainable	Suitable

sustainably because economics tempt us to liquidate it and reinvest the capital gained thereby in investments paying higher interest or dividend rates.

North American pines provide a clear non-fishery analog [123]. In the southeastern USA, loblolly pines (*Pinus taeda*, Pinaceae) on warm, low-elevation sites with good rainfall are key resources for the timber industry. They grow fast enough to log on 25–35 year rotations; high resilience can make them sufficiently economically attractive to log sustainably. But some other species in the same genus are much less productive, the extreme example being bristlecone pines (*P. longaeva*) of eastern California. In their high-elevation, nutrient-poor, cold, dry, windy environment (note analogs to the deep sea), these exceedingly long-lived trees grow crooked, making them unsuitable for saw timber, but their weather-beaten beauty would nonetheless make them tempting to cut. However, their annual biomass accumulation is exceedingly small, and recruitment is slow and episodic (like that of deep-sea fishes such as orange roughy). As Clark's Law explains, it would be economically rational to log them all and reinvest the proceeds, but that would be mining, not sustainable forestry. Because low productivity makes *P. longaeva* so vulnerable, the US government prohibits their logging [124].

More than 2500 years ago, Aesop's fable *The Goose that Laid the Golden Eggs* taught that greed destroys the source of good. High biomass old-growth whales [20], trees [125] and deep-sea fishes [82] all tempt us to overexploit. Ludwig et al. [126] recommended that claims of sustainable "harvesting" should not be trusted. Many nations have consciously made especially vulnerable species, such as whales and giant trees, safe from exploitation. But for reasons worth examining thoughtfully, fishes are treated differently, by rules that owe less to Aesop than to Oscar Wilde, who said "I can resist everything but temptation."

Large biomass concentrations of deep-sea fishes on some seamounts and other limited areas cannot be sustainably exploited because, even there, their productivity is generally too low, much lower than for continental shelves where people overfished so many fish stocks. These deep-sea biomass concentrations exist primarily because they had sufficient time for occasional recruitment episodes to accumulate. But they do not rebuild quickly or reliably, at least not within the time frame of fisheries. Catches generally reduce biomass until the deep-sea fishes cease being economically attractive. Thus, the centuries-old analogy between cod fisheries and mines cited in this paper's introduction is even truer in the deep sea, where the interaction of ecology (high biomass but low productivity/resilience) and economics (the incentive to convert stock biomass to capital that generates higher interest rates) compels fisheries to drive deep-sea fish stocks down to uneconomic levels serially, mining the deposits and moving on.

Now that fisheries have driven fish biomass and productivity far below their potential in productive shallow waters near fishing ports (the lower right quadrant of Table 3, the best places to fish), humankind is now exploiting the last high-biomass old-growth fish concentrations in the deep sea (the lower left quadrant, the worst places to fish). The great majority of deep-sea fisheries are unsustainable unless governments consciously choose to supersede the economically rational but destructive incentives of Clark's Law by instituting precautionary regulation. In many cases, that likely means not fishing inherently vulnerable populations and stringently enforcing such regulations.

Is low productivity in the overwhelming majority of deep-sea fishes an inconvenient truth that fishery managers, countries, Regional Fishery Management Organizations (RFMOs) and United Nations bodies will choose to overlook? Can humans resist the temptation of temporarily profitable concentrations of biomass whose low productivity incentivizes us to fish unsustainably?

And can our institutions act before it is too late? The next two sections of this paper are relevant to those questions.

## 10. Subsidies and sustainability

Deep-sea demersal fish species are more vulnerable to exploitation than the fishes whose depletion led to fishing farther from land and into the deep sea. This is, in part, because low growth rates relative to the available market discount rate for capital make it desirable for fishermen to mine, rather than sustainably exploit deep-sea fishes. That is true even in the absence of fisheries subsidies [127]. But many governments actually increase the economic incentive for doing this by subsidizing fish mining.

It is well-documented that almost all governments around the world provide subsidies to their fishing industries [128–130]. Sumaila et al. [131] estimated that the fisheries subsidy to high seas bottom trawling fleets, globally, is about US \$162 million per year, which constitutes 25% of the total landed value of the fleet's catch. Economic data for bottom trawlers suggest that the profit achieved by this vessel group is normally not more than 10% of landed value. Hence, their worldwide contribution to economic activity is limited.

The implication of this finding is that, without subsidies, most of the world's bottom trawl fleet operating in the high seas would be operating at a loss and unable to fish, thereby reducing the current threat to deep-sea and high seas fish stocks. It is also worth noting that the total catch by these fleets is less than 1% of the tonnage or value of the global marine catch [108,131], implying that they contribute next to nothing to global food security.

