Rapid worldwide depletion of predatory fish communities

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Supplementary information

Data sources, treatment and interpretation

Longlining data Longlining data obtained from the Japanese fishery agency were used to calculate the yearly catch-per-unit-effort across a global 5x5° grid. Catch-per-unit-effort data are in most cases a conservative estimator of abundance [1]. However, the reliability of the longline CPUE series has been questioned for 4 principle reasons:

First, it has been claimed for some selected species that the declines in CPUE could not be accounted for by the estimated catches. However, when a careful analysis of fisheries with good catch data is undertaken (for example for southern bluefin tuna), there has been no difficulty in explaining the trends in CPUE (see assessments carried out by the Commission for the Conservation of Southern Bluefin Tuna; URL: www.ccsbt.org and Ref. 2). Similarly, there is no difficulty in accounting for the changes in abundance of western Atlantic bluefin tuna by estimated catches (www.iccat.es). However, reliable inference of age-structure is rarely available for the early years of a fishery, so simple models without age-structure are usually fit to such data. The notion that catches cannot explain declines in CPUE appears to be based upon the application of overly simplistic models, assuming simple logistic population dynamics. However, where this suggestion has been tested, it has not been found valid. For example, rapid declines in North Atlantic swordfish and blue marlin CPUE were consistent with a simple model that includes age structure [3-5]. The only clear cases where the magnitude of the CPUE trends are not reconcilable with age-structured models concern yellowfin tuna [6], which we discuss next.

Second, it has been suggested that the longline CPUE declines may not represent true changes in abundance because catches for some species have remained stable, or increased after the decline in longline CPUE has occurred (Ref. 6 and A. Fonteneau pers com.). This pattern is found consistently in all three oceans for yellowfin tuna, but not for

other major species. For example, the catches and estimates of maximum sustainable yield for Atlantic yellowfin tuna increased gradually from 1970-1995 (Ref. 7). The increase in yellowfin productivity in the Eastern Pacific Ocean (EPO) occurred in about 1984-85 (Ref. 8), while the increase in the Western Central Pacific Ocean (WCPO) occurred in about 1975-76 (Ref. 9). The earlier occurrence in the WCPO corresponds to earlier depletion of other large predators in this region. These species have higher age at maturity than yellowfin, and therefore less potential for rapid increases. The pattern for yellowfin is most easily explained as an increase in survival of juvenile fish, likely linked to the 10-fold declines in their predators. Such patterns are clearly predicted by ecosystem models that take species interactions into account [10,11]. Similar changes due to release from predation or competition appear to occur in billfishes and some groundfishes, as seen in Fig. 3 of our ms. Traditional assessments have largely ignored such interactions among species and the effects of fishing down predator biomass on remaining stocks. The alternative hypothesis is that only a minor part of the yellowfin adult recruitment is available to the longline gear [6], or any other gear. This hypothesis is difficult to test, and has little support for other species. We emphasize that this objection concerns yellowfin tuna, and is not generally applicable to the interpretation of longline CPUE trends. For example, Fontenau finds that bigeye tuna CPUE corresponds to true adult abundance [6].

The third reason that has been raised as to why the CPUE data are not consistent with changes in abundance is that they are not consistent with changes in the length of fish caught over time. This objection has been raised primarily for some billfish, such as white and blue marlin [12]. However, recent work has shown that this objection is not valid because of the unusual pattern of growth of the marlins [5].

Fourth, it has been suggested that the changes in the average depth at which longline fishing occurs makes the trends in CPUE difficult to interpret. However, these changes occurred around 1980, well after the CPUE declines had occurred. While the deeper depth of the hooks may reduce the catch of surface-dwelling marlins, depth has little effect on the catch rates of swordfish, and increases the catch rate for albacore and bigeye tuna [13]. Different studies vary on the effects of depth on yellowfin catch rates. Thus, the shift in depth of hooks appears to increase the estimated relative abundance of

the major species caught during the period (bigeye and albacore) or have little consistent effect (yellowfin, swordfish). Increasing depth will reduce the estimates of the marlins, but these species represent only a very small proportion of the catch since 1975. In conclusion, we argue that the decline in CPUE can be reconciled with catch data when considering age structure and multi-species interactions. We also stress that the very high initial catch rates observed throughout the world's oceans were verified by independent scientific surveys as discussed in the text.

Finally, it has been hypothesized that during the initial stages of exploitation the decline in CPUE overestimated the decline in abundance because some fish may have been genetically determined to be more vulnerable to longline gear, and the decline only took place in the vulnerable portion of the population [14], whereas a large "hidden biomass" remains. This hypothesis is difficult to test, and although we cannot refute it, we consider it somewhat unlikely that satellite technology, greatly improved fishing gear, the use of spotter airplanes and similar technological advances continue to miss large, unseen stock components.

