

Rapid worldwide depletion of predatory fish communities

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Serious concerns have been raised about the ecological effects of industrialized fishing^{1–3}, spurring a United Nations resolution on restoring fisheries and marine ecosystems to healthy levels⁴. However, a prerequisite for restoration is a general understanding of the composition and abundance of unexploited fish communities, relative to contemporary ones. We constructed trajectories of community biomass and composition of large predatory fishes in four continental shelf and nine oceanic systems, using all available data from the beginning of exploitation. Industrialized fisheries typically reduced community biomass by 80% within 15 years of exploitation. Compensatory increases in fast-growing species were observed, but often reversed within a decade. Using a meta-analytic approach, we estimate that large predatory fish biomass today is only about 10% of pre-industrial levels. We conclude that declines of large predators in coastal regions⁵ have extended throughout the global ocean, with potentially serious consequences for ecosystems^{5–7}. Our analysis suggests that management based on recent data alone may be misleading, and provides minimum estimates for unexploited communities, which could serve as the ‘missing baseline’⁸ needed for future restoration efforts.

Ecological communities on continental shelves and in the open ocean contribute almost half of the planet’s primary production⁹, and sustain three-quarters of global fishery yields¹. The widespread decline and collapse of major fish stocks has sparked concerns about the effects of overfishing on these communities. Historical data from coastal ecosystems suggest that losses of large predatory fishes,

as well as mammals and reptiles, were especially pronounced, and precipitated marked changes in coastal ecosystem structure and function⁵. Such baseline information is scarce for shelf and oceanic ecosystems. Although there is an understanding of the magnitude of the decline in single stocks¹⁰, it is an open question how entire communities have responded to large-scale exploitation. In this paper, we examine the trajectories of entire communities, and estimate global rates of decline for large predatory fishes in shelf and oceanic ecosystems.

We attempted to compile all data from which relative biomass at the beginning of industrialized exploitation could be reliably estimated. For shelf ecosystems, we used standardized research trawl surveys in the northwest Atlantic Ocean, the Gulf of Thailand and the Antarctic Ocean off South Georgia, which were designed to estimate the biomass of large demersal fish such as codfishes (Gadidae), flatfishes (Pleuronectidae), skates and rays (Rajidae), among others (see Supplementary Information for detailed species information). In all other shelf areas for which we could obtain data, industrialized trawl fisheries occurred before research surveys took place. For oceanic ecosystems, we used Japanese pelagic longlining data, which represent the complete catch-rate data for tuna (Thunnini), billfishes (Istiophoridae) and swordfish (Xiphiidae) aggregated in monthly intervals, from 1952 to 1999, across a global 5° × 5° grid. Pelagic longlines are the most widespread fishing gear, and the Japanese fleet the most widespread longline operation, covering all oceans except the circumpolar seas. Longlines, which resemble long, baited transects, catch a wide range of species in a consistent way and over vast spatial scales. We had to restrict our analysis of longlining data to the equatorial and southern oceans, because industrialized exploitation was already underway in much of the Northern Hemisphere before these data were recorded^{11,12}. Longlining data were separated into temperate, subtropical and tropical communities (see Methods).

For each shelf and oceanic community, *i*, we estimated

$$N_i(t) = N_i(0)[(1 - \delta_i)e^{-rt} + \delta_i] \quad (1)$$

where $N_i(t)$ is the biomass at time *t*, $N_i(0)$ is the initial biomass

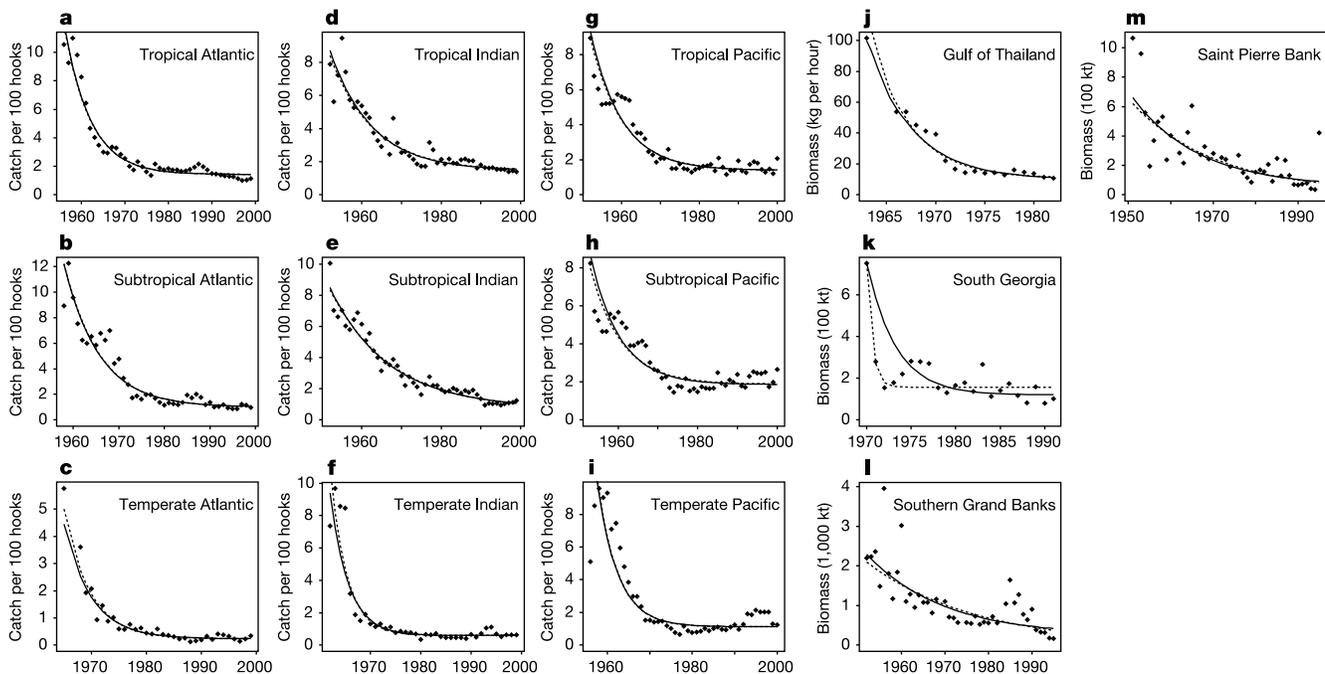


Figure 1 Time trends of community biomass in oceanic (a–i) and shelf (j–m) ecosystems. Relative biomass estimates from the beginning of industrialized fishing (solid

points) are shown with superimposed fitted curves from individual maximum-likelihood fits (solid lines) and empirical Bayes predictions from a mixed-model fit (dashed lines).

Table 1 Meta-analysis of time trends in predatory fish biomass

Region	$r_i (\times 100)$			$\delta_i (\times 100)$		
	Individual fit	CL	Mixed model	Individual fit	CL	Mixed model
Tropical Atlantic	16.6	13.5–19.7	16.7	12.1	10.0–14.5	11.9
Subtropical Atlantic	12.9	10.1–15.7	13.0	8.1	6.4–10.2	8.3
Temperate Atlantic	21.4	15.8–26.9	20.3	4.7	3.2–6.9	5.3
Tropical Indian	9.2	7.1–11.4	9.5	17.6	14.9–20.6	16.8
Subtropical Indian	6.5	5.1–7.8	6.8	8.2	5.5–12.3	9.2
Temperate Indian	30.7	23.7–37.8	27.7	5.5	3.9–7.7	6.3
Tropical Pacific	12.1	9.4–14.8	12.4	15.5	13.0–18.6	14.9
Subtropical Pacific	12.8	8.5–17.1	13.5	23.5	18.9–29.3	21.5
Temperate Pacific	20.8	14.3–27.3	20.4	8.2	5.6–12.1	8.5
Gulf of Thailand	25.6	18.2–33.0	22.2	9.3	6.8–12.6	9.8
South Georgia	166.6	2.2–331.1	30.8	20.9	17.5–25.0	16.0
Southern Grand Banks	4.0	2.9–5.1	5.7	0.0	–	10.0
Saint Pierre Banks	5.1	0.1–10.1	6.3	2.7	0.0–36600	7.9
Mixed model mean			16.0			10.3
Mixed model CL			10.7–21.3			7.7–13.9
Distribution			4.5–31.6			4.6–23.6

Two parameters were estimated: r_i is the initial rate of decline (in per cent per year), and δ_i the residual biomass proportion at equilibrium (in per cent). Point estimates and 95% confidence limits (CL) are presented for the individual maximum likelihood fits, and for the mixed-effects model that combined all data (see Methods for details). The random-effects distribution (95% limits) provides a measure of the estimated parameter variability across communities.

before industrialized exploitation, and r_i is the initial rate of decline to δ_i , the fraction of the community that remains at equilibrium. The initial rate of decline in total biomass—that is, the fraction lost in the first year—is $(1 - \delta_i)(1 - e^{-r_i})$. Then we combined all data using nonlinear mixed-effects models¹³, where $r_i \sim N(\mu_r, \sigma_r^2)$ and $\log \delta_i \sim N(\mu_\delta, \sigma_\delta^2)$, to estimate a global mean and variance of r_i and δ_i .

In the open ocean communities, we observed surprisingly consistent and rapid declines, with catch rates falling from 6–12 down to 0.5–2 individuals per 100 hooks during the first 10 years of exploitation (Fig. 1a–i). Rates of decline were similar in tropical and subtropical regions, but consistently highest in temperate regions in all three oceans (Fig. 1c, f, i and Table 1). Temperate regions also showed the lowest equilibrium catch rates (Table 1). Spatial pattern

of expansion and decline of pelagic fisheries are shown in Fig. 2. During the global expansion of longline fisheries in the 1950s to 1960s, high abundances of tuna and billfish were always found at the periphery of the fished area (Fig. 2a–c). Most newly fished areas showed very high catch rates, but declined to low levels after a few years. As a result, all areas now sustain low catch rates, and some formerly productive areas have been abandoned (Fig. 2d). In shelf communities, we observed declines of similar magnitude as in the open ocean. The Gulf of Thailand, for example, lost 60% of large finfish, sharks and skates during the first 5 years of industrialized trawl fishing (Fig. 1j). The highest initial rate of decline was seen in South Georgia (Fig. 1k), which has a narrow shelf area that was effectively fished down during the first 2 years of exploitation¹⁴. Less-than-average declines were seen on the Southern Grand Banks

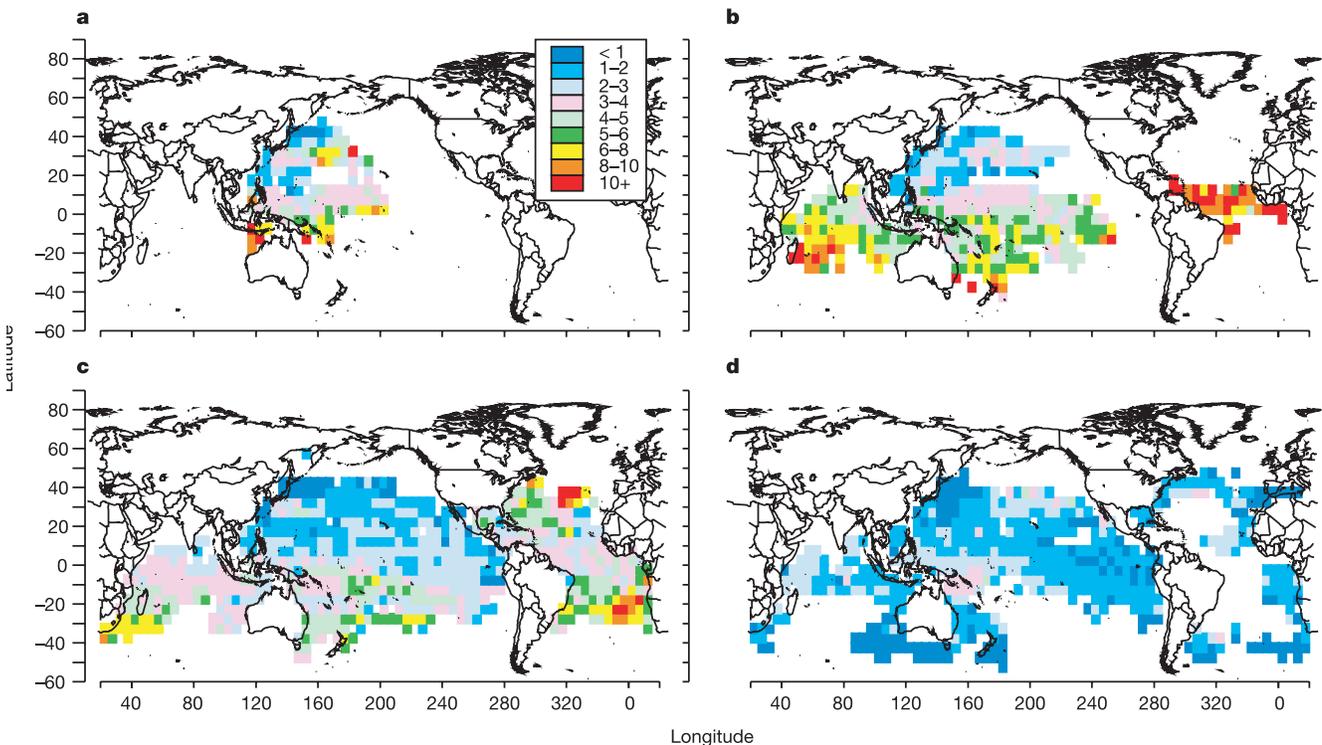


Figure 2 Spatial patterns of relative predator biomass in 1952 (a), 1958 (b), 1964 (c) and 1980 (d). Colour codes depict the number of fish caught per 100 hooks on pelagic

longlines set by the Japanese fleet. Data are binned in a global $5^\circ \times 5^\circ$ grid. For complete year-by-year maps, refer to the Supplementary Information.

(Fig. 1l) and Saint Pierre Bank (Fig. 1m); these communities may already have been affected by intense pre-industrial fisheries¹⁵.

By combining all data using a mixed-effects model, we estimated that the mean initial rate of decline, r_i , is 16% per year, and the mean residual equilibrium biomass, δ_i , is 10% of pre-exploitation levels (Table 1). So, an 80% decline typically occurred within 15 years of industrialized exploitation, which is usually before scientific monitoring has taken place. The proportion of residual biomass, δ_i , showed remarkably little variation between communities (Table 1): the mixed-effects model estimates imply that 95% of communities would have a residual biomass proportion between 5% and 24%. We believe that these still represent conservative estimates of total predator declines for the following reasons: (1) pre-industrial removals from some of the shelf communities¹⁵; (2) gear saturation at high catch rates in the early longlining data, as well as higher initial levels of shark damage leading to an underestimation of initial biomass¹⁶ (see Supplementary Information); (3) increasing fishing power of longline vessels over time owing to improved navigation and targeting of oceanographic features¹⁷; and (4) targeting of some migratory species, such as southern bluefin tuna (*Thunnus maccoyii*), at their tropical spawning grounds before widespread exploitation in temperate areas occurred¹⁸. Furthermore, declines in other large predators such as sharks are not fully captured by our data, but may be of similar or greater magnitude than those of bony fishes^{19,20}.

