

sulphide complexes, indicating that Cu sulphide clusters are more stable than Cu organic complexes. This explains why laboratory cultures of oceanic phytoplankton have been observed to increase the production of total dissolved sulphides when the concentrations of free Cu and Zn in the culture media were increased<sup>22</sup>. Although the data that we report here suggest that metal sulphide formation is a means of detoxifying trace metals for organisms, further toxicological studies are needed to quantify the roles both sulphides and 'natural' organic ligands play in controlling Cu toxicity in natural waters.

Sulphur complexation may have a dramatic effect on the acute toxicity of other, less abundant, class B metals (for example, Ag, Cd, Hg). The speciation of these trace metals should be dominated by sulphide complexation, because Zn and Fe sulphides (acid volatile sulphides) will provide a pool of sulphides available for complexation and metal replacement reactions. In laboratory experiments, we found that  $\text{Ag}^+$  ions quickly replaced Zn ions in metal sulphide clusters, suggesting that acid volatile sulphides are available for reaction with class B metals. Indeed, this chemistry has been observed for Cd in freshwater and marine sediments: added Cd replaced Fe in solid FeS, which resulted in a dramatic reduction in the Cd toxicity to a variety of organisms<sup>23</sup>. □

## Methods

Water samples were collected following clean protocols, and filtered in a class 100 clean room using 0.2- $\mu\text{m}$  Nuclepore filters.  $\text{DS}_T$  concentrations were determined by square-wave voltammetry on a hanging-drop mercury electrode following Cr(II) reduction in acid<sup>15</sup>. Acidic Cr(II) reduction of the water samples produced  $\text{H}_2\text{S}$ , which was purged and trapped in 1 M NaOH, and then analysed by voltammetry. Acidic Cr(II) reduction was selected for its ability to dissolve both Zn and Fe sulphides and reductively dissolve pyrite and the Cu(poly)sulphides produced during Cu sulphide formation<sup>59</sup>. Sulphide liberated with 3 M HCl was also measured, and resulted in similar sulphide concentrations to the Fe and Zn sulphide concentrations measured electrochemically. Total dissolved metals were measured using either graphite furnace atomic absorption spectrometry or inductively coupled mass spectrometry.

Metal sulphide identification was performed following the square-wave voltammetry procedure<sup>2</sup> using a DLK-100 voltammetric analyser (Analytical Instrument Systems) and a 6-mm glassy carbon rotating-disk electrode (ROTEL). In summary, an acid titration was performed on the water sample to induce dissociation of the metal sulphide complexes. Free sulphide released was electrochemically measured at discrete pH values, which correspond to Cu sulphide (pH < 5), Zn sulphide (pH < 6.7) and  $\text{FeSH}^+$  (pH > 6.7) dissociation. To prevent double counting, the free sulphide was purged before the next acidification. FeS (ref. 13) and polysulphides (ref. 14) were measured directly by their discrete peak potentials at ambient pH.

Laser ablation FTMS was performed using a Finnegan FTMS 2000 laser desorption mass spectrometer run in negative-ion mode. The laser source was a  $\text{CO}_2$  laser with an output at 10.6  $\mu\text{m}$  wavelength. The ionization delay was set at either 1 or 5 s. FTMS analysis was performed on vacuum-dried aqueous solutions, fresh precipitates, and crushed minerals. Laboratory solutions were prepared using 1  $\mu\text{M}$  aliquots of  $\text{M}^{2+}$  and  $\text{HS}^-$  at pH 7.5. Filtered river water samples were freeze-dried before FTMS analysis. The effects of freeze-drying appear to be minimal. Aqueous solutions were found to primarily contain lower-molecular-mass species, unlike either fresh precipitates or sulphide minerals. Additional corroborating evidence was provided by electrospray FTMS analysis of an aqueous solution of Zn sulphides, which showed  $\text{Zn}_3\text{S}_4$  as the primary metal sulphide species<sup>24</sup>.