## 11. The legal regime in the least protected place on earth

The exceptional biological and economic vulnerability of many deep-sea fish species, and subsidies to deep-sea fishing fleets, in combination, make them exceptionally difficult to manage sustainably. Thus, any effective legal regime would have to ensure that deep-sea fisheries are: (1) governed by highly precautionary rules, (2) supported by adequate data and scientific information, (3) established by a transparent management body, and (4) effectively implemented [132]. At present, none of these preconditions are being met in most areas of the high seas [7,133], and only rarely are they met within the EEZs of coastal states [134].

Within EEZs, only a handful of countries have a robust scientific basis for making management recommendations, and most lack transparent and participatory processes to convert those recommendations into policy. Moreover, only 17% of coastal states have the capacity for effective enforcement [134]. Nevertheless, within EEZs, governments have the legal authority (if not always the capacity) to unilaterally improve management processes and to control access to fisheries. Thus, at least some deep-sea fisheries should stand a chance of being sustainable. The black scabbardfish fishery in Madeira is one – albeit rare – example.

However, most of the world's deep-sea ecosystems are in international waters (the high seas), where sustainability of deep-sea fisheries hinges on a more complex web of interdependent actors, including flag states, port states, market states and RFMOs governed by an unfinished legal regime [132,135].

Under international law, all states have the right for their nationals to fish on the high seas (article 116) [136]. However, all states have a reciprocal responsibility to manage and control their fishing vessels and nationals on the high seas, and to cooperate to ensure conservation of living marine resources (articles 117–119) [136]. Under the FAO Code of Conduct for Responsible Fisheries [137] and the UN Fish

Stocks Agreement for straddling and highly migratory fish stocks [138], these duties are further elaborated in terms of ecosystem-based and precautionary management and the roles of RFMOs with respect to the use of science, transparency and participation.

Unfortunately, as a result of lax flag state control, illegal, unreported and unregulated (IUU) fishing persists [139,140]. Moreover, due to conflicts of interest within many RFMOs, decisions to reduce catches of target stocks are made slowly, scientific advice and ecosystem impacts are often ignored, and even when strong measures are adopted, opt-out provisions can enable major players to ignore the rules [140]. This is a recipe for disaster in the deep.

The good news is that this deep-sea “tragedy of the commons” has been recognized, and actions to redress at least some of these shortcomings are being put into place [141]. In 2006, the United Nations General Assembly (UNGA) adopted a resolution on “Sustainable Fisheries” [142] calling on states to undertake an explicit set of time-limited actions to ensure sustainability of deep-sea fisheries on the high seas and to protect vulnerable deep-sea ecosystems, consistent with the precautionary and ecosystem approaches.

The UNGA also requested that FAO develop “Guidelines for the management of deep-seas fisheries on the high seas.” These Guidelines, adopted in August 2008, call for rigorous management of deep-sea fisheries throughout all stages of their development, and for keeping catch rates low until knowledge, management capacity and measures for monitoring, control and surveillance increase [143].

A review of progress in implementing the UNGA resolution in late 2009 revealed that, while a number of RFMOs had adopted measures such as closed areas to reduce the impact of fishing on deep-sea habitats, few RFMOs had taken steps to ensure the sustainability of deep-sea fisheries [144]. As a result, the UNGA adopted a new resolution with clear language calling for States and RFMOs not to authorize deep-sea fisheries unless an impact assessment had been performed and measures adopted to prevent significant impacts on deep-sea ecosystems. It then explicitly called for States and RFMOs, where scientific information is uncertain, unreliable or inadequate, to “adopt precautionary management measures to ensure that fishing effort, capacity and catch levels did not exceed levels consistent with the sustainability of the fish stocks and non-target species.” [UNGA resolution 64/72, paragraph 119(d) (emphasis added) [142].

Improved adherence to the 2006 and 2009 UNGA resolutions and FAO Guidelines could help towards achieving sustainability of deep-sea fisheries. However, until states fully implement their obligations, including through better flag state and RFMO performance, and better data, the preconditions for sustainability for deep-sea fisheries on the high seas will not be met. And as unlikely as that is in deep-sea portions of countries’ EEZs, it is even less likely on the high seas under current conditions. A UNGA review of progress by States and RFMOs in implementing the 2006 and 2009 resolutions in late 2011 provides an opportunity for all States to insist that deep-sea fisheries on the high seas be managed on a sustainable basis, or not allowed to proceed.

## 12. Conclusion

After briefly reviewing key aspects of the biology of deep-sea fishes, the authors of this paper conclude that sustainable exploitation is feasible for very few of them under prevailing economic conditions and governance arrangements. The authors do note that catches of a handful of species can be or can give the appearance of being sustained, primarily ones that (a) can occur shallower than 200 m, (b) have relatively high population resilience and (c) are fished with low-tech, non-trawl methods.