One mechanism that could compensate for the effects of overfishing is the increase in non-target species due to release from predation or competition²¹. In our analyses, we see evidence for species compensation in both oceanic billfish and shelf groundfish communities (Fig. 3). According to the longlining data and to early surveys^{11,12}, blue marlin was initially the dominant billfish species, but declined rapidly in the 1950s (Fig. 3a). Simultaneous increases in faster-growing species such as sailfish were observed, followed by a decrease, possibly due to increased 'bycatch' mortality (Fig. 3a; neither species was targeted by the Japanese fleet). Coincidentally, swordfish catch rates increased until these fish became prime targets of other fleets in the late 1980s. Surprisingly consistent patterns of compensatory increase and decline were seen in most pelagic communities (see Supplementary Information). Similarly, in the North Atlantic demersal communities, we observed rapid initial declines, particularly in large codfishes, but also in skates and rockfish. Although the dominant codfishes declined sixfold between 1952 and 1970, sixfold increases were seen in the flatfishes, which were not initially targeted by the trawl fishery (Fig. 3b). Some increase in the gadoids occurred when implementation of the 200-mile limit in 1977 curtailed foreign overfishing in Canadian waters. However, as in the billfish data, we observed an ultimate decline in all species groups (Fig. 3b) as fishing pressure from Canadian and other fleets intensified in the late 1980s, leading to the collapse of all major groundfish stocks¹⁰. We conclude that some species compensation was evident, but often reversed within a decade or less, probably because of changes in targeting or bycatch.

Our analysis suggests that the global ocean has lost more than 90% of large predatory fishes. Although it is now widely accepted that single populations can be fished to low levels, this is the first analysis to show general, pronounced declines of entire communities across widely varying ecosystems. Although the overall magnitude of change is evident, there remains uncertainty about trajectories of individual tuna and billfish species. Assessments of these species are continually improved by the international management agencies. However, most scientists and managers may not be aware of the true magnitude of change in marine ecosystems, because the majority of declines occurred during the first years of exploitation, typically before surveys were undertaken. Management schemes are usually implemented well after industrialized fishing has begun, and only serve to stabilize fish biomass at low levels. Supporting evidence for these conclusions comes from the United Nations Food and Agriculture Organization (FAO) data set, which indicates declining global catches²² and a consistent decline in the mean trophic level of the catch²³, which is a result of removing predatory fishes. Furthermore, on seamounts and on continental slopes, where virgin communities are fished, similar dynamics of extremely high catch rates are observed, which decline rapidly over the first 3–5 years of exploitation²⁴. We suggest that this pattern is not unique to these communities, but simply a universal feature of the early exploitation of ecosystems.

Our results have several important management implications. First, we need to consider potential ecosystem effects of removing 90% of large predators. Fishery-induced top-down effects are evident in coastal⁵ and shelf²⁵ ecosystems, but little empirical information is available from the open oceans. This is worrisome, as any ecosystem-wide effect is bound to be widespread, and possibly difficult to reverse, because of the global scale of the declines (Fig. 2). Another serious problem in heavily depleted communities is the extinction of populations, particularly those with high ages of maturity²⁶. Local extinctions can go unnoticed even in closely monitored systems such as the northwest Atlantic²⁷, let alone in the open ocean. Finally, the reduction of fish biomass to low levels may compromise the sustainability of fishing, and support only relatively low economic yields³. Such concerns have motivated a recent UN resolution to restore fish stocks to healthy

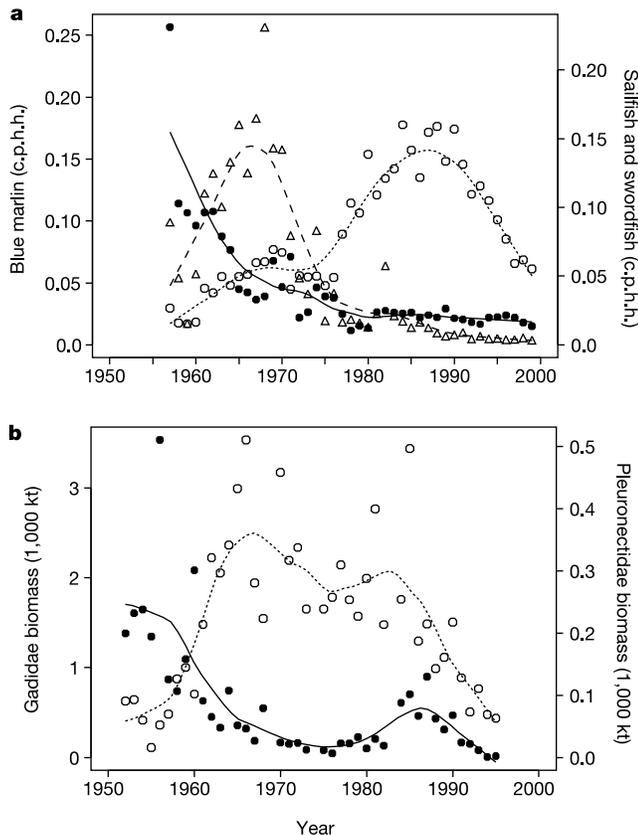


Figure 3 Compensation in exploited fish communities. **a**, Oceanic billfish community in the tropical Atlantic, showing the catch per 100 hooks (c.p.h.h.) of blue marlin (*Makaira nigricans*; solid circles, solid line), sailfish (*Istiophorus platypterus*; open triangles, dashed line) and swordfish (*Xiphias gladius*; open circles, dotted line). **b**, Demersal fish community on the Southern Grand Banks, 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.

levels⁴. Our analysis shows that it is appropriate and necessary to attempt restoration on a global scale, and provides a benchmark against which community recovery could be assessed. □

Methods

Data selection

For shelf communities, we compiled data from research trawl surveys from the Southern Grand Banks (43–46° N, 49–53° W) and Saint Pierre Banks (45–47° N, 55–58° W) (ref. 28), the Gulf of Thailand (9–14° N, 100–105° W) (ref. 29) and South Georgia (53–56° S, 35–40° W) (ref. 14). All other trawl data sets that we considered (for example, North Sea, Georges Bank and Alaska) did not capture the beginning of industrialized exploitation. We included only demersal predators; pelagic species, which were not well sampled by the trawl gear, were excluded. Longlining data obtained from the Japanese Fishery Agency were divided into temperate (Atlantic, 40–45° S; Indian, 35–45° S; Pacific, 30–45° S), subtropical (Atlantic, 10–40° S; Indian, 10–35° S; Pacific, 15–30° S) and tropical communities (Atlantic, 20° N–10° S; Indian, 15° N–15° S; Pacific, 10–15° S). These divisions were based on their dominant species: yellowfin (*T. albacares*), albacore (*T. alalunga*) or southern bluefin tuna (*T. maccoyii*), respectively, and excluded areas previously fished by the Japanese, Spanish and US fleets. Running the models with alternative divisions ($\pm 5^\circ$) did not change the results significantly. The catch rates in each community were determined as the sum of the catches divided by the sum of the effort in each region in each year. Years with very low effort (<20,000 hooks for the entire region) were excluded. Alternative treatment of the data, including removing seasonal effects and taking the average catch rates over $5^\circ \times 5^\circ$ squares, had little effect on the results. For longlines, we assume that the catch rate is an approximate measure of relative biomass, which is probably conservative because the average individual weights of fish in exploited populations tend to decline over time. Our data capture the abundance of larger fishes that are vulnerable to baited hooks and bottom trawls, respectively. Many smaller species have low catchabilities and are not recorded reliably by these methods. Changes in the longline fishery occurred around 1980 when the fishery began to expand into deeper regions; however, this was only after the declines in biomass were observed. For more details on species composition, data treatment and interpretation of trends, refer to the Supplementary Information.

Data analysis

Our model (equation (1)) assumes that for each community, *i*, the rate of decline to equilibrium is exponential with rate *r_i*, from a pre-exploitation biomass *N_i(0)*, where *t* = 0 is the first year of industrialized fishing. Exploitation continues until equilibrium is approached, where a residual proportion, δ_i , of the biomass remains. We fit this model separately to each community under the assumption of a lognormal error distribution using nonlinear regression (Procedure NLIN in SAS, version 8). We also used nonlinear mixed-effects models¹³ to determine whether the patterns were similar across communities. Mixed-effect models were fitted by maximizing the likelihood integrated over the random effects using adaptive gaussian quadrature (Procedure NLMIXED in SAS). To account for the fact that biomass was recorded in different units (kilotonnes (kt), catch rates), the initial biomass, *N_i(0)*, was assumed to be a fixed effect for each community with appropriate units. For South Georgia, *N_i(0)* was fixed at the first biomass estimate to capture the high initial rate of decline. This first estimate (750 kt; ref. 14) was considered to be realistic because it was very close to the sum of total removals (514 kt; ref. 30) plus the residual biomass estimate (160 kt; ref. 14) after the first 2 years of fishing. Autocorrelation in the residuals of some time series may cause the standard errors to be underestimated. The results were robust to alternative error assumptions (separate error variances for the time series and alternative error distributions); for example, under the assumption of normal errors, the rate of decline was 13.9% and residual biomass was 10.9%, respectively.

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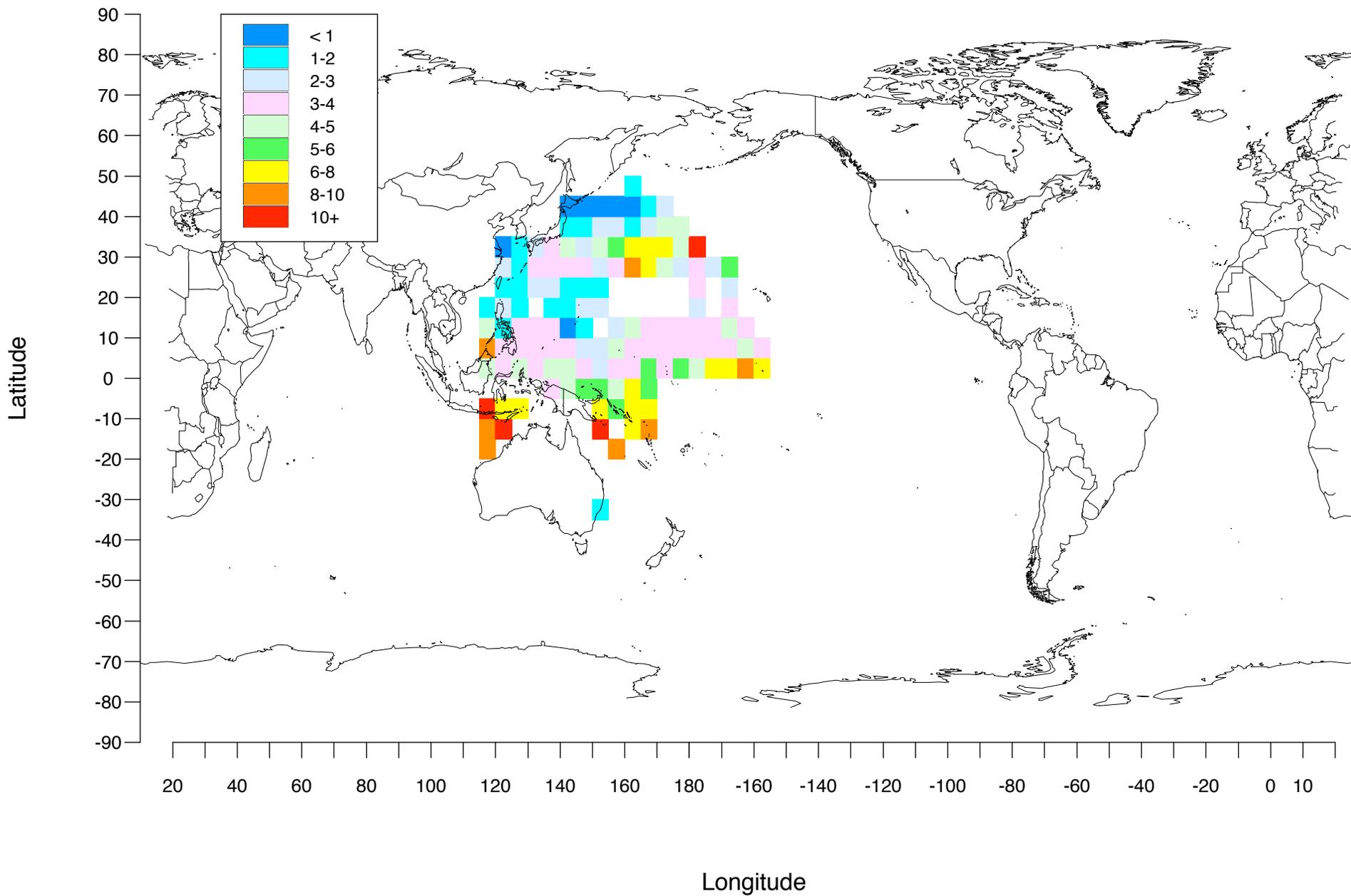
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Attractor dynamics of network UP states in the neocortex