FTMS spectra were analysed using the OPUS utilities isotope program<sup>25</sup> to calculate isotopic distributions for discrete metal sulphide stoichiometries. Isotope ratios used for species determinations were  $^1\text{H}$  99.98% and  $^2\text{H}$  0.02%. Oxygen ratios were  $^{16}\text{O}$  99.76%,  $^{17}\text{O}$  0.04% and  $^{18}\text{O}$  0.2%. Sulphur ratios were  $^{32}\text{S}$  95.02%,  $^{33}\text{S}$  0.75% and  $^{34}\text{S}$  4.21% and  $^{36}\text{S}$  0.02%. Cu ratios were  $^{63}\text{Cu}$  69.17% and  $^{65}\text{Cu}$  30.83%. Zn ratios were  $^{64}\text{Zn}$  48.6%,  $^{66}\text{Zn}$  27.9%,  $^{67}\text{Zn}$  4.1%,  $^{68}\text{Zn}$  18.8% and  $^{70}\text{Zn}$  0.6%. Fe ratios were  $^{54}\text{Fe}$  5.8%,  $^{56}\text{Fe}$  91.72%,  $^{57}\text{Fe}$  2.2% and  $^{58}\text{Fe}$  0.28%. Abundance (%) was related to the largest species present in the water sample, which was typically  $\text{SO}_4^{2-}$ .

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# Collapse and recovery of marine fishes

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Over-exploitation and subsequent collapse of marine fishes has focused attention on the ability of affected populations to recover to former abundance levels<sup>1–3</sup> and on the degree to which their persistence is threatened by extinction<sup>4,5</sup>. Although potential for recovery has been assessed indirectly<sup>1</sup>, actual changes in population size following long-term declines have not been examined empirically. Here I show that there is very little evidence for rapid recovery from prolonged declines, in contrast to the perception that marine fishes are highly resilient to large population reductions<sup>6,7</sup>. With the possible exception of herring and related species that mature early in life and are fished with highly selective equipment, my analysis of 90 stocks reveals that many gadids (for example, cod, haddock) and other non-clupeids (for example, flatfishes) have experienced little, if any, recovery as much as

15 years after 45–99% reductions in reproductive biomass. Although the effects of overfishing on single species may generally be reversible<sup>1</sup>, the actual time required for recovery appears to be considerable. To exempt marine fishes from existing criteria used to assign extinction risk<sup>6,7</sup> would be inconsistent with precautionary approaches to fisheries management and the conservation of marine biodiversity.

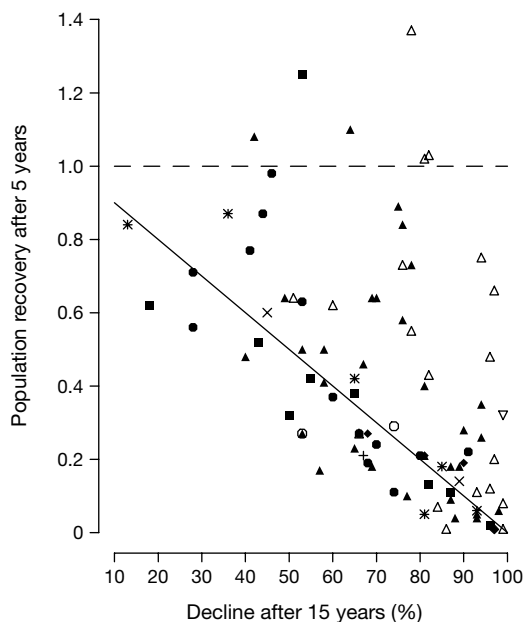
Worldwide overfishing has raised concerns that extraordinary collapses in abundance may significantly increase the extinction probability of targeted<sup>4</sup> (for example, Atlantic cod, *Gadus morhua*) and incidentally harvested<sup>8</sup> (for example, barndoor skate, *Raja laevis*) marine fishes<sup>5,6</sup>. This is reflected by the work of national and international agencies responsible for assigning risk categories to potentially endangered species. Present and past fisheries for Atlantic cod, whose over-exploitation and collapse have been well documented<sup>2,9–11</sup>, provide one example. On the basis of global estimates of decline, the International Union for Conservation of Nature (IUCN) listed<sup>4</sup> Atlantic cod as ‘vulnerable’ in 1996, the same status applied 2 years later by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC)<sup>12</sup>. Other marine fishes assigned to risk categories by these agencies include the Pacific sardine (*Sardinops sagax*; Clupeidae)<sup>12</sup>, haddock (*Melanogrammus aeglefinus*; Gadidae)<sup>4</sup>, Bering wolffish (*Anarhichas orientalis*; Anarhichadidae)<sup>4</sup>, and the pleuronectid flatfishes Atlantic halibut (*Hippoglossus hippoglossus*) and yellowtail flounder (*Pleuronectes ferrugineus*)<sup>4</sup>.