The surplus production of deep-sea fishes is generally low, but their biomass can be attractively high. Large withdrawals of this biological capital (high catch rates) in the early years of some deep-sea fisheries have repeatedly misled the fishing industry and resource managers into believing that deep-sea stocks can be sustainably exploited. This belief is often endorsed by agencies interested in the large economic returns that these fisheries usually generate in their early years.

As Clark [11], Roberts [12] and Large et al. [14] observe, deep-sea fishing is fish mining. Deep-sea fisheries exaggerate a general feature of marine fisheries, the pernicious disconnect between the natural spatiotemporal patterns of productivity of stocks and the perceived need for continuous high catches that has fueled the growth of the global fishing enterprise by serially depleting fish stocks. The serial collapses that took 50 years in coastal marine fisheries takes only 5–10 years in the deep sea. These fisheries also often rely extensively on bottom trawling, and a sustainable combination of low catches with limited ecosystem impact is a difficult, almost impossible, balance to achieve [145].

Given the widespread subsidization of energy-intensive deep-sea fisheries and the relatively tiny catches they generate globally, there is a persuasive argument that the best policy would be to shut these fisheries down and redirect subsidies currently allocated to them toward (1) compensating the impacted fishers and (2) helping to rebuild fish populations in highly productive waters closer to fishing ports and markets, places far more conducive to sustainable fisheries. Those involved in deep-sea fisheries should bear the burden of proving their sustainability if these fisheries are to develop, or continue.

Ending deep-sea fisheries would be particularly appropriate for the high seas outside the EEZs of maritime countries, where fisheries from just a few countries are harming the biodiversity that is a vital interest for all humankind.

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## References

- [1] Pauly D. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 1995;10:430.
- [2] Roberts C. *The unnatural history of the sea*. Washington DC: Island Press; 2007.
- [3] Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 2001;293(5530):629–38.
- [4] Rick TC, Erlandson JM. Coastal exploitation. *Science* 2009;325(5943):952–3.