Rosa Cossart, Dmitry Aronov & Rafael Yuste

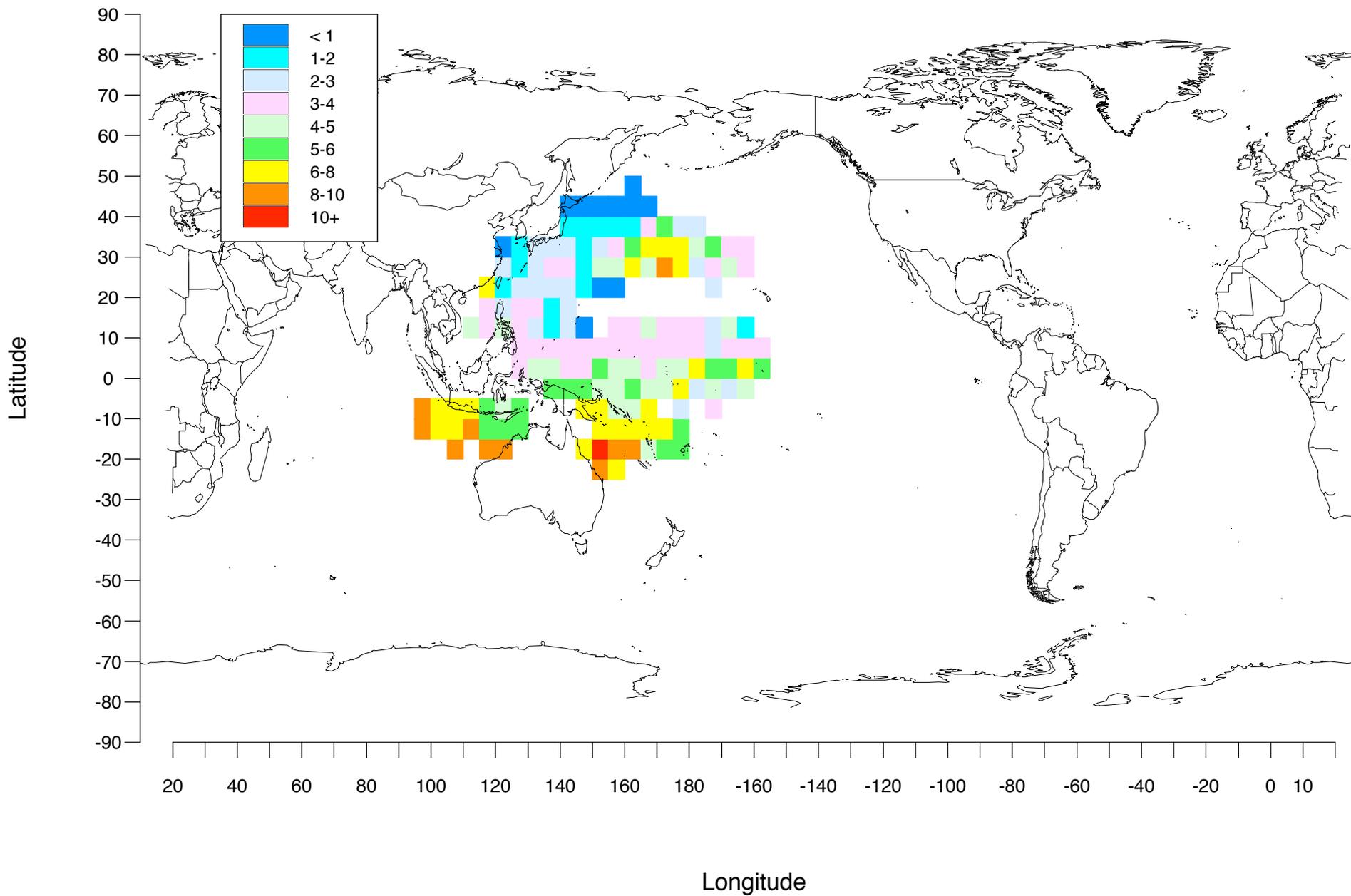
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The cerebral cortex receives input from lower brain regions, and its function is traditionally considered to be processing that input through successive stages to reach an appropriate output^{1,2}. However, the cortical circuit contains many interconnections, including those feeding back from higher centres^{3–6}, and is continuously active even in the absence of sensory inputs^{7–9}. Such spontaneous firing has a structure that reflects the coordinated activity of specific groups of neurons^{10–12}. Moreover, the membrane potential of cortical neurons fluctuates spontaneously between a resting (DOWN) and a depolarized (UP) state^{11,13–16}, which may also be coordinated. The elevated firing rate in the UP state follows sensory stimulation¹⁶ and provides a substrate for