There are, however, concerns that quantitative listing criteria based on temporal trends in abundance, such as those applied by IUCN<sup>13</sup> and COSEWIC<sup>14</sup>, may significantly over-estimate extinction threats to marine fishes and should be modified to account for

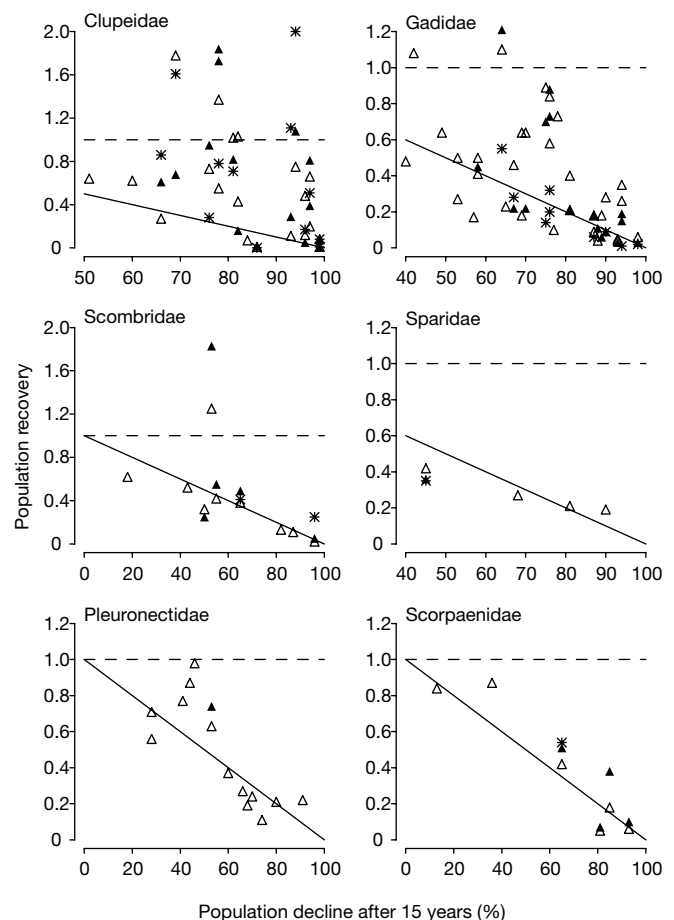
the great natural variability in abundance, high reproductive potential and remarkable ability to recover from population collapse perceived to be characteristic of marine fishes, relative to other taxa<sup>6,7</sup>. Theoretical analyses also suggest that there is nothing intrinsic to the population dynamics of exploited marine fishes that would prevent them from increasing at low population sizes<sup>1</sup>, although the assumption that their per capita reproductive success increases at low population levels may not be as general as previously thought<sup>3</sup>.