- [5] Myers RA, Worm B. Rapid worldwide depletion of predatory fish communities. *Nature* 2003;423:280–3.
- [6] Watson R, Pauly D. Systematic distortions in world fisheries catch trends. *Nature* 2001;414:534–6.
- [7] FAO. State of world fisheries and aquaculture 2008. Rome: FAO Fisheries and Aquaculture Department; 2009. 84p. Available:.
- [8] Pauly D, Alder J, Bakun A, Heileman S, Kock KH, et al. Marine systems. In: Hassan R, Scholes R, Ash N, editors. Ecosystems and human well-being: current states and trends, vol. 1. Washington DC: Millennium Ecosystem Assessment and Island Press; 2005. p. 477–511. [Chapter 18].
- [9] Morato T, Watson R, Pitcher TJ, Pauly D. Fishing down the deep. *Fish and Fisheries* 2006;7:24–34.
- [10] Merrett NR, Haedrich RL. Deep-sea demersal fish and fisheries. London: Chapman & Hall; 1997. p. 282.
- [11] Clark M. Are deepwater fisheries sustainable? The example of orange roughy (*Hoplostethus atlanticus*) in New Zealand Fisheries Research 2001;51:123–35.
- [12] Roberts C. Deep impact: the rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* 2002;17(5):242–5.
- [13] Glover AG, Smith CR. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environmental Conservation* 2003;30(3):219–41.
- [14] Large PA, Hammer C, Bergstad OA, Gordon JDM, Lorange P. Deep-water fisheries of the Northeast Atlantic: II assessment and management approaches. *Journal of Northwest Atlantic Fisheries Science* 2003;31:151–63.
- [15] Perez JAA, Wahrlich R, Pezzuto PR, Schwingel PR, Lopes FRA, Rodrigues-Ribeiro M. Deep-sea fishery off southern Brazil: recent trends of the Brazilian fishing industry. *Journal of Northwest Atlantic Fisheries Science* 2003;31:1–18.
- [16] Thiel H. Anthropogenic impacts on the deep sea. In: Tyler PA, editor. Ecosystems of the deep oceans, vol. 28. Ecosystems of the world. Amsterdam, The Netherlands: Elsevier Science; 2003. p. 427–72.
- [17] Davies AJ, Roberts JM, Hall-Spencer J. Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. *Biological Conservation* 2007;138(3–4):299–312.
- [18] Sissenwine MP, Mace PM. Can deep-water fisheries be managed sustainably? *FAO Fisheries Report* 838; 2007. p. 61–111.
- [19] Natural Environment Research Council. Deep sea fish stocks threatened; 2009. Available: <<http://www.sams.ac.uk/sams-news/Media%20releases/deep-sea-fish-stocks-threatened-1>> [accessed June 8, 2010].
- [20] Clark CW. The economics of overexploitation. *Science* 1973;181(4100):630–4.
- [21] Clark CW. Profit maximization and the extinction of animal species. *Journal of Political Economy* 1973;81(4):950–61.
- [22] Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, et al. Impacts of biodiversity loss on ocean ecosystem services. *Science* 2006;314(5800):787–90.
- [23] Danovaro R, Gambi C, Dell'Anno A, Corinaldeci C, Fraschetti S, et al. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Current Biology* 2008;18(1):1–8.
- [24] Morato T, Cheung WWL, Pitcher TJ. Vulnerability of seamount fish to fishing: fuzzy analysis of life history attributes. *Journal of Fish Biology* 2006;68:209–21.
- [25] FAO. State of the world fisheries and aquaculture. Rome (Italy): FAO Fisheries and Aquaculture Department; 2004.
- [26] Pauly D, Alder J, Bennett E, Christensen V, Tyedmers P, et al. The future for fisheries. *Science* 2003;302(5649):1359–61.
- [27] Pauly D, Watson R, Alder J. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of The Royal Society: Biological Sciences* 2005;360:5–12.
- [28] Cheung WWL, Watson R, Morato T, Pitcher TJ, Pauly D. Intrinsic vulnerability in the global fish catch. *Marine Ecology Progress Series* 2007;333:1–12.
- [29] Baker KD, Devine JA, Haedrich RL. Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. *Environmental Biology of Fishes* 2009;85:79–88.
- [30] Ryther JH. Photosynthesis and fish production in the sea. *Science* 1969;166:72–6.
- [31] McAllister DE, Baquero J, Spiller G, Campbell RA. Global trawling ground survey. Ocean Voice International: Marine Conservation Biology Institute, World Resources Institute; 1999.
- [32] Lutz MJ, Caldeira K, Dunbar RB, Behrenfeld MJ. Seasonal rhythms of net primary production and particulate organic carbon flux describe biological pump efficiency in the global ocean. *Journal of Geophysical Research* 2007;112:C10011, doi:10.1029/2006JC003706.
- [33] Genin A, Dower JF. Seamount plankton dynamics. In: Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, editors. Seamounts: ecology, fisheries and conservation. Oxford, UK: Blackwell Publishing; 2007. p. 85–100.
- [34] White M, Bashmachnikov I, Aristegui J, Martins A. Physical processes and seamount productivity. In: Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, editors. Seamounts: ecology, fisheries and conservation. Oxford (UK): Blackwell Publishing; 2007. p. 65–84.