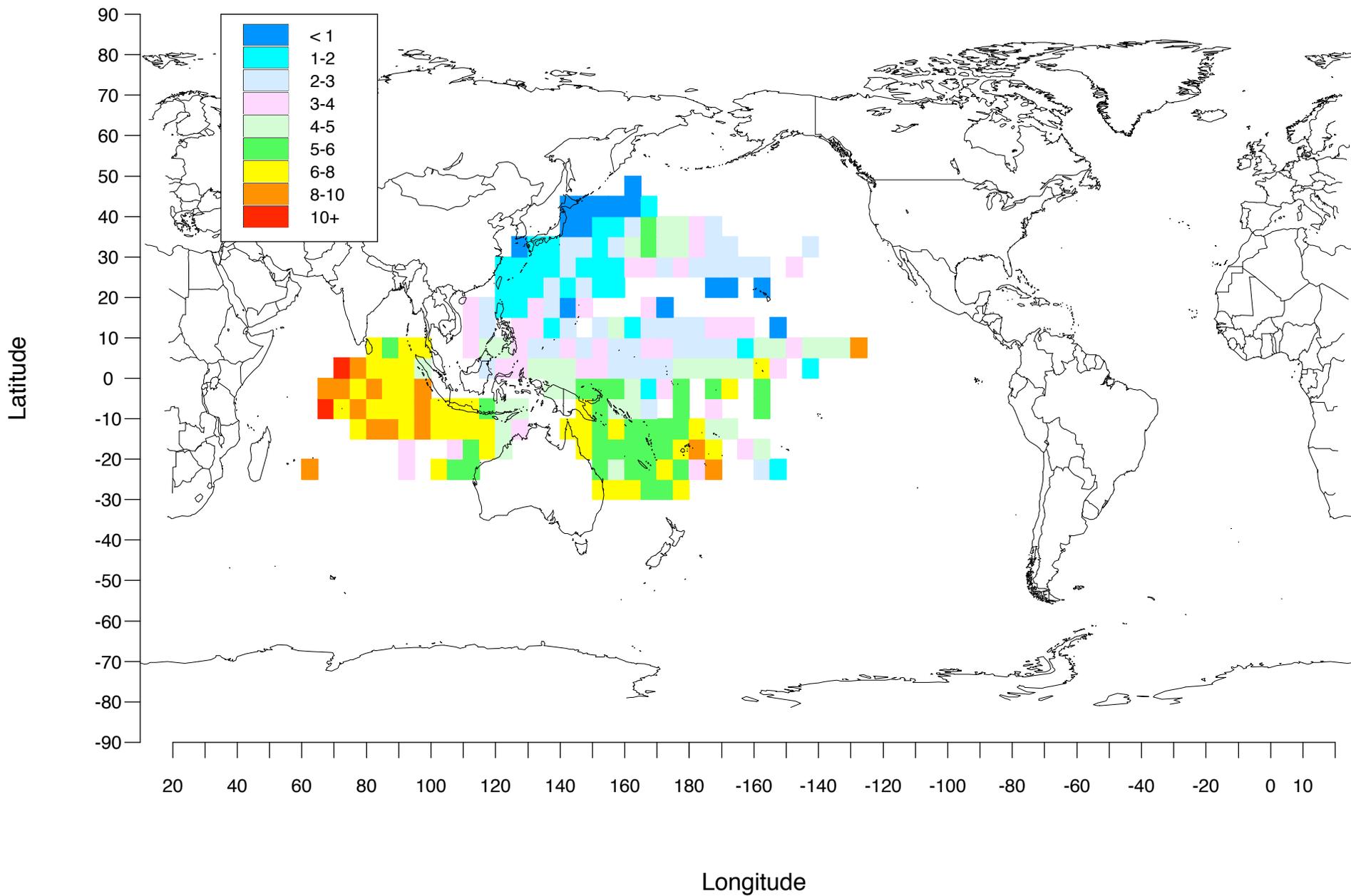
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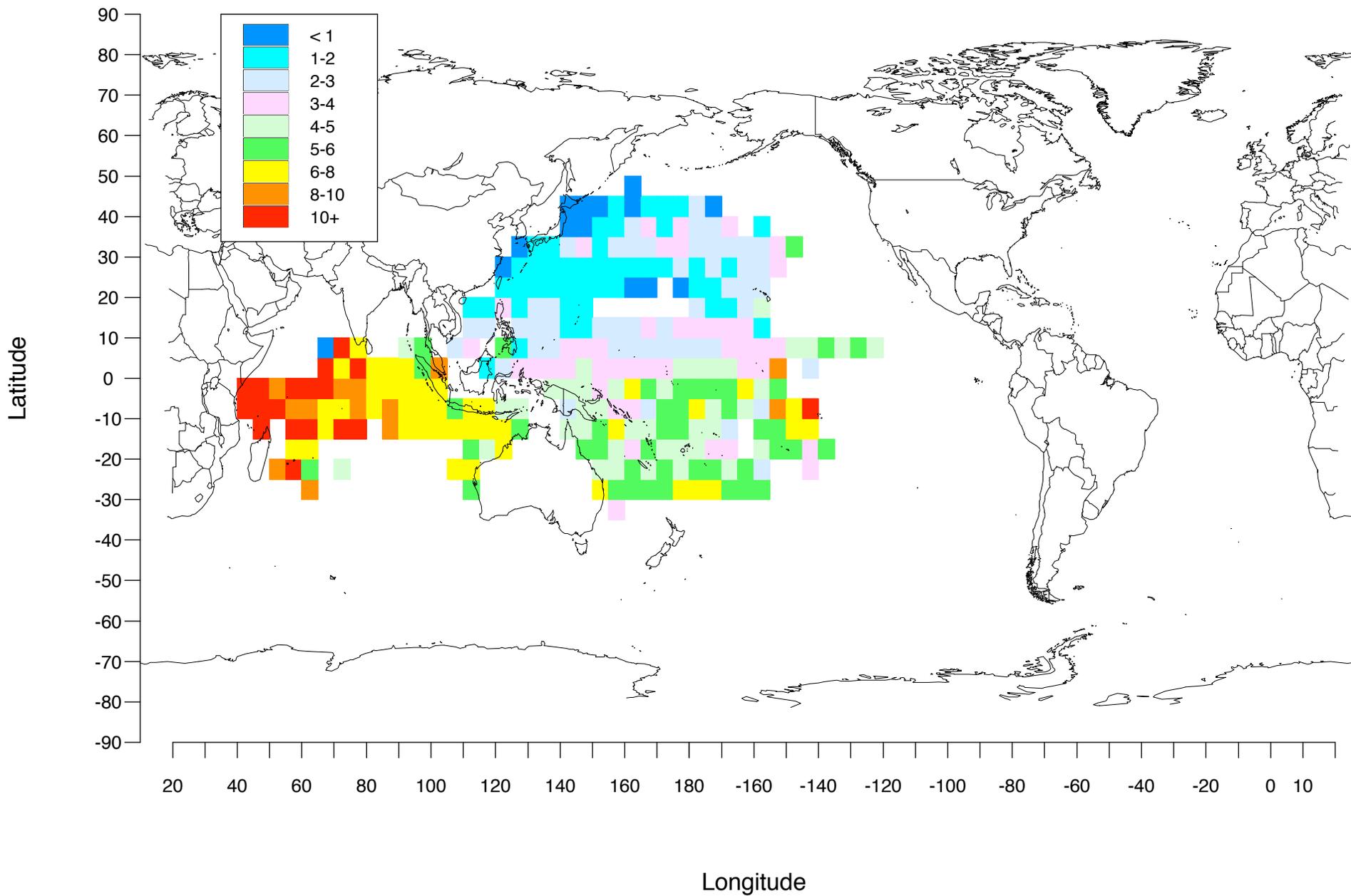
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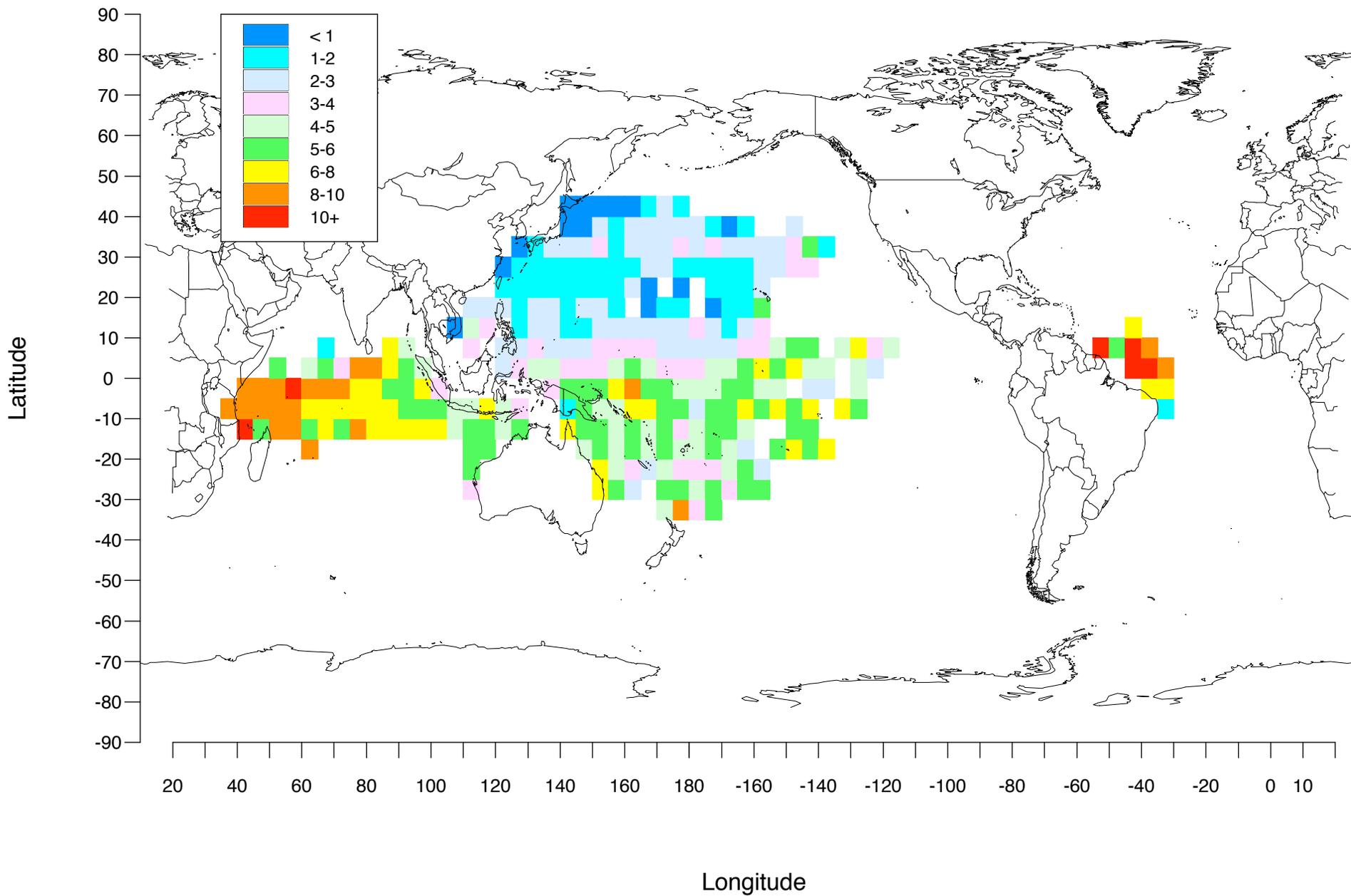
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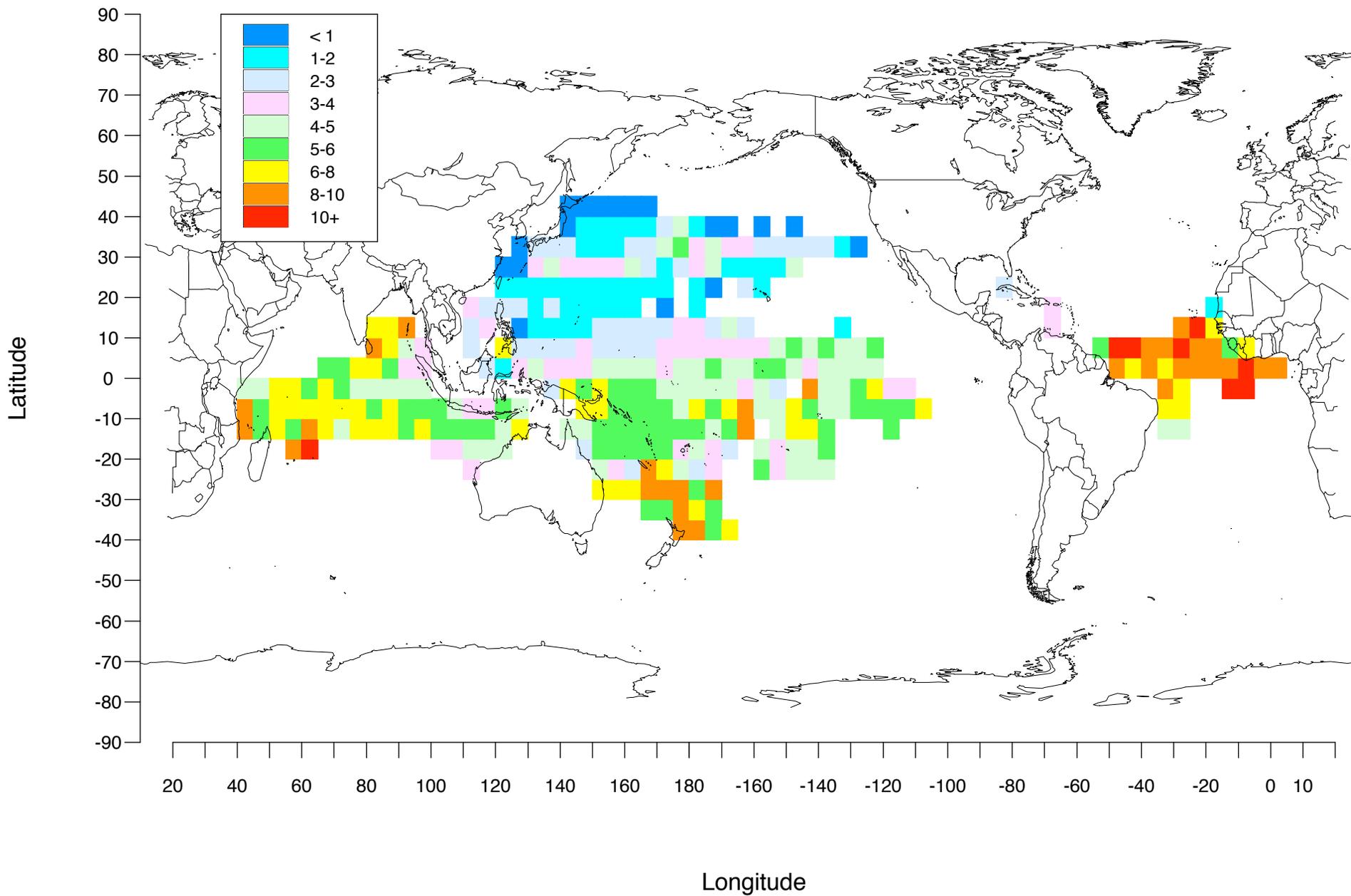
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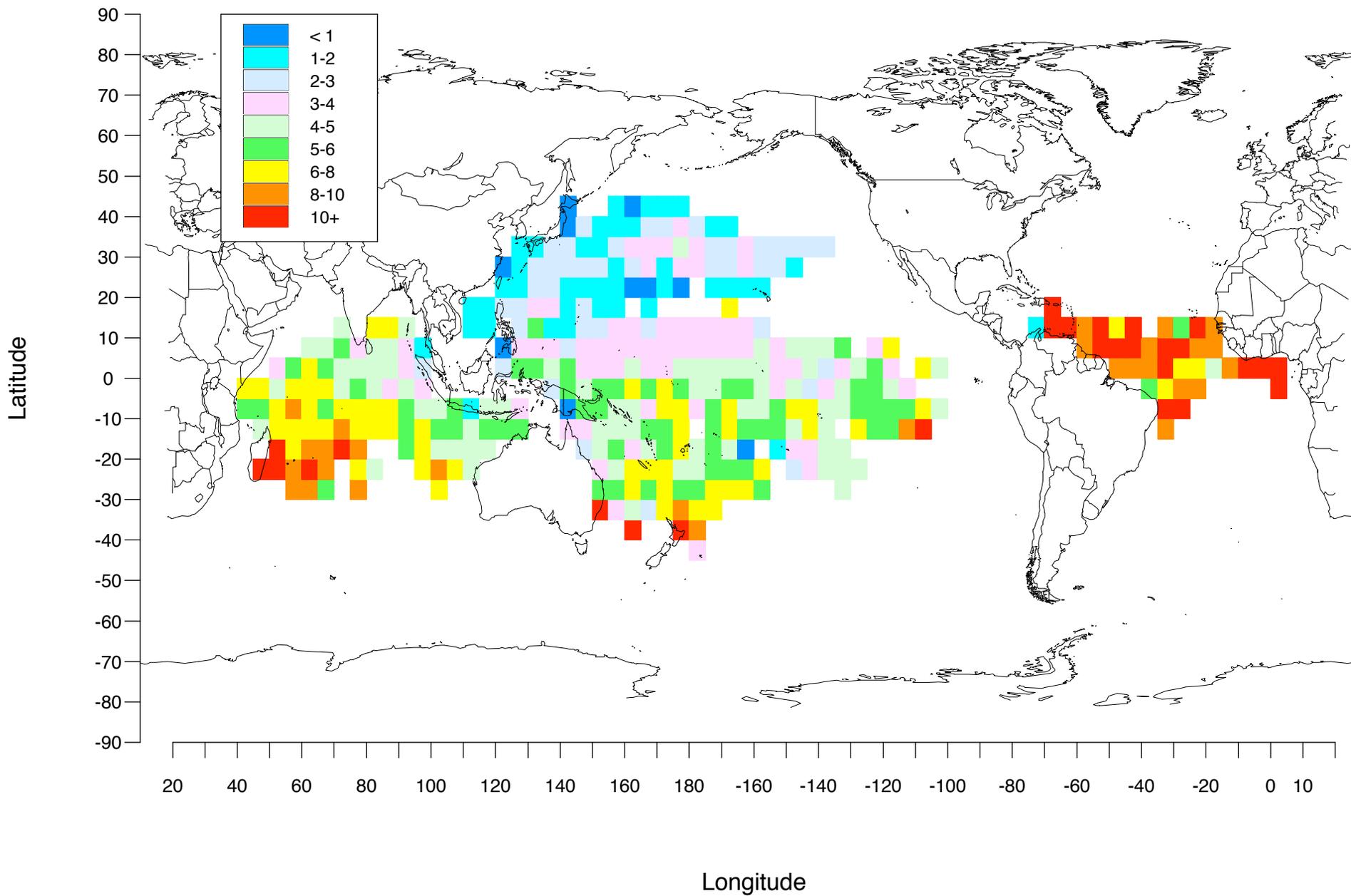