Shark damage on logline sets Because shark damaged tuna were discarded and not recorded as catches in Japanese longlining operations, high levels of shark damage in initial years would bias trends towards an underestimation of initial biomass. High initial levels of shark damage and a marked decline of shark damage over time are well documented. We review the data for the tropical Pacific and the Gulf of Mexico as an example. Between 1953 and 1956 the percentage of tunas damaged by sharks in the tropical Pacific ranged from 12.4-26.3 percent, depending on the season [15]. Between 1954 and 1963 the proportional shark damage declined to 10.3 percent [16], and between 1995 and 2000 only 2.6 of tuna were damaged by sharks [17]. Similar changes were found in the Gulf of Mexico. Exploratory long-line surveys carried out by the U.S. Fish and Wildlife Service in the early 1950's found that around 30% of the yellowfin tuna was damaged to some extent by sharks, and 20% were too damaged to be canned [18,19]. We have examined data in the same area reported by scientifically trained observers who report catch data to the U.S. National Marine Fisheries Service. In the 1990's we found that of 11,230 yellowfin tuna observed, only 3.8% were damaged by all sources, including sharks.

These declines in shark damage are consistent with the general decline in shark numbers both in shark targeted [20] and bycatch fisheries [21]. Other data that report damage by sharks and marine mammals (killer and false killer whales) suggest that damage rates by marine mammals per trip or per set may have increased in some areas [22]. However, these data may be regarded with caution because both trip duration and number of hooks per set have increased over time.

Gulf of Thailand trawl survey data The trawl fisheries in the Gulf of Thailand represent one of the largest demersal fisheries in Southeast Asia, with catches peaking at 800 kt per year. In this fishery, some 150 species make a contribution. The Gulf of Thailand time series was extracted from Table 1 in Ref. 23. We included only larger demersal predators in our analysis, excluding small fish such as threadfin breams and ponyfishes, as well as invertebrates, and pelagics. Exclusion of these groups had little effects on the overall magnitude of decline. For complete species information refer to Table S1.

South Georgia trawl survey data The South Georgia time series was extracted from Fig. 1 in Ref. 24. The authors combined virtual population analysis (VPA) estimates (1970-74) with subsequent survey data (1975-91) in order to derive an approximate estimate of original demersal fish biomass in South Georgia at 750 kt. In their analysis, they considered several species of icefish and notothenias (or rockcod), which are by far the most abundant demersal fishes in this area (see Table S1). The problem is that information on species other than the dominant rockcod *Notothenia rossii* was fragmentary in the early years, and there may have been some initial under-reporting of catches. However, this would make the results only more conservative, as the magnitude of the decline would be underestimated. We used the approximate estimates of other species biomass provided by the authors. These suggest a residual biomass of 160 kt after the first two years of fishing. Together with the total removals of 514 kt (after CCAMLR catch statistics [25]), this comes close to the total biomass estimate of 750 kt, supporting this number as a reasonable estimate of total biomass prior to industrial exploitation.

Northwest Atlantic data The Northwest Atlantic data cover the North Atlantic Fisheries Organization (NAFO) areas 3NO (Southern Grand Banks) and 3Ps (St. Pierre Bank), respectively. From 1947 to 1970 fixed location research trawl surveys were used to estimate groundfish abundance in these areas. Stratified random trawl surveys began in 1971 and 1972, on the Southern Grand Bank and St. Pierre Bank, respectively. The data collected prior to 1971 were converted to the new stratification scheme by determining in which stratum the original stations were located. Fourteen strata from the Southern Grand Bank, with depths ranging from 57-183 meters, and eleven strata from the St. Pierre Bank, with depths ranging from 56-274 meters, could be used for analysis. In each stratum, several tows per year were conducted. After 1995 the survey gear changed to a shrimp trawl with drastically different selectivity; thus we analyzed only the data before 1996. Individual estimates of biomass were calculated for fish identified to genus or species. Survey catches were standardized for different catchabilities using correction factors determined from the area surveyed by each gear. Neither of the correction factors was large and is unlikely to have a profound effect on the observed trends in biomass. Absolute indices of abundance were calculated by dividing the biomass estimates by these correction factors. In addition, we used published conversion factors for the variation in diel catchability for over 50 species in the Northwest Atlantic [26]. The survey area is primarily stratified along depth zones. For the purpose of this analysis, strata of equal depths were combined within each region and then biomass estimates were calculated from these data. Further details can be found in Ref. 27.

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Table S1. Species included in the data sets