- [35] Rowe GT, Merrett N, Sheppard J, Needler G, Hargrave B, et al. Estimates of direct biological transport of radioactive waste in the deep sea with special reference to organic carbon budgets. *Oceanologica Acta* 1986;9:199–208.
- [36] Ministry of Fisheries-New Zealand. Report for the fisheries assessment plenary, May 2009: stock assessments and yield estimates; 2009. p. 1036.
- [37] Koslow JA. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *Journal of Fisheries Biology* 1996;49(Suppl. A):54–74.
- [38] Pauly D. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 1980;39:175–92.
- [39] McCann K, Shuter B. Bioenergetics of life history strategies and the comparative allometry of reproduction. *Canadian Journal of Fisheries and Aquatic Sciences* 1997;54:1289–98.
- [40] Roff DA. The evolution of life histories: theory and analysis. New York: Chapman and Hall; 1992.
- [41] Winemiller K, Rose K. Patterns of life history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 1992;49:2196–218.
- [42] Froese R, Binohlan C. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fishery Biology* 2000;56:758–73.
- [43] Koslow JA, Boehlert GW, Gordon JDM, Haedrich RL, Lorange P, et al. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 2000;57:548–57.
- [44] Morato T, Clark MR. Seamount fishes: ecology and life histories. In: Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, et al., editors. Seamounts: ecology, fisheries, and conservation. Blackwell Fisheries and Aquatic Resources Series 12. Oxford: Blackwell Publishing; 2007. p. 170–188, p. 527 [Chapter 9].
- [45] Jennings S, Reynolds JD, Mills SC. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London: Series B* 1998;265:333–9.
- [46] Dulvy NK, Sadovy Y, Reynolds JD. Extinction vulnerability in marine populations. *Fish and Fisheries* 2003;4:25–64.
- [47] Hutchings JA, Reynolds JD. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 2004;54:297–309.
- [48] Winemiller KO. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 2005;62:872–85.
- [49] Allain V. Reproductive strategies of three deep-water benthopelagic fishes from the northeast Atlantic Ocean. *Fisheries Research* 2001;51:165–76.
- [50] Rideout RM, Rose GA, Burton MPM. Skipped spawning in female iteroparous fishes. *Fish and Fisheries* 2005;6:50–72.
- [51] Minto C, Nolan CP. Fecundity and maturity of orange roughy (*Hoplostethus atlanticus* Collett 1889) on the Porcupine Bank, Northeast Atlantic. *Environmental Biology of Fishes* 2006;77:39–50.
- [52] Sadovy Y. The threat of fishing to highly fecund fishes. *Journal of Fisheries Biology* 2001;59(Suppl A):90–108.
- [53] Denney NH, Jennings S, Reynolds JD. Life-history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London: Series B* 2002;269:2229–37.
- [54] Berkeley SA, Hixon MA, Larson RJ, Love MS. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 2004;29(8):23–32.
- [55] Cheung WWL, Pitcher TJ, Pauly D. A fuzzy logic expert system to estimate intrinsic extinction vulnerability of marine fishes to fishing. *Biological Conservation* 2005;124:97–111.
- [56] Froese R, Pauly D, editors. FishBase; 2009. Available: <[www.fishbase.org](http://www.fishbase.org)>, version (04/2009).
- [57] Stevens JD, Bonfil R, Dulvy NK, Walker PA. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 2000;57:476–94.
- [58] Sverdrup HU, Johnson MW, Fleming RH. The oceans—their physics, chemistry and general biology. New York: Prentice-Hall; 1961.
- [59] FAO. Report and documentation of the expert consultation on deep-sea fisheries in the high seas. FAO Fisheries Report No. 838. Rome (Italy): FAO; 2007. p. 203.
- [60] McAllister MK, Pikitch EK, Babcock EA. Using Demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences* 2001;58(9):1871–90.
- [61] Gulland JA. The fish resources of the oceans. Surrey, England: FAO/Fishing News Books; 1971. p. 425.
- [62] Hoenig JM. Empirical use of longevity data to estimate mortality rates. *Fish B-NOAA* 1984;81:4.
- [63] Beverton Jensen AL and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 1996;53:820–2.
- [64] Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society of London: Series B* 2005;262:2337–44.
- [65] Sumaila UR, Walters C. Intergenerational discounting: a new intuitive approach. *Ecological Economics* 2005;52:135–42.
- [66] Gordon HS. The economic theory of a common-property resource: the fishery. *Journal of Political Economy* 1954;62(2):124–42.
- [67] Hardin G. The tragedy of the commons. *Science* 1968;162:1243–8.
- [68] Berkes F, Hughes TP, Steeneck RS, Wilson JA, Bellwood DR, et al. Globalization, roving bandits, and marine resources. *Science* 2006;311:1557–8.