I made use of the most comprehensive numerical fisheries data base available, maintained by R. A. Myers, Department of Biology, Dalhousie University, Halifax, Canada, at <http://fish.dal.ca/welcome.html>. I recorded the largest 15-year percentage decline in mature fish biomass experienced by each stock and subsequent population sizes 5, 10 and 15 years thereafter. The 15-year interval was considered short enough to obtain a reasonably large sample of populations, and long enough to be biologically meaningful, approximating the three-generation time period specified by quantitative at-risk criteria used by species-listing organizations such as IUCN and COSEWIC.

After a decline, any increase in population size,  $N$ , could be interpreted as some sort of recovery. Graphically, recovery  $t$  years after a 15-year decline can be determined from a plot of  $N_{t+15}/N_0$  on the ordinate against magnitude of population decline on the abscissa, that is,  $1 - N_{15}/N_0$ . On such a plot, populations exhibiting no recovery, that is,  $N_{t+15} = N_{15}$ , would fall on a straight line with



**Figure 1** Bivariate association between population decline and subsequent population size for 90 marine fish stocks. The ordinate refers to the size of a population 5 years after the proportionately largest 15-year decline experienced by that population, relative to its size at the beginning of its 15-year decline. Populations that experienced some recovery are represented by points to the right of the solid line. Fully recovered stocks are represented by points on and above the dashed line. One datum—a 69% population decline of one clupeid followed by a 1.78 recovery—has been omitted for clarity. Slanted crosses, Engraulidae; upward triangles, Clupeidae; downward triangles, Osmeridae; filled triangles, Gadidae; stars, Scorpaenidae; upright crosses, Anoplopomatidae; filled diamonds, Sparidae; diamonds, Nototheniidae; filled squares, Scombridae; filled circles, Pleuronectidae; circles, Soleidae.



**Figure 2** Population recovery within and among six families of marine fishes 5 (triangles), 10 (filled triangles) and 15 (stars) years after the greatest proportionate 15-year decline experienced by each stock. The dashed and solid lines represent the ‘full recovery’ and ‘no recovery’ lines, respectively.

slope of  $-1$  extending from  $(0,1)$  to  $(1,0)$ . Those continuing to decline would fall below this line, whereas those exhibiting some recovery would fall above this line. Similarly, populations falling on the line with slope of  $0$  extending from  $(0,1)$  to  $(1,1)$  would be said to have fully recovered, that is,  $N_{t+15} = N_0$ , whereas those above this second line would have increased relative to the size from which their population declines had begun.

Among those for which data were available, 90 marine fish stocks (representing 38 species among 11 families) experienced 15-year declines of 13 to 99%, followed by 5-year changes in population size ranging from 0.3 to 178% of the size from which the declines began. Of these 90 stocks, 37 (41%) continued to decline after the 15-year period, 46 (51%) exhibited some recovery, and 7 (8%) had fully recovered (Fig. 1). Subsequent population size was negatively correlated with magnitude of population decline (Fig. 1, Table 1; correlation coefficients will have been over-estimated slightly because of autocorrelated data).

Population sizes 5 years thereafter were significantly correlated with population declines within most of the six numerically dominant families in the analysis (representing 83 of the 90 stocks; Fig. 2, Table 1): Clupeidae (for example, herring, *Clupea harengus*; sprat, *Sprattus sprattus*), Gadidae (for example, cod, haddock), Scombridae (for example, mackerel, *Scomber* spp.; tuna, *Thunnus* spp.), Sparidae (for example, snapper, *Pagrus auratus*), Scorpaenidae (for example, redfish, *Sebastes* spp.), and Pleuronectidae (for example, plaice, *Pleuronectes* spp.; Greenland halibut, *Reinhardtius hippoglossoides*). The association was not significant within the clupeids or the scombrids, although the correlation was highly significant within the latter family when the outlier stock (eastern Pacific yellowfin tuna, *T. albacares*) was removed from the analysis. Among families, clupeids (80% of the stocks) were most likely to have experienced some level of recovery (Fig. 2).