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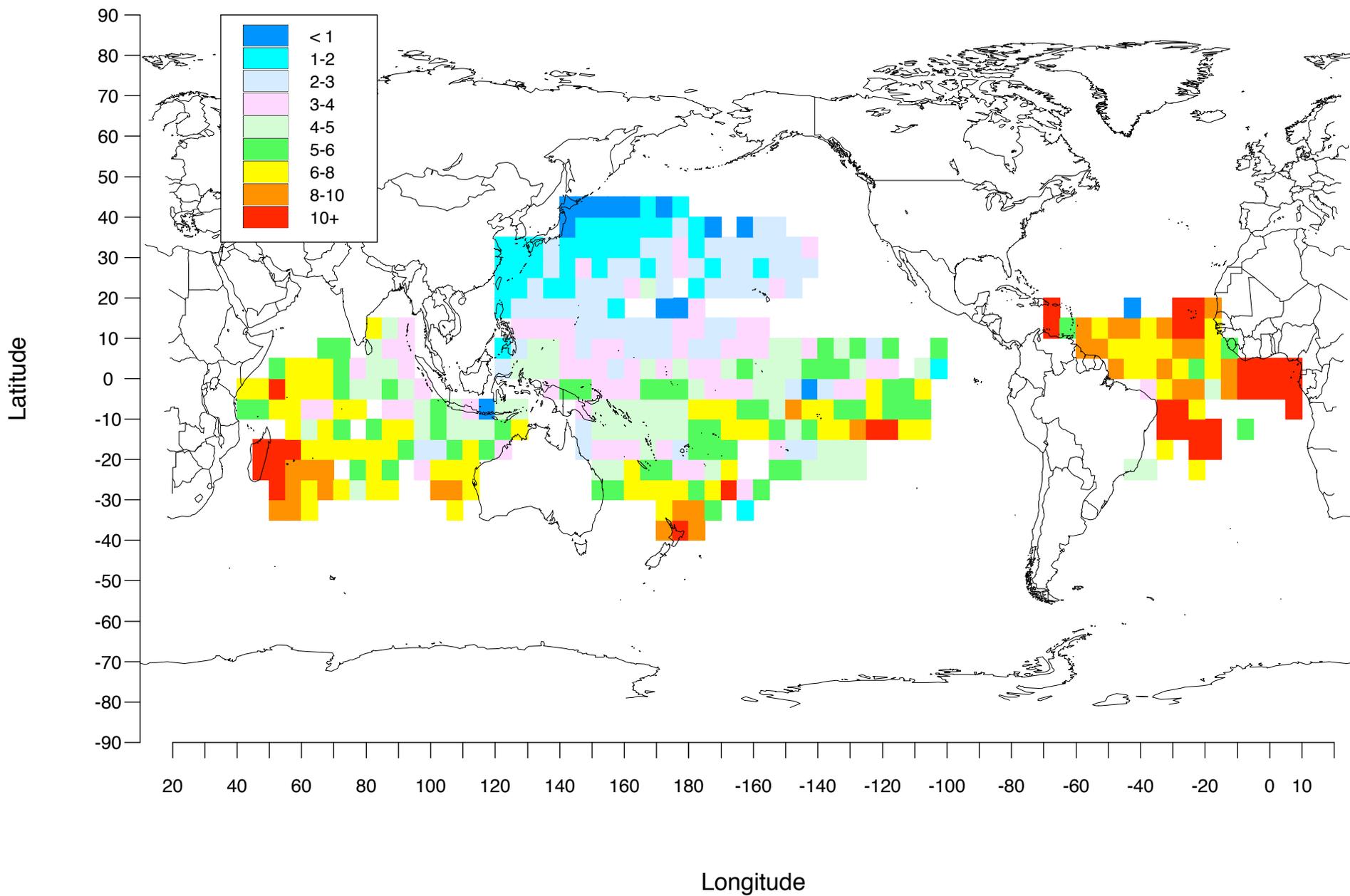
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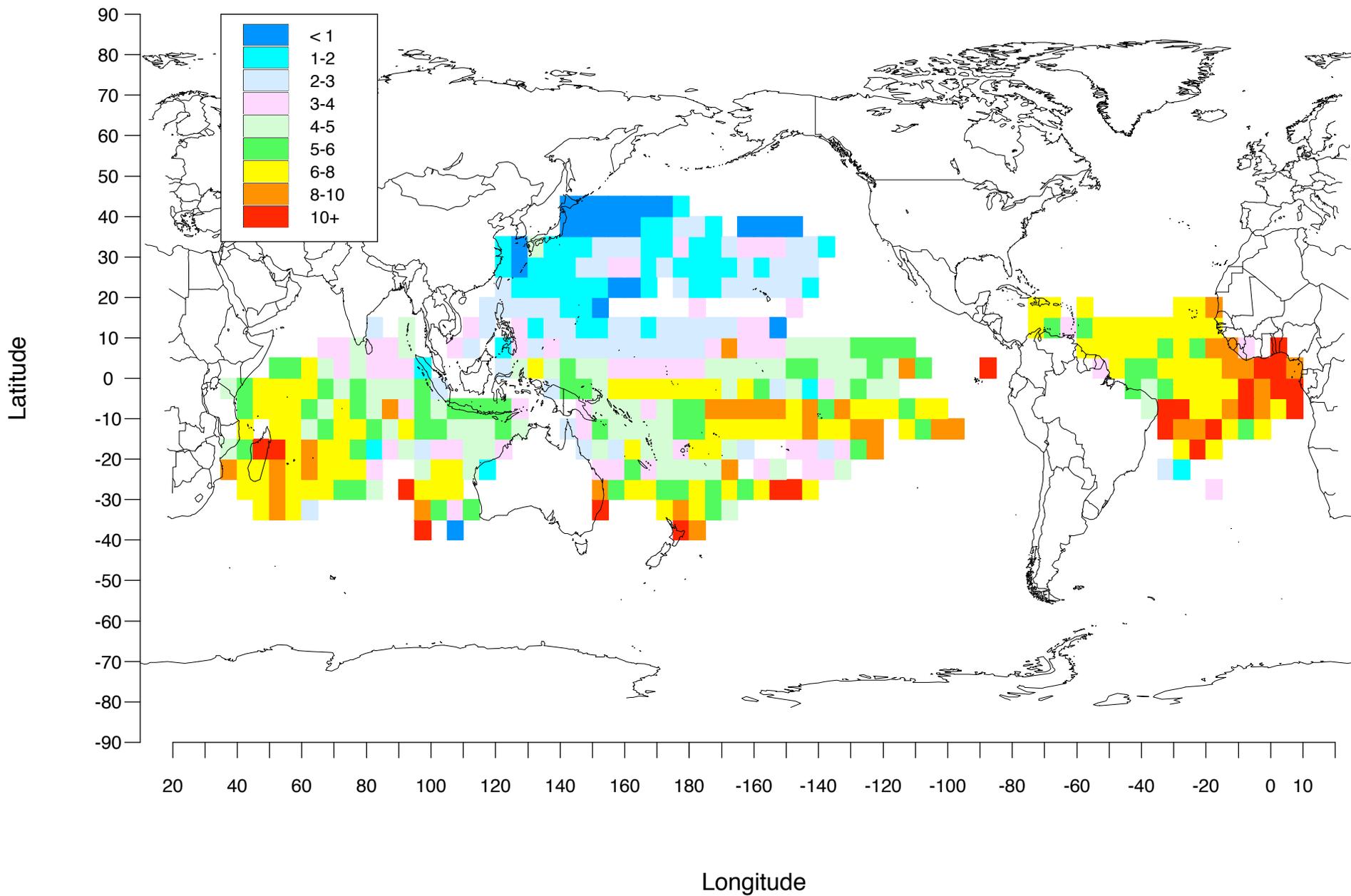
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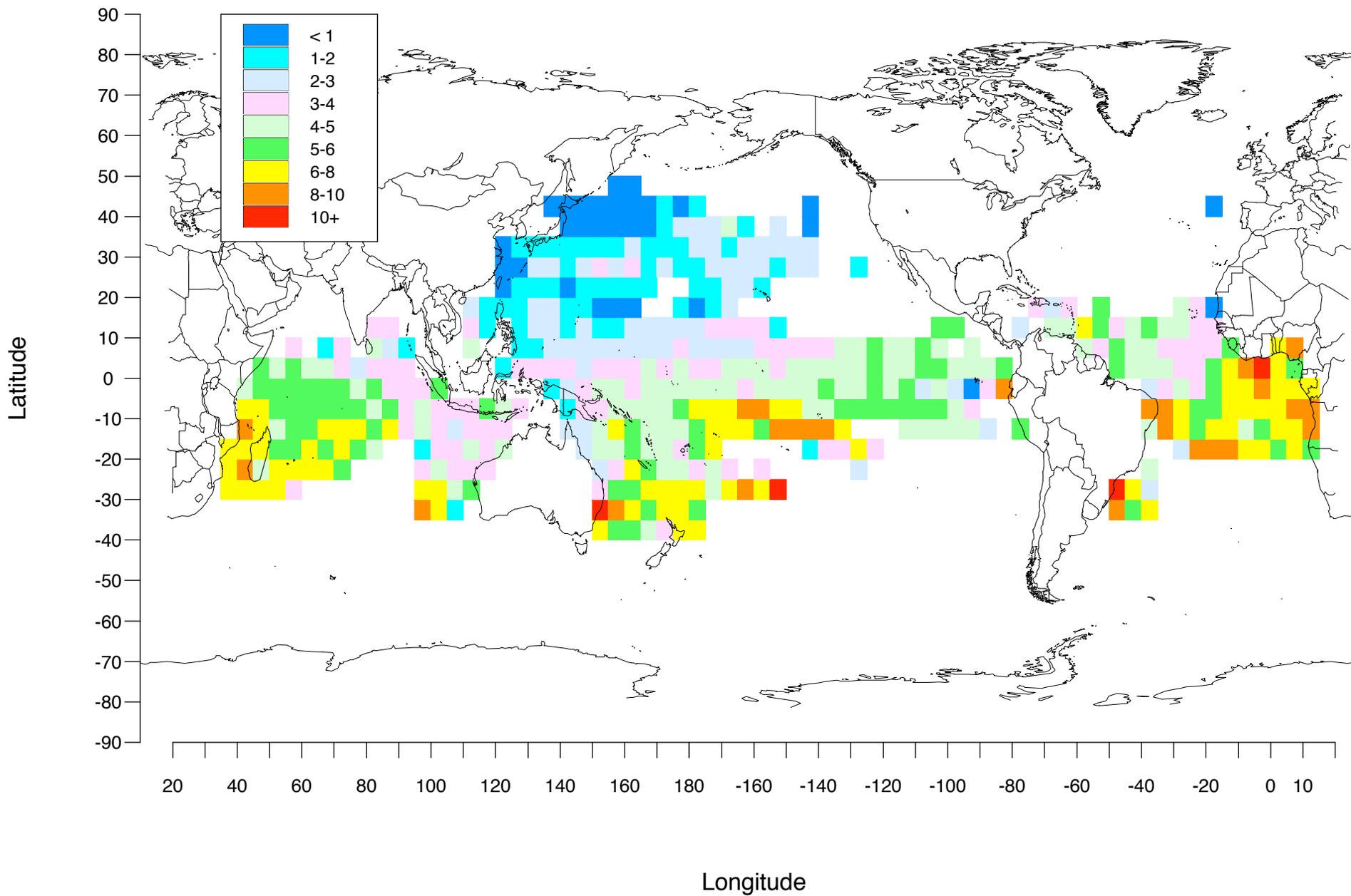
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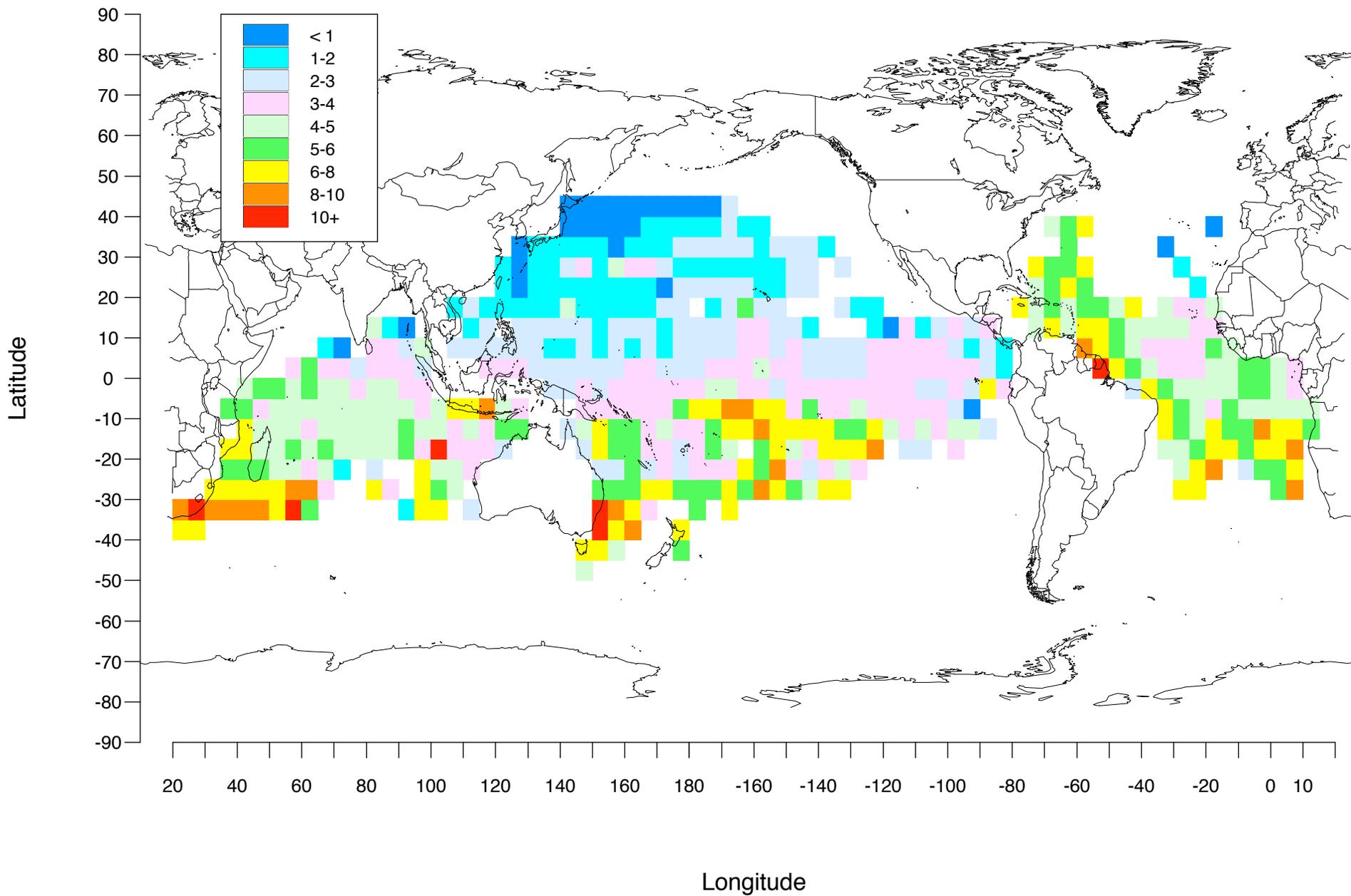