- [69] Ostrom E. A general framework for analyzing sustainability of social-ecological systems. *Science* 2009;325:419–22.
- [70] Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, et al. Population diversity and the portfolio effect in an exploited species. *Nature* 2010;465:609–12.
- [71] Norse EA. Ecosystem-based spatial planning of marine fisheries: why and how? *Bulletin of Marine Science* 2010;86:179–95.
- [72] Garcia VB, Lucifora IO, Myers RA. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society of London: Series B* 2008;275:83–9.
- [73] Kyne PM, Simpfendorfer CA. Collation and Summarization of Available Data on Deepwater Chondrichthyan: biodiversity, Life History and Fisheries. Bellevue, WA: Marine Conservation Biology Institute; 2007. 137 p.
- [74] Graham KJ, Andrew NL, Hodgson KE. Changes in relative abundance of sharks and rays on Australian south east fishery trawl grounds after twenty years of fishing. *Marine Freshwater Research* 2001;52:549–61.
- [75] Devine JA, Baker KD, Haedric RL. Deep-sea fishes qualify as endangered. *Nature* 2006;439:29.
- [76] Priede IG, Froese R, Bailey DM, Bergstad OA, Collins MA, et al. The absence of sharks from abyssal regions of the world's oceans. *Proceedings of the Royal Society of London: Series B* 2006;273:1435–41.
- [77] IUCN. Overview of the conservation of deep-sea chondrichthyan. Report of the IUCN Shark Specialist Group; 2007. 34 p.
- [78] Cavanagh RD, Kyne PM. The conservation status of deep-sea chondrichthyan fishes. In: Shotton R, editor. *Proceedings of the Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries. Part 2: Conference poster papers and workshop papers.* FAO Fisheries Proceedings No. 3/2. Rome (Italy): FAO; 2005. p. 366–80. Available.
- [79] Last PR, Stevens JD. Sharks and rays of Australia. Australia: CSIRO; 1994.
- [80] Clark MR, Vinnichenko VI, Gordon JDM, Beck-Bulat GZ, Kukharev NN, et al. Large scale distant water trawl fisheries on seamounts. In: Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, editors. *Seamounts: ecology, fisheries, and conservation.* Blackwell fisheries and aquatic resources series 12. Oxford: Blackwell Publishing; 2007. p. 361–99.
- [81] Clark MR, Anderson OF, RICC Francis, Tracey DM. The effects of commercial exploitation on orange roughy (*Hoplostethus atlanticus*) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. *Fisheries Research* 2000;45(3):217–38.
- [82] Francis RICC, Clark MR. Sustainability issues for orange roughy fisheries. *Bulletin of Marine Science* 2005;76:337–51.
- [83] Bax NJ, Tilzey R, Lyle J, Wayne SE, Kloser R, et al. Providing management advice for deep-sea fisheries: lessons learned from Australia's orange roughy fisheries. *FAO Fisheries Proceedings No. 3/1*; 2005. p. 259–72.
- [84] Boyer DC, Kirchner CH, McAllister MK, Staby A, Staalesen B. The orange roughy fishery of Namibia: lessons to be learned about managing a developing fishery. *South African Journal of Marine Science* 2001;23:205–21.
- [85] Branch TA. A review of orange roughy *Hoplostethus atlanticus* fisheries, estimation methods, biology and stock structure. *South African Journal of Marine Science* 2001;23:181–203.
- [86] Paya I, Montecinos M., Ojeda V., Cid L. An overview of the orange roughy (*Hoplostethus* sp.) fishery off Chile. *FAO Fisheries Proceedings No. 3/2*; 2005. p. 97–116.
- [87] Japp DW, James A. Potential exploitable deepwater resources and exploratory fishing off the South African coast and the development of the deepwater fishery on the south Madagascar ridge. *FAO Fisheries Proceedings No. 3/1*; 2005. p. 162–168.
- [88] Clark MR. Deep-sea seamount fisheries: a review of global status and future prospects. *Latin American Journal of Aquatic Research* 2009;37(3):501–12.
- [89] Japp D.W., Wilkinson S. Deep-sea resources and fisheries. *FAO Fisheries Report* 838; 2007. p. 39–59.
- [90] Dunn M. Orange roughy. What might the future hold? *New Zealand Science Review* 2007;63(3–4):70–5.
- [91] Sasaki T. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. In: Uchida RN, Hayasi S, Boehlert GW, editors. *Environment and Resources of Seamounts in the North Pacific.* NOAA Technical Report NMFS 43; 1986. p. 21–30.
- [92] Borets LA. Some results of studies on the biology of the pelagic armourhead (*Pentaceros richardsoni* Smith). *Investigations of the biology of fishes and fishery oceanography.* Vladivostok: TINRO; 1975 pp. 82–90 [In Russian].
- [93] Kulikov MY, Darnitsky VB. Abundance dynamics of benthopelagic fishes in the Northwest Pacific and possible reasons behind that. *Oceanographic basis of biological productivity in the Northwestern Part of the Pacific.* Vladivostok: TINRO; 1992 pp. 4–19 [In Russian].
- [94] Orlov AM, Iwamoto T, editors. *Grenadiers of the world oceans: biology, stock assessment, and fisheries, vol. 63.* Symposium: American Fisheries Society; 2008.
- [95] Moore J. Deep-sea finfish fisheries: lessons from history. *Fisheries* 1999;24:16–21.
- [96] Noronha AC. A fish from Madeira. The black scabbardfish or *Aphanopus carbo*. Porto, Portugal: Renascença Portuguesa; 1925. 15 p. [In Portuguese].
- [97] Freitas M, Biscoito M. Four chondrichthyes new for the archipelago of Madeira and adjacent seamounts (NE Atlantic Ocean). *Bocagiana* 2007;221:7.
- [98] Martins R, Ferreira C. Line fishing for black scabbardfish (*Aphanopus carbo* Lowe, 1839) and other deep water species in the eastern mid-Atlantic to the north of Madeira. In: Hooper AG, editor. *Deep-water fisheries of the north atlantic oceanic slope.* Dordrecht: Kluwer Academic Publishers; 1995. p. 323–35.