Data 10 and 15 years subsequent to the 15-year population declines were available for 45 and 25 stocks, respectively, comprised primarily of clupeids and gadids (69 and 84%, respectively). Among all stocks, the magnitude of decline negatively influenced population size 10 years, but not 15 years, after the declines (Fig. 3, Table 1). However, when clupeid data were excluded, population decline was strongly and significantly associated with both 10- and 15-year population recovery sizes among non-clupeids, notably gadids. Indeed, 15 years after their declines, 12% of marine stocks (all clupeids) had exhibited full recovery, whereas 40% (primarily gadids, but some clupeids) had experienced no recovery at all (Fig. 3). Furthermore, when clupeids were excluded from the analyses the regression coefficients for the 5- and 15-year recovery

intervals (Table 1) were very close to the no-recovery line intercept and slope of  $1$  and  $-1$ , respectively, emphasizing the limited recoveries experienced by most marine fishes.

These data suggest that, after prolonged decline, clupeids are more likely to recover to previously experienced population sizes and are more resilient than other marine fishes. Such an increased rate of recovery may be attributable to the younger age at which clupeids mature relative to gadids, scorpaenids, scombrids, sparids and pleuronectids<sup>15</sup>, and the higher intrinsic rate of increase that earlier maturity generally effects<sup>16</sup>. Higher reproductive rates may also mitigate the negative influence of environmental stochasticity on the persistence of populations at small sizes<sup>17,18</sup>. In addition, being at a lower trophic level than other families considered here, clupeids may be better able to 'track' temporal and spatial fluctuations in primary and secondary productivity.

The apparent increased resilience of many clupeids relative to other stocks, however, may reflect different management responses to population declines and the different species selectivities of fishing gear. Clupeids are typically fished by deploying purse seines or mid-water trawls on schools identified visually or acoustically. The species uniformity of clupeid schools results in bycatches of incidentally harvested fishes one to two orders of magnitude lower than those of the bottom-deployed seines and trawls used to catch groundfish<sup>19</sup>. Thus, it may be comparatively easy to eliminate fishing mortality on affected clupeid stocks because of the high species selectivity of clupeid fishing technology. By contrast, the collapse of a groundfish stock rarely results in cessation of bottom-trawling in the affected region, meaning that fishing mortality on the collapsed stock can be reduced, but rarely eliminated, because of the comparatively low species selectivity of the fishing gear used to capture a broad diversity of demersal marine fishes.

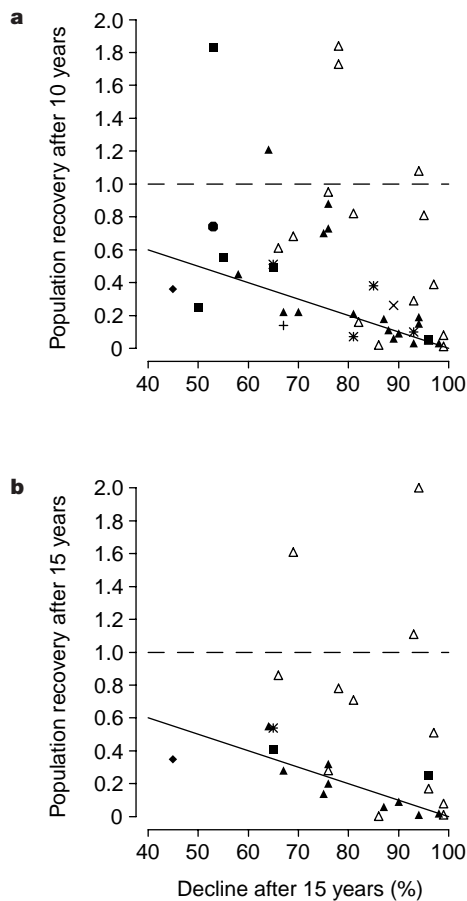
The failure of many marine fish stocks to recover rapidly to former levels of abundance might arguably<sup>6,7</sup> be attributed to management strategies designed to maintain populations at 50% of their virgin biomass to maximize sustainable yields<sup>20</sup>. But this seems a highly improbable explanation for the present observations, given the lengthy histories of direct and indirect exploitation<sup>21,22</sup> that have preceded the formal collection of data on fish numbers and biomass by fishery management agencies. In addition to the proposed influences of age at maturity, reproductive rate and fishing gear selectivity on recovery rates, it seems likely that ecosystem-level consequences of exploitation, for example, food webs altered by changes to species community structure, are also important<sup>23,24</sup>.