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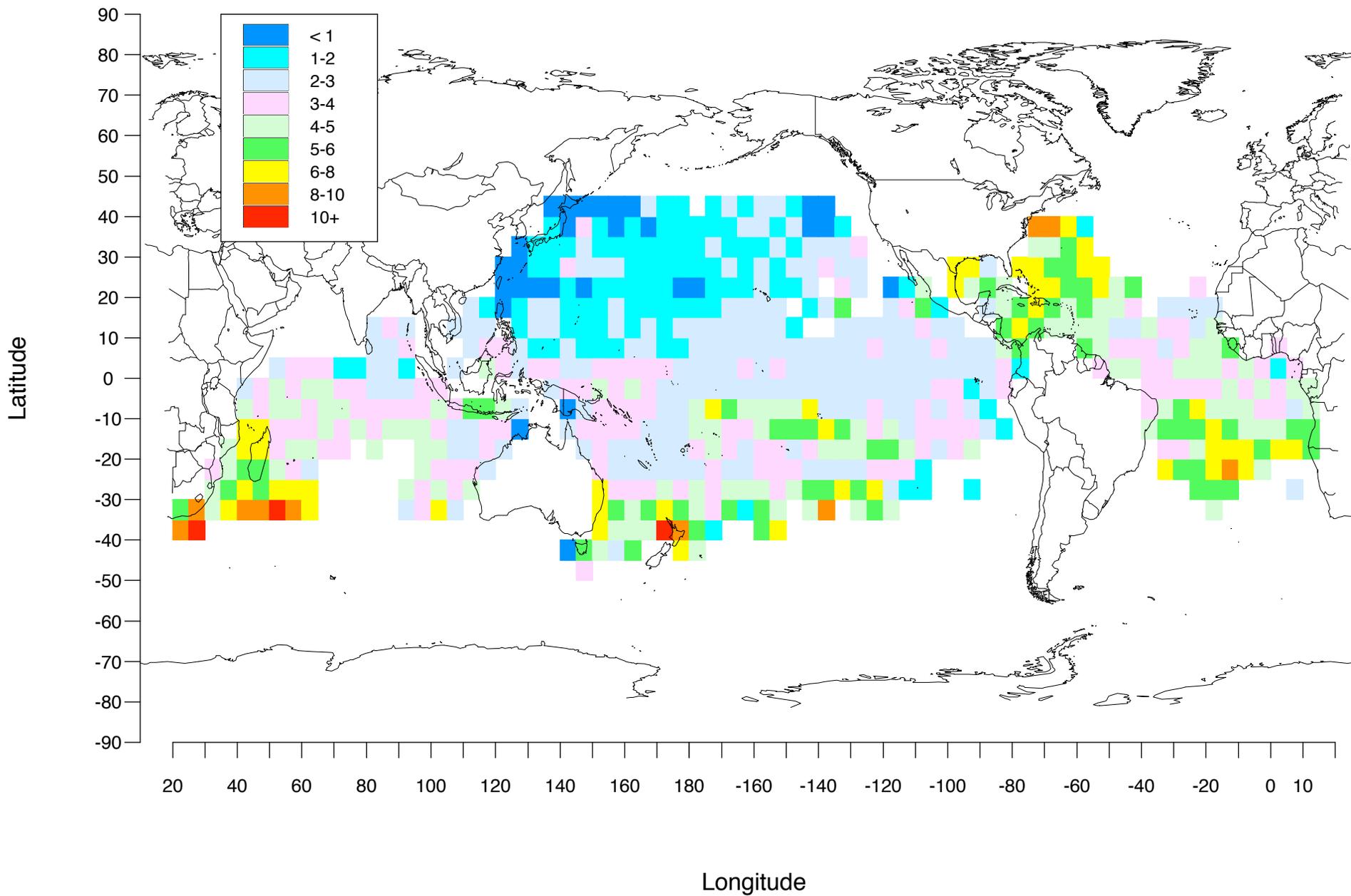
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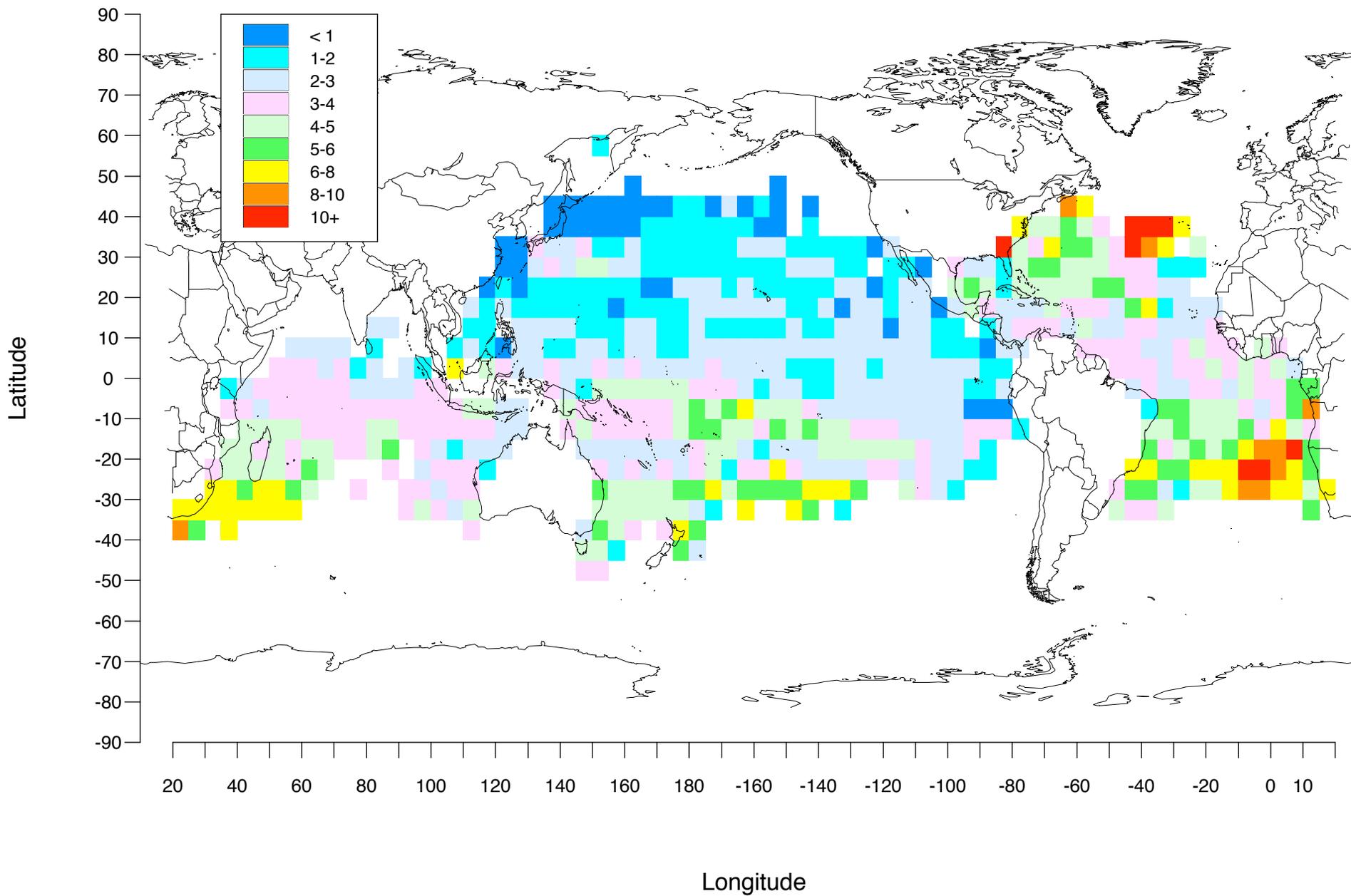
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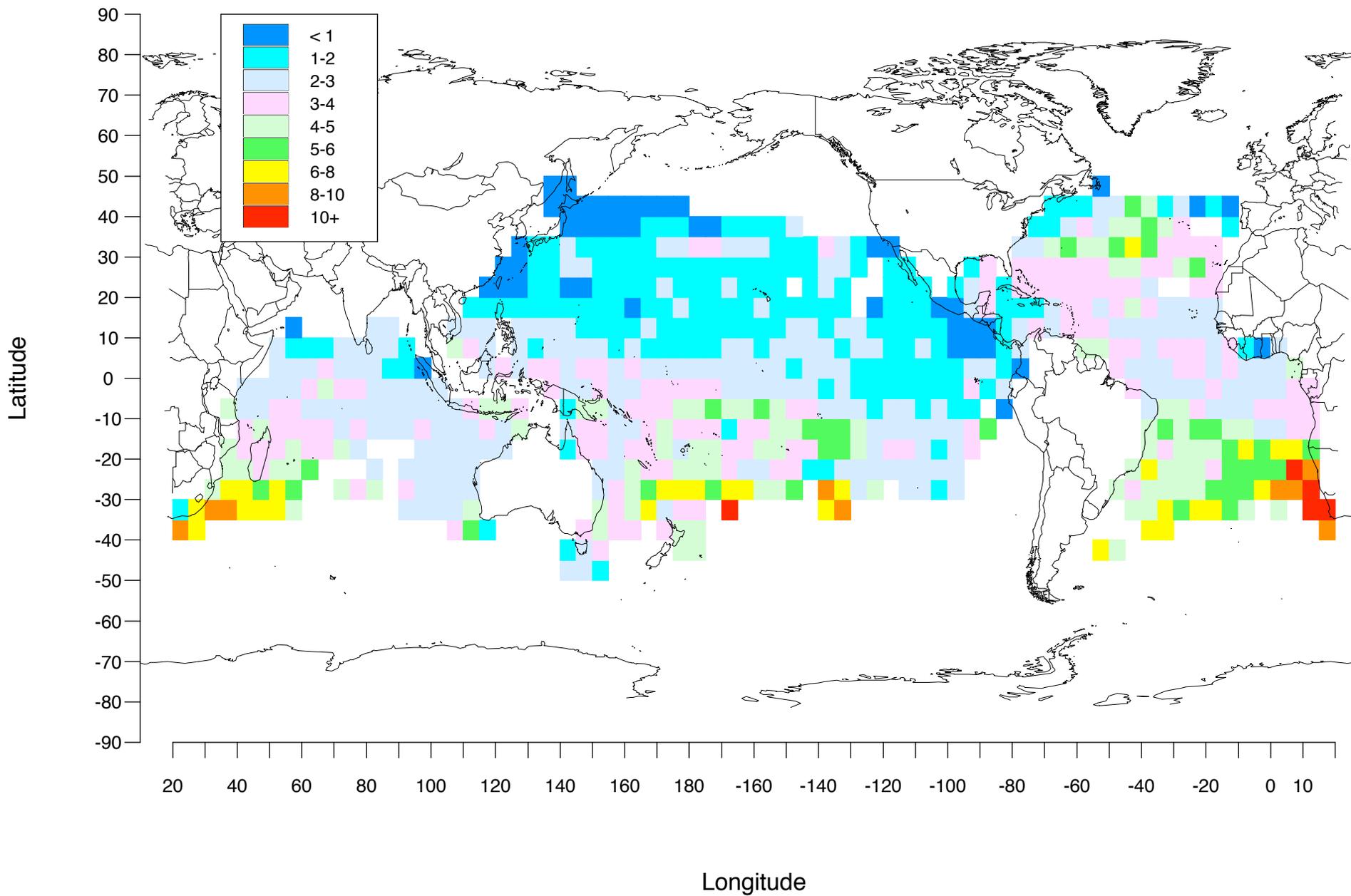
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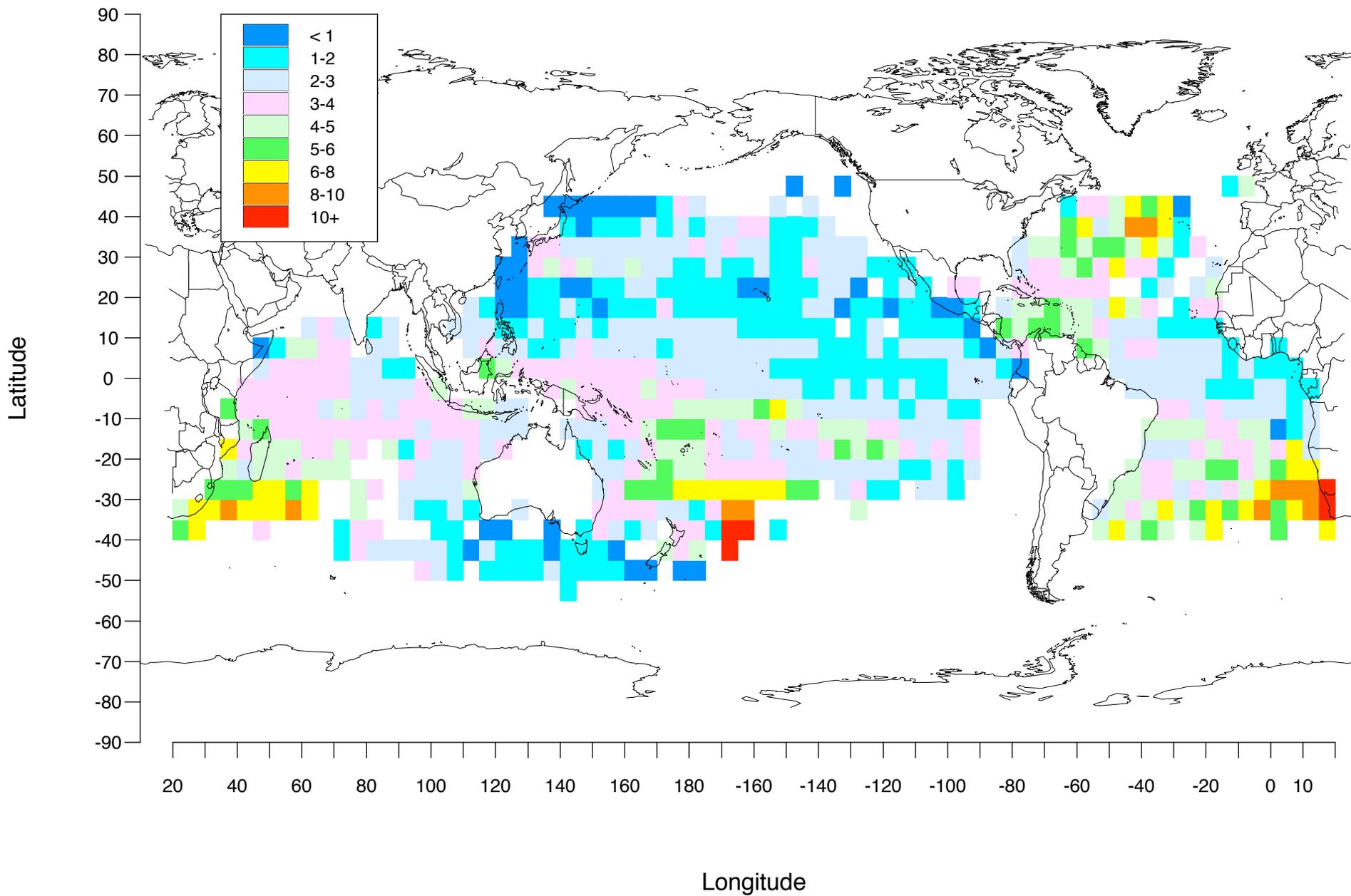
Catch Per Hundred Hooks, Year = 1964