Common Name	Scientific Name	Dataset		
		Japanese longlining		
		Pacific	Indian	Atlantic
Albacore tuna	*Thunnus alalunga*	Y	Y	Y
Atlantic blue marlin	*Makaira nigricans*			Y
Atlantic bluefin tuna	*Thunnus thynnus*			Y
Bigeye tuna	*Thunnus obesus*	Y	Y	Y
Black marlin	*Makaira indica*	Y	Y	Y
Broadbill swordfish	*Xiphias gladius*	Y	Y	Y
Indo-Pacific blue marlin	*Makaira mazara*	Y	Y	
Longbill spearfish	*Tetrapturus pfluegeri*			Y
Pacific bluefin tuna	*Thunnus orientalis*	Y		
Sailfish	*Istiophorus platypterus*	Y	Y	Y
Shortbill spearfish	*Tetrapturus angustirostris*	Y	Y	
Skipjack tuna	*Katsuwonus pelamis*	Y	Y	Y
Southern bluefin tuna	*Thunnus maccoyii*	Y	Y	Y
Striped marlin	*Tetrapturus audax*	Y	Y	
White marlin	*Tetrapturus albidus*			Y
Yellowfin tuna	*Thunnus albacares*	Y	Y	Y
		Gulf of Thailand trawl survey		
Bigeye	*Priacanthus* sp.		Y	
Cutlassfishes	Trichiuridae		Y	
Drums and croakers	Sciaenidae		Y	
Emperors	Lethrinidae		Y	
False trevally	*Lactarius lactarius*		Y	
Goatfishes	Mullidae		Y	
Groupers	Serranidae		Y	
Grunts	*Pomadasys* sp.		Y	
Indian spiny turbot	*Psettodes erumei*		Y	
Jacks and pompanos	Carangidae		Y	
Lizardfish	*Saurida* sp.		Y	
Pike conger	*Muraenesox* sp.		Y	
Rays	Rajidae		Y	
Sea catfishes	Ariidae		Y	
Sharks	Chondrichthyes		Y	
Snappers	Lutjanidae		Y	
Sweetlips	*Plectorhinchus* sp.		Y	
		South Georgia trawl survey		
Green notothenia	*Gobionotothen gibberifrons*		Y	
Mackerel icefish	*Champsocephalus gunnari*		Y	
Marbled notothenia	*Notothenia rossii*		Y	
Scotia Sea icefish	*Champsocephalus aceratus*		Y	

South Georgia icefish	*Pseudochaenichthys georgianus*	Y	
		NW Atlantic trawl surveys	
		Grand Banks	St. Pierre Bank
American plaice	*Hippoglossoides platessoides*	Y	Y
Atlantic Cod	*Gadus morhua*	Y	Y
Atlantic halibut	*Hippoglossus hippoglossus*	Y	Y
Barndoor skate	*Raja laevis*	Y	Y
Broadhead wolffish	*Anarhichas denticulatus*	Y	Y
Haddock	*Melanogrammus aeglefinus*	Y	Y
Longfin Hake	*Urophycis chesteri*	Y	Y
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	Y	Y
Mailed sculpin	*Triglops sp.*	Y	
Marlin-spike	*Nezumia bairdi*		Y
Monkfish	*Lophius americanus*	Y	Y
Pollock	*Pollachius virens*		Y
Redfish	*Sebastes* sp.	Y	Y
Sea raven	*Hemitripterus americanus*	Y	Y
Shorthorn sculpin	*Myoxocephalus scorpius*	Y	Y
Silver hake	*Merluccius bilinearis*	Y	Y
Smooth skate	*Raja senta*	Y	Y
Spotted wolffish	*Anarhichas minor*	Y	Y
Striped wolffish	*Anarhichas lupus*	Y	Y
Thorny skate	*Raja radiata*	Y	Y
White hake	*Urophycis tenuis*	Y	Y
Winter skate	*Raja ocellata*		Y
Witch flounder	*Glyptocephalus cynoglossus*	Y	Y
Yellowtail flounder	*Limanda ferruginea*	Y	Y

Fig. S1. Spatial patterns of relative predator biomass from 1952-2000. Color codes depict the number of fish caught per 100 hooks on pelagic longlines set by the Japanese fleet. Data are binned in a global 5°x5° grid.

Fig. S2. Compensation in oceanic billfish communities, with blue marlin (*Makaira nigricans*, *M. mazara*, filled circles, solid line, left scale in **a-f**), sailfish (*Istiophorus platypterus*, open triangles, dashed line, right scale in **a-f**), and swordfish (*Xiphias gladius*, open circles, dotted line, right scale in **a-f**). Concurring changes in white marlin (*Tetrapturus albidus*, **g-h)**, black marlin (*Makaira indica,* closed diamonds, solid linein **i-l**) and striped marlin (*Tetrapturus audax,* open diamonds, dotted line in **i-l**) are also shown. Blue marlin and black marlin are relatively larger, long-lived species, which declined rapidly as fishing pressure increased in the 1950s. Sailfish, white marlin and striped marlin increased during the same time. Swordfish was initially not targeted and increased slowly from 1950-1980 in most regions. Recent declines in swordfish are likely due to directed fisheries (other than Japanese) targeting this species[28]. Whereas most changes occurred during the time when the fishery was relatively stable (1952-1980), some of the later species dynamics could be confounded by changes in fishing practise, like the expansion into deeper waters around the late 1970s. Lines represent best fits using a local regression smoother.

Fig. S3. Compensation in demersal fish communities on the Southern Grand Banks **(a)** and Saint Pierre Banks **(b)**, showing the biomass of codfishes (Gadidae, solid circles, solid line), and flatfishes (Pleuronectidae, open circles, dotted line). Lines represent best fits using a local regression smoother.