The suggestion that marine fishes should be exempt from existing

**Table 1 Linear regressions for associations between recovery and decline in marine fishes**

Recovery period	Family	Regression equation	Number of stocks	<i>P</i>	<i>r</i>
5 years	Clupeidae	$y = 1.78 - 1.48x$	20	0.062	-0.42
	Gadidae	$y = 1.14 - 1.00x$	31	0.003	-0.52
	Scombridae	$y = 0.80 - 0.79x$	8	<0.001	-0.96
	Sparidae	$y = 0.65 - 0.53x$	4	0.013	-0.99
	Scorpaenidae	$y = 1.11 - 1.13x$	6	0.004	-0.95
	Pleuronectidae	$y = 1.16 - 1.19x$	13	0.0013	-0.79
	All	$y = 1.00 - 0.82x$	90	<0.0001	-0.46
	All except Clupeidae	$y = 1.04 - 0.94x$	70	<0.0001	-0.64
10 years	Clupeidae	$y = 2.74 - 2.46x$	15	0.083	-0.46
	Gadidae	$y = 1.86 - 1.87x$	16	0.007	-0.65
	All	$y = 1.41 - 1.19x$	45	0.012	-0.37
	All except Clupeidae	$y = 1.46 - 1.42x$	30	0.001	-0.56
15 years	Clupeidae	$y = 3.01 - 2.47x$	12	0.33	-0.32
	Gadidae	$y = 1.22 - 1.28x$	9	0.002	-0.88
	All	$y = 1.06 - 0.60x$	25	0.58	-0.12
	All except Clupeidae	$y = 0.91 - 0.87x$	13	0.004	-0.74

Regression equations describing mature population size (*y*) 5, 10 and 15 years following a 15-year population decline relative to the population size at the beginning of the decline ( $N_0$ ), as a function of population decline (*x*, proportional decline in mature fish biomass over a period of 15 years, that is,  $1 - N_{15}/N_0$ ). The regression equation for the Scombridae excludes the outlying eastern Pacific yellowfin tuna stock for which the 5-year recovery population size was 1.25 times the maximum during the 15-year decline (Fig. 2). Inclusion of this datum yields the following regression for the scombrids:  $y = 0.99 - 0.93x$ ,  $P = 0.078$ ,  $r = -0.62$ . Low *P*-values indicate rejection of the hypothesis of full recovery.



**Figure 3** Population recovery of marine fishes 10 (upper panel) and 15 years (lower panel) after the greatest proportionate 15-year decline experienced by each stock. The dashed and solid lines represent the ‘full recovery’ and ‘no recovery’ lines, respectively. The families corresponding to each symbol are those given in the caption to Fig. 1. **a**, 10 years; **b**, 15 years after decline.

quantitative criteria used to assign extinction risk<sup>6,7</sup> would be inconsistent with a precautionary approach to fisheries management and to the conservation of marine biodiversity. This is particularly important if, rather than providing estimates of extinction probability, the primary utility of at-risk designations lies in their reflection of the likelihood that species or populations will recover to former levels of abundance. I have found that 5–15 years after 15-year declines of 50 and 80% (the three-generation thresholds for the IUCN’s ‘endangered’ and ‘critically endangered’ categories), gadid and other non-clupeid populations, on average, have increased marginally or not at all. Thus, although the effects of overfishing may indeed be generally reversible<sup>1</sup>, the time required for population recovery in many marine fishes appears to be considerably longer than previously believed. □