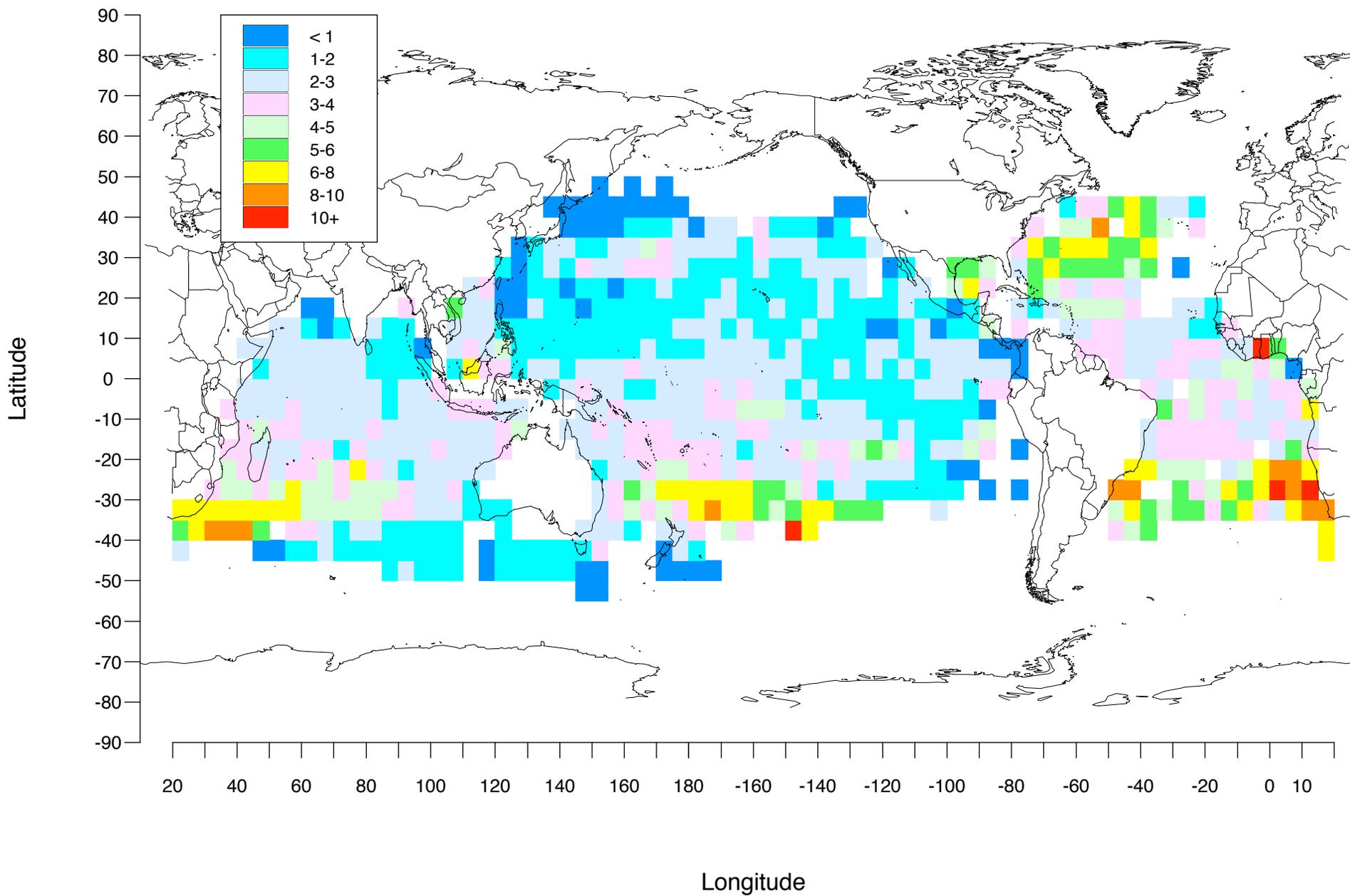
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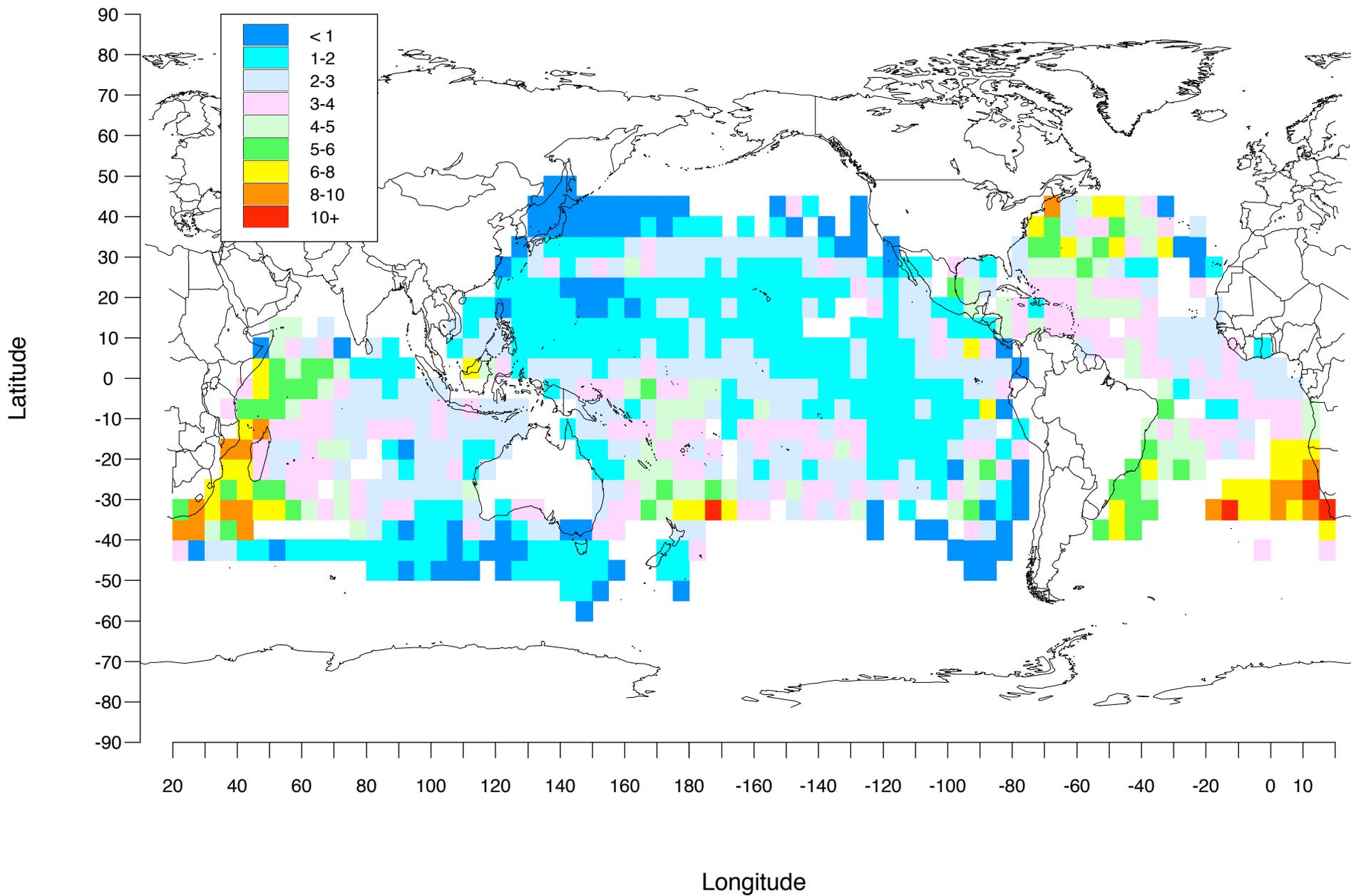
Catch Per Hundred Hooks, Year = 1966