- [99] Morales-Nin B, Canha A, Casas M, Figueiredo I, Gordo LS, et al. Inter-calibration of age readings of deepwater black scabbardfish, *Aphanopus carbo* (Lowe, 1839). *ICES Journal of Marine Science* 2002;59:352–64.
- [100] Figueiredo I, Bordalo-Machado P, Reis S, Sena-Carvalho D, Blasdale T, Newton A, et al. Observations on the reproductive cycle of the black scabbardfish (*Aphanopus carbo* Lowe, 1839) in the NE Atlantic. *ICES Journal of Marine Science* 2003;60(4):774–9.
- [101] Shotton R. The deep-water fisheries. In: *Review of the state of world marine fishery resources.* FAO Fisheries Technical Paper. Rome (Italy): FAO Marine Resources Service, Fishery Resources Division; 2005. p. 188–200.
- [102] Probert PK, Christiansen S, Gjerde KM, Gubbay S, Santos RS. Management and conservation of seamounts. In: Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, Santos R, editors. *Seamounts: ecology, fisheries and conservation.* Oxford (UK): Fish and Aquatic Resources Series, Blackwell; 2007. p. 443–75.
- [103] Bordalo-Machado P, Figueiredo I. The fishery for black scabbardfish (*Aphanopus carbo* Lowe, 1839) in the Portuguese continental slope. *Reviews in Fish Biology and Fisheries* 2009;19:49–67.
- [104] ICES. Report of the working group on the biology and assessment of deep-sea fisheries resources. *ICES CM 2008/ACOM 14*; 2008. 531 p.
- [105] Grigg RW. Precious corals in Hawaii: Discovery of a new bed and revised management measures for existing beds. *Marine Fisheries Review* 2002;64:13–20.
- [106] Parrish FA, Baco AR. State of deep coral ecosystems in the US Pacific Islands region: Hawaii and the US Pacific Territories. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G, editors. *The state of deep coral ecosystems of the United States.* Technical Memorandum CRCP-3; 2007. p. 155–94.
- [107] Anderson OF, Clark MR. Analysis of bycatch in the fishery for orange roughy (*Hoplostethus atlanticus*) on the south Tasman Rise. *Marine Freshwater Research* 2003;54:643–52.
- [108] Gianni M. High seas bottom fisheries and their impact on the biodiversity of vulnerable deep-sea ecosystems. Gland, Switzerland: International Union for Conservation of Nature & Natural Resources; 2004. Available.
- [109] Rice J. Impacts of mobile bottom gears on seafloor habitats, species and communities a review and synthesis of selected international reviews. DFO CSAS Research Document 2006/057; 2006.
- [110] NMFS. Final programmatic supplemental groundfish environmental impact statement for Alaska groundfish fisheries. Juneau: NOAA, NMFS; 2004.
- [111] Watling L, Norse EA. Disturbance of the seabed by mobile fishing gear: a comparison with forest clearcutting. *Conservation Biology* 1998;12:1180–97.
- [112] Chuenpagdee R, Morgan LE, Maxwell S, Norse EA, Pauly D. Shifting gears: Assessing collateral impacts of fishing methods in U.S. waters. *Frontiers in Ecology and Environment* 2003;1:517–24.
- [113] Fuller SD, Picco C, Ford J, Tsao C-F, Morgan LE, et al. How we fish matters: addressing the ecological impacts of Canadian fishing gear. *Ecology Action Centre, Living Oceans Society, Marine Conservation Biology Institute*; 2008. 25 p.
- [114] FAO. Impact of trawling and scallop dredging on benthic habitats and communities. *FAO Fisheries Technical Paper 472.* Rome (Italy): FAO; 2005; 58 p.
- [115] Emeis KC, Benoit JR, Deegan LA, Gilbert AJ, Lee V, et al. Group 4: unifying concepts for integrated coastal management. In: von Bodungen G, Turner K, editors. *Science and integrated coastal management.* Berlin: Dahlem University Press; 2001. 378 p.
- [116] Druffel ER, Griffin MS, Witter A, Nelson E, Southon J, et al. *Gerardia*: bristlecone pine of the deep-sea? *Geochimica et Cosmochimica Acta* 1995;59:5031–6.
- [117] Roark EB, Guilderson TP, Dunbar RB, Ingram BL. Radiocarbon based ages and growth rates: Hawaiian deep-sea corals. *Mar Ecology Progress Series* 2006;327:1–14.
- [118] Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA. Extreme longevity in proteinaceous deep-sea corals. *Proceedings of the National Academy of Sciences* 2009;106(13):5204–8.
- [119] Williams A, Schlacher TA, Rowden AA, Althaus F, Clark MR, Bowden DA, et al. Seamount megabenthic assemblages fail to recover from trawling impacts. *Marine Ecology* 2010;31(Suppl. 1):183–99.
- [120] Freiwald A, Fossà JH, Grehan A, Koslow T, Roberts JM. Cold water coral reefs. Cambridge: UNEP-WCMC; 2004.
- [121] Rogers AD, Clark MR, Hall-Spencer J, Gjerde KM. The science behind the guidelines: a scientific guide to the FAO draft international guidelines (December 2007) for the management of deep-sea fisheries in the high seas and examples of how the guidelines may be practically implemented. Switzerland: IUCN; 2008. 39 p.
- [122] Sethi SA, Branch TA, Watson R. Global fishery development patterns are driven by profit but not trophic level. *Proceedings of the National Academy of Sciences: Early Edition* 2010. June 21.
- [123] CAB International. *Pines of silvicultural importance.* New York: CABI Publishing; 2002. 562 p.
- [124] Cohen MPA. *Garden of bristlecones: tales of change in the Great Basin.* Reno: University of Nevada Press; 1998. 308 p.
- [125] Norse EA. *Ancient forests of the Pacific Northwest.* Washington, DC: Island Press; 1990. 327 p.
- [126] Ludwig D, Hilborn R, Walters C. Uncertainty, resource exploitation and conservation: lessons from history. *Science* 1993;260(17):36.