**Methods**

Data used in the analyses presented here were available for the following families, species, and stocks/populations at (<http://fish.dal.ca/welcome.html>). Clupeidae: Atlantic menhaden, *Brevoortia tyrannus* (west Atlantic); herring, *Clupea harengus* (central British Columbia (BC), Downs, east Bering Sea, Gulf of Maine, Hokkaido, International Council for the Exploration of the Sea (ICES) VIa N, Iceland (spring and summer spawners), Northwest Atlantic Fisheries Organization (NAFO) 4-5, North Sea, north and south Strait of Georgia (BC), Norway (spring spawners), Prince Rupert (BC), Queen Charlotte Island (BC), southeastern Alaska); Spanish sardine, *Sardinops sagax* (California, South Africa); and sprat, *Sprattus sprattus* (Baltic 26-28). Engraulidae: anchovy, *Engraulis encrasicolus* (Black Sea); and northern anchovy, *E. mordax* (California). Gadidae: Atlantic cod, *Gadus morhua* (Baltic (22/24 & 25-32), Greenland offshore, ICES VIa, Iceland, NAFO (2)3KL, 3NO, 3Pn4RS, 3Ps, 4TVn, 4VsW & 4X), northeast Arctic, North Sea, West Greenland); haddock, *Melanogrammus aeglefinus* (ICES VIa, Iceland, NAFO (4)TVW, 4X & 5Z), NE

Arctic, North Sea); whiting, *Merlangius merlangius* (western Black Sea, North Sea); silver hake, *Merluccius bilinearis* (NAFO 5Ze, Mid-Atlantic Bight); pollock, *Pollachius virens* (ICES VI, Iceland, northeast Arctic, North Sea); and Norway pout, *Trisopterus esmarkii* (North Sea). Nototheniidae: icefish, *Notothenia rossii* (South Georgia). Scombridae: chub mackerel, *Scomber japonicus* (southern California); king mackerel, *Scomberomorus cavalla* (western Gulf of Mexico); albacore tuna, *Thunnus alalunga* (south Pacific); yellowfin tuna, *T. albacares* (east Pacific, Indian Ocean); southern bluefin tuna, *T. maccoyii* (south Pacific); bigeye tuna, *T. obesus* (east Pacific, west Atlantic); and Atlantic bluefin tuna, *T. thynnus* (west Atlantic). Sparidae: New Zealand snapper, *Pagrus auratus* (Hauraki Gulf, New Zealand SNA 8); and yellow sea bream, *Tauti tumifrons* (central China Sea, Japan). Pleuronectidae: petrale sole, *Eopseta jordani* (southern British Columbia); American plaice, *Hippoglossoides platessoides* (NAFO 3LNO); Pacific halibut, *Hippoglossus stenolepis* (north Pacific); common dab, *Limanda limanda* (Belt Sea); longhead dab, *L. propinqua* (western Kamchatka Shelf); flounder, *Platichthys flesus* (Baltic 24/25); yellowtail flounder, *Pleuronectes ferrugineus* (ICES VIIId, North Sea); plaice, *P. platessa* (Irish Sea, Kattegat, North Sea); and Greenland halibut, *Reinhardtius hippoglossoides* (east Bering Sea, northeast Arctic). Soleidae: sole, *Solea vulgaris* (ICES VIIId, North Sea). Anoplopomatidae: sablefish, *Anoplopoma fimbria* (western United States). Scorpaenidae: Pacific ocean perch, *Sebastes alutus* (Aleutian Islands, Goose Island Gully (BC), Gulf of Alaska); shortspine thornyhead, *S. alaskanus* (Gulf of Alaska); and redbfish, *Sebastes* spp. (Iceland, northeast Arctic). Osmeridae: caplin, *Mallotus villosus* (Barents Sea).

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