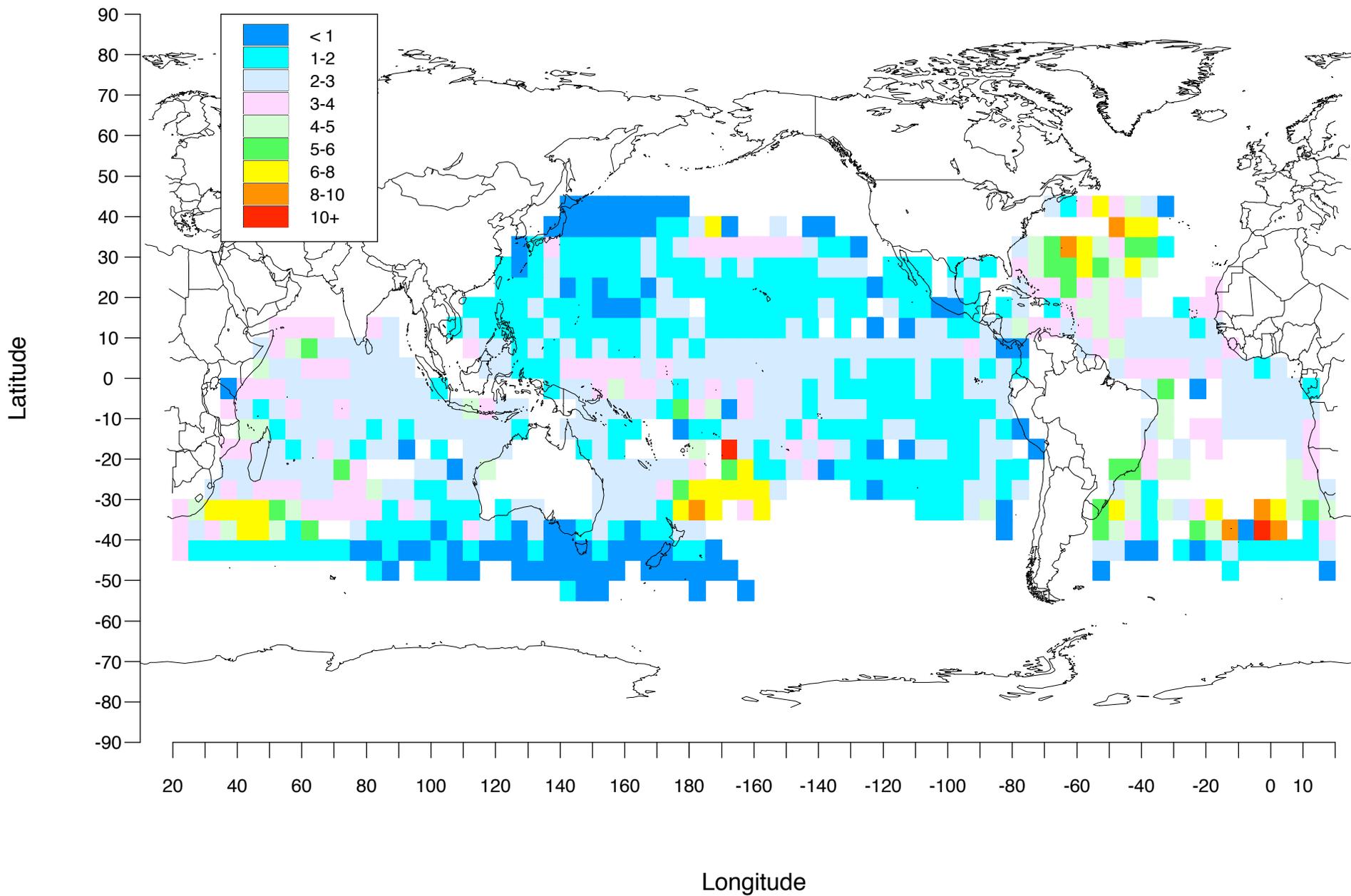
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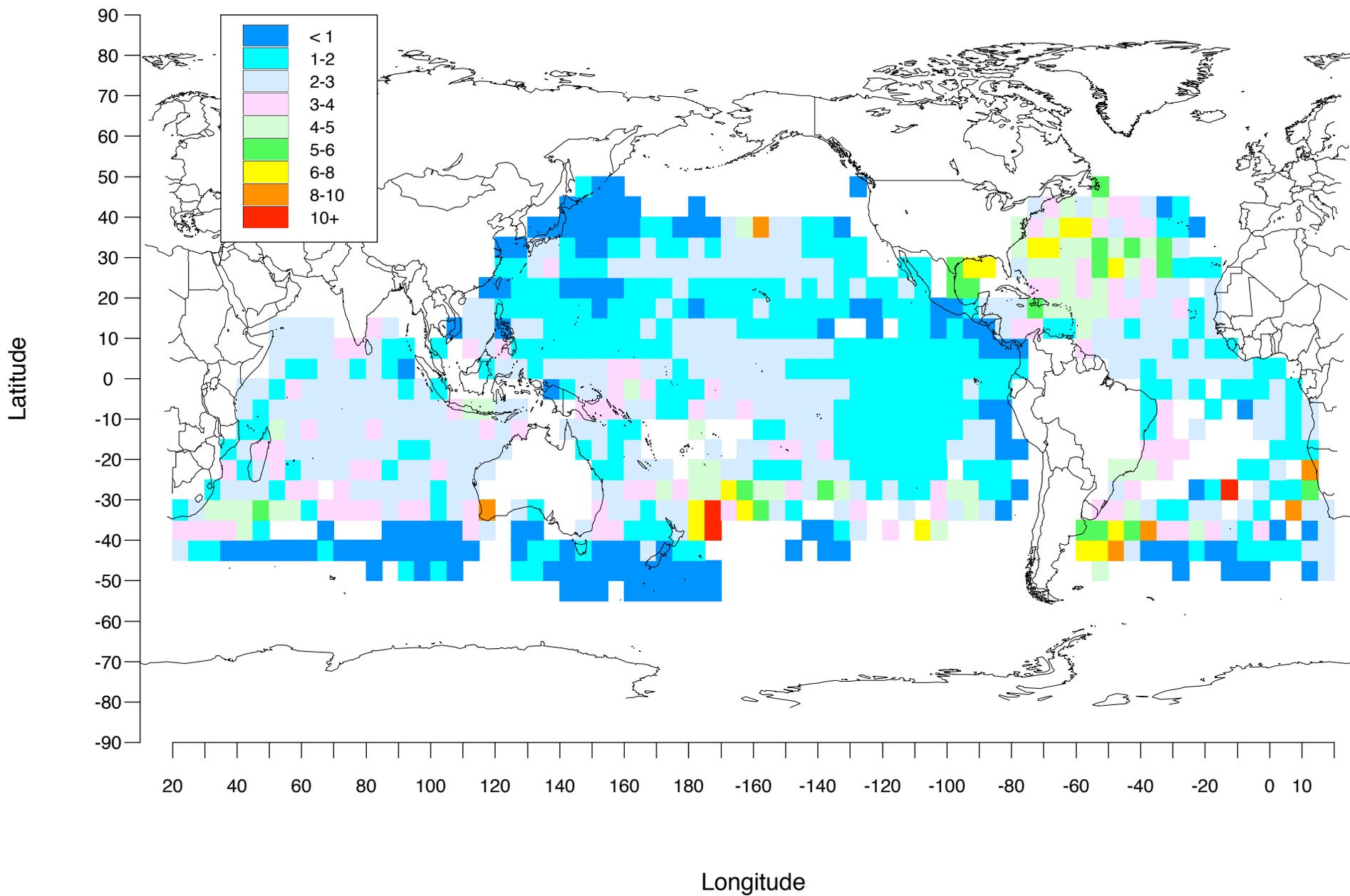
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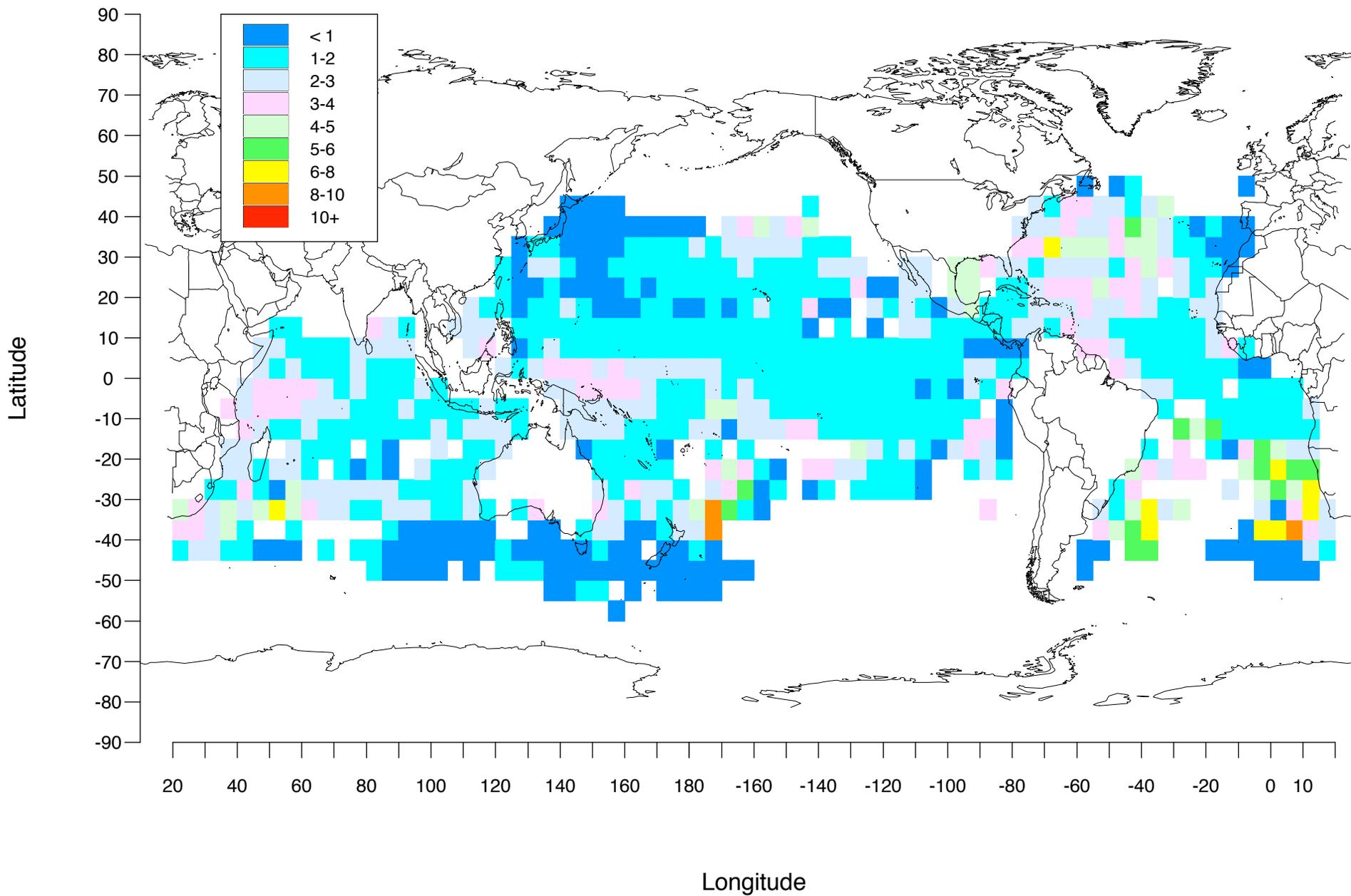
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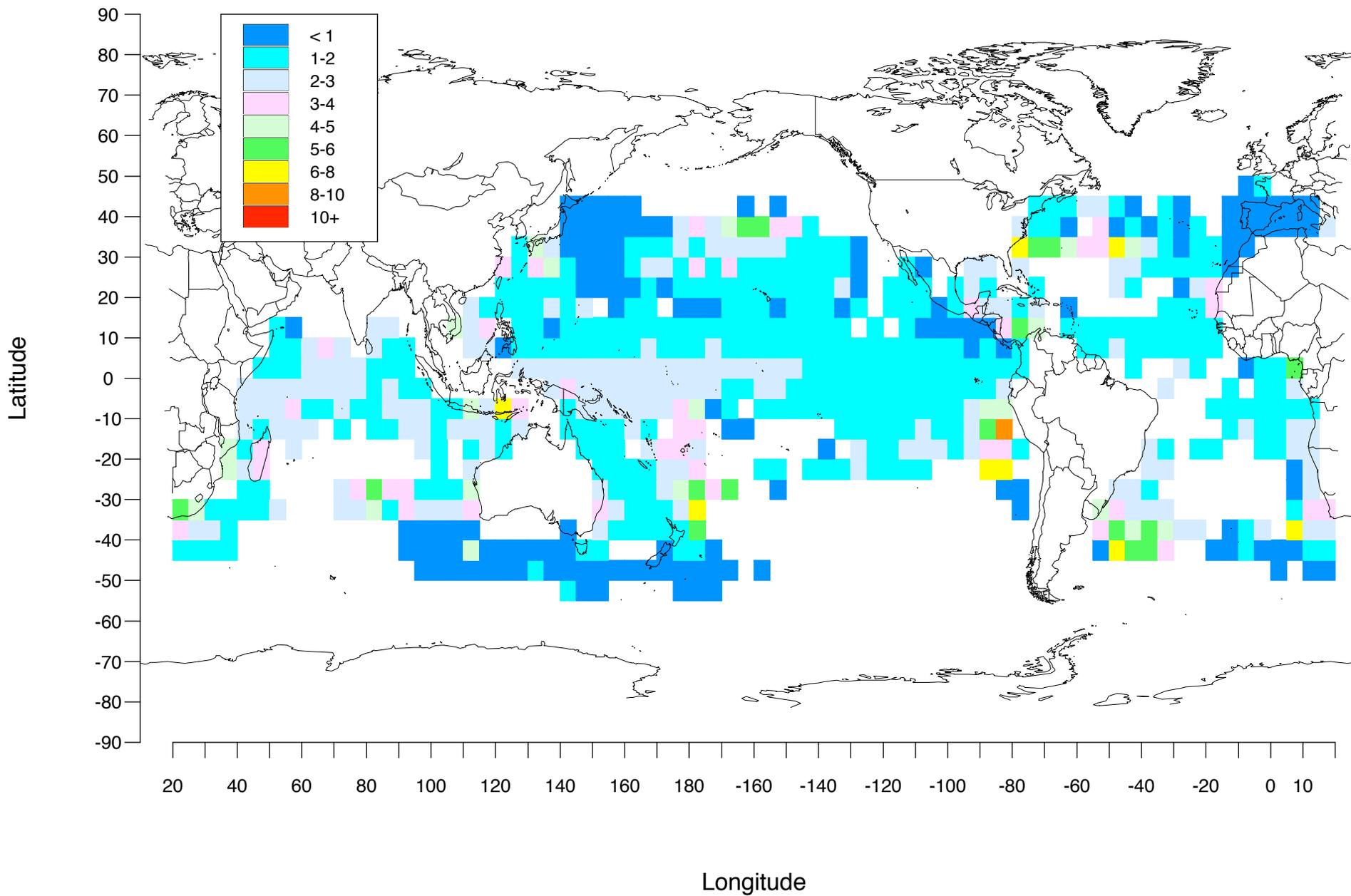
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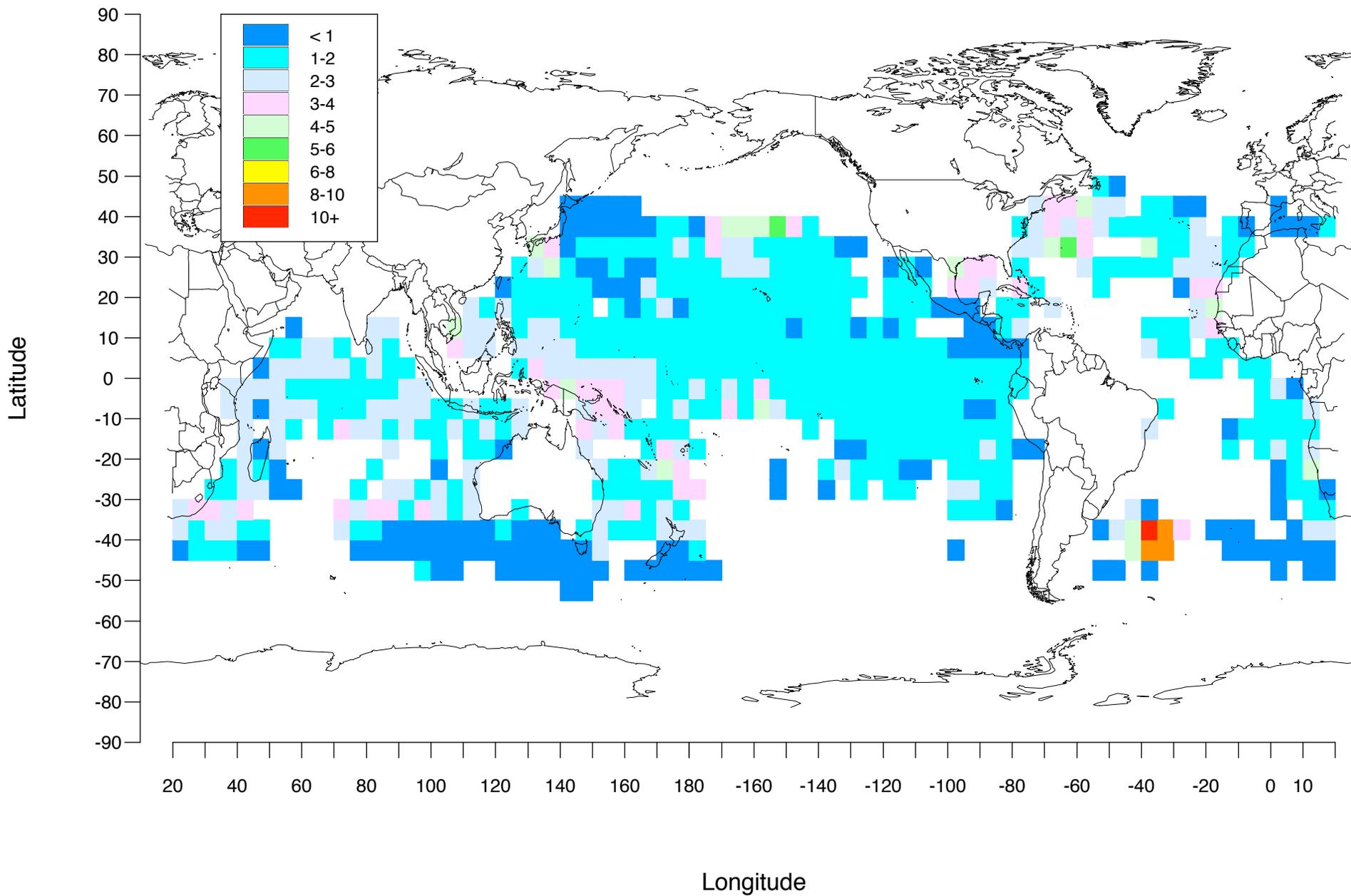
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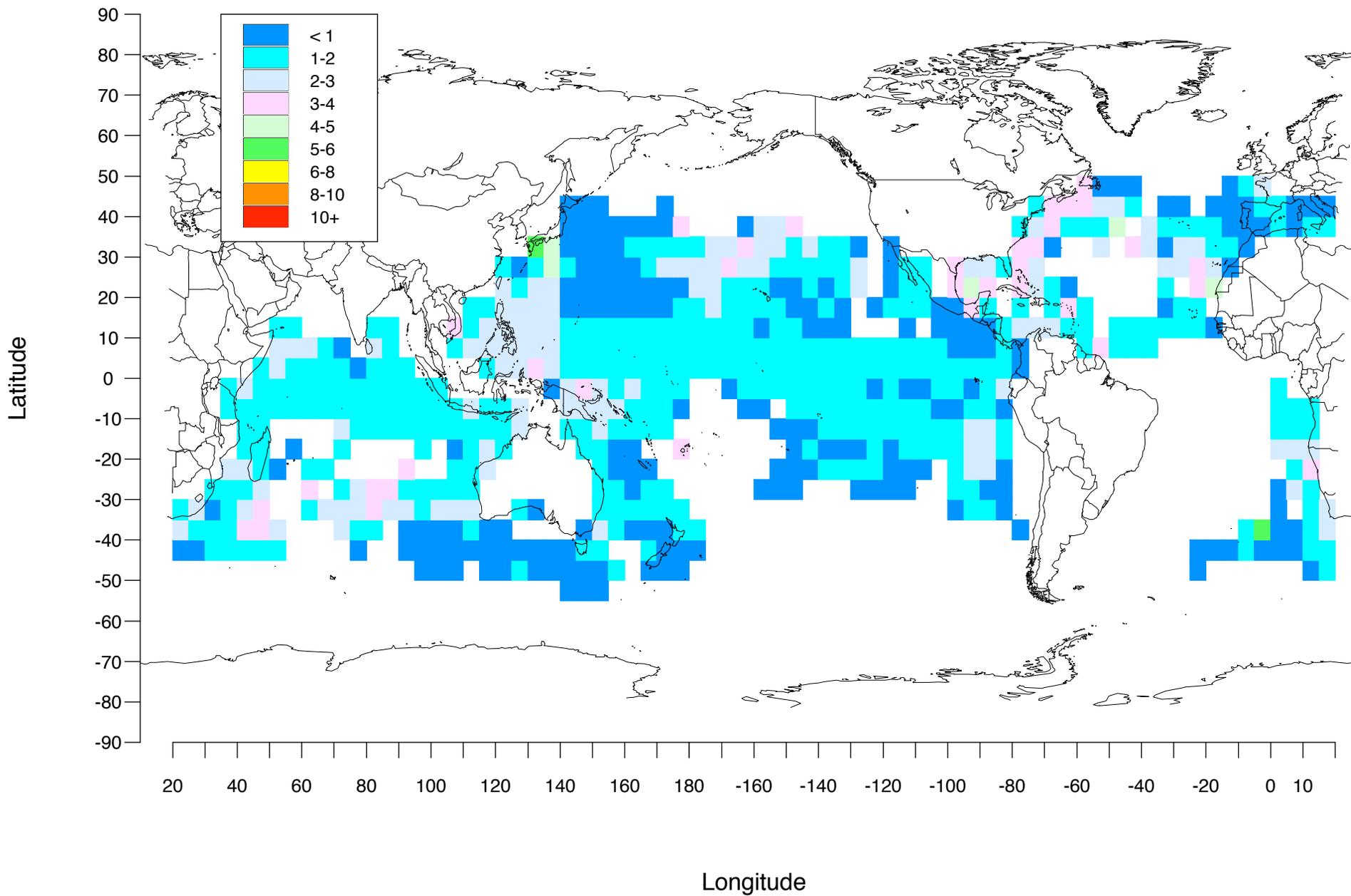
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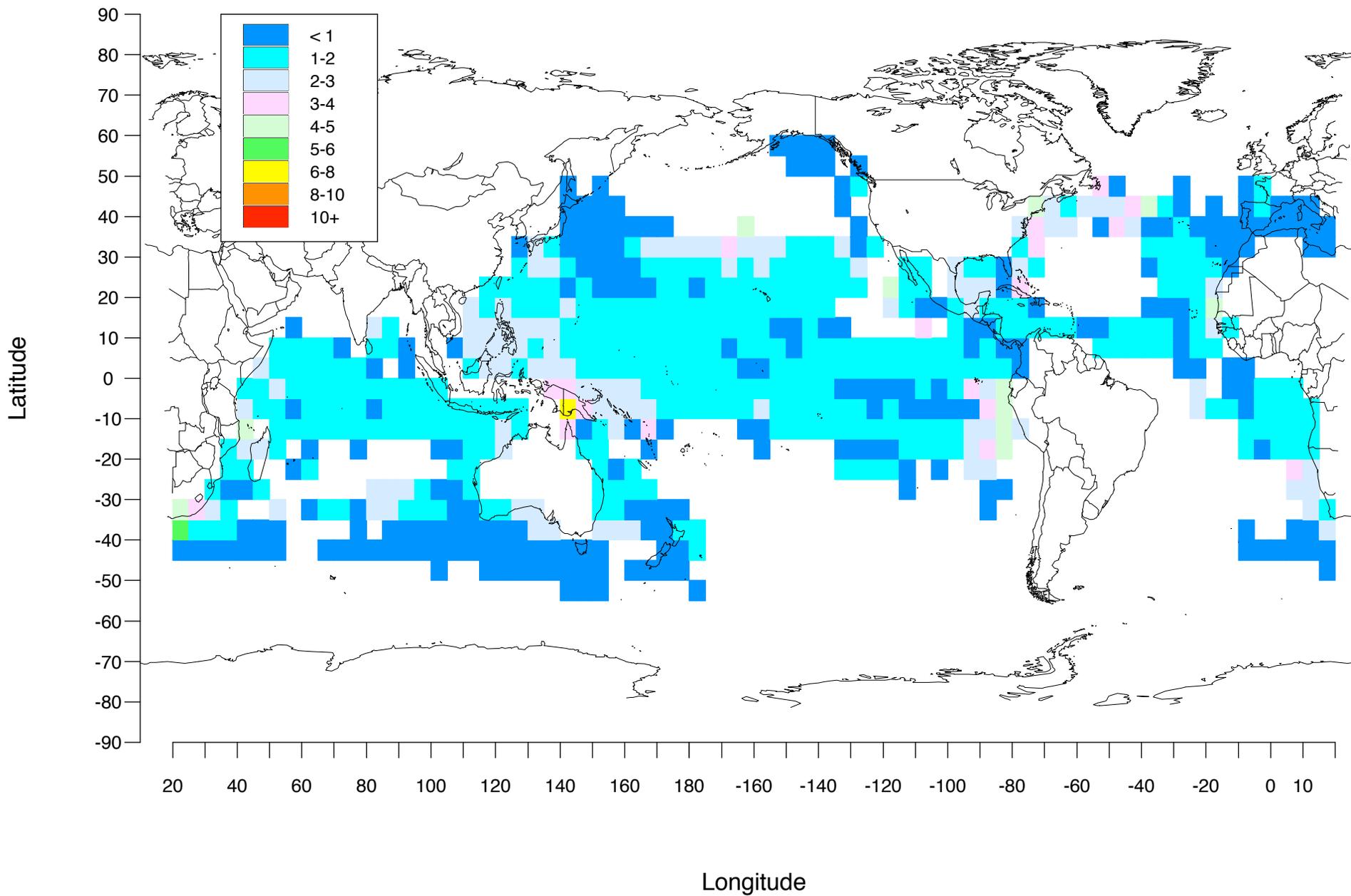
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