- [127] Clark CW, Munro G, Sumaila UR. Limits to the privatization of fishery resources. *Land Economics* 2010;86(2):209–18.
- [128] Milazzo M. Subsidies in world fisheries: a re-examination. World Bank Technical Paper No. 406. Washington, DC: The World Bank; 1998.
- [129] Sumaila UR, Pauly D, editors. Catching more bait: a bottom-up re-estimation of global fisheries subsidies. Vancouver: Fisheries Centre, the University of British Columbia. Fisheries Centre Research Reports, vol. 14, no. 16; 2006. 114 p.
- [130] Sharp R, Sumaila UR. Quantification of U.S. marine fisheries subsidies. *North American Journal of Fish Management* 2009;29:18–32.
- [131] Sumaila UR, Khan A, Teh L, Watson R, Tyedmers P, et al. Subsidies to high seas bottom trawl fleets and the sustainability of deep-sea demersal fish stocks. *Marine Policy* 2009;34(3):495–7.
- [132] Special Issue of the *International Journal of Marine and Coastal Law* 2004;19(3):209–22.
- [133] Bensch A, Gianni M, Gréboval D, Sanders JS, Hjort A. Worldwide review of bottom fisheries in the high seas. FAO Fisheries and Aquaculture Technical Paper No. 522; 2008. p. 145.
- [134] Mora C, Myers RA, Coll M, Simone L, Pitcher TJ, et al. Management effectiveness of the world's marine fisheries. *PLoS Biology* 2009;7(6): e1000131, doi:10.1371/journal.pbio.1000131.
- [135] Hayashi M. Global governance of deep-sea fisheries. Special Issue of the *International Journal of Marine and Coastal Law* 2004;19(3):289–98.
- [136] United Nations. Convention on the Law of the Sea (UNCLOS). 1833 U.N.T.S 397; 1982.
- [137] FAO. Code of Conduct for Responsible Fisheries. Rome (Italy): FAO; 1995. Available:.
- [138] United Nations. United Nations agreement on straddling fish stocks and highly migratory fish stocks. *International Legal Materials* 1995;34: 1547–80. Available <[http://www.un.org/Depts/los/convention\\_agreements/convention\\_overview\\_fish\\_stocks.htm](http://www.un.org/Depts/los/convention_agreements/convention_overview_fish_stocks.htm)>.
- [139] High Seas Task Force. Closing the net: stopping illegal fishing on the high seas; 2006. Available: <<http://www.high-seas.org/docs/HSTFfinal/HSTF-Final-Report-09-03-06.pdf>>.
- [140] Lodge MW, Anderson D, Løbach T, Munro G, Sainsbury K, et al. Recommended best practices for regional fisheries management organizations. Report of an independent panel to develop a model for improved governance by Regional Fisheries Management Organizations. London: The Royal Institute of International Affairs; 2007. 141 p. Available: <[http://www.chathamhouse.org.uk/files/9710\\_rfmo0807.pdf](http://www.chathamhouse.org.uk/files/9710_rfmo0807.pdf)>.
- [141] IUCN. Letter to the acting director of the UN Division for Ocean Affairs and Law of the Sea, 20 April 2009, a submission for the review of implementation of paragraphs 83 to 90 of General Assembly Resolution 61/105; 2009.
- [142] United National General Assembly. Resolution on sustainable fisheries A/RES/61/105, paragraphs 80–91; 2006. Available: <<http://daccessdds.un.org/doc/UNDOC/GEN/N06/500/73/PDF/N0650073.pdf?OpenElement/>>.
- [143] FAO. International guidelines for the management of deep-sea fisheries in the high seas. Rome (Italy): FAO; 2009. 92 p.
- [144] Gianni M.. Review of the implementation of the provisions of UNGA resolution 61/105 related to the management of high seas bottom fisheries, Submission to the UN Division for Oceans Affairs and the Law of the Sea; 2009.
- [145] Watling L, Haedrich RL, Devne J, Drazen J, Dunn MR, Gianni M, et al. Can ecosystem-based deep-sea fishing be sustained? In: Proceedings of the International scientific workshop France: Neuville-Bosc; 2010.
- [146] FAO. FishStat Plus—Universal software for fishery statistical time series; 2009c. Available: <<http://www.fao.org/fishery/statistics/software/fishstat/>>.
- [147] Musick JA. Criteria to define extinction risk in marine fishes. *Fisheries* 1999;24(12):6–14.
- [148] Yanagimoto T. Outline of Japanese trawl fishing on seamounts in the Central North Pacific (1969–1997). Reports on the research and stock assessments of groundfish in the North Pacific in 1998/1999. Kushiro (Japan): Fisheries Agency of Japan, Hokkaido National Fisheries Research Institute; 1999. 1–13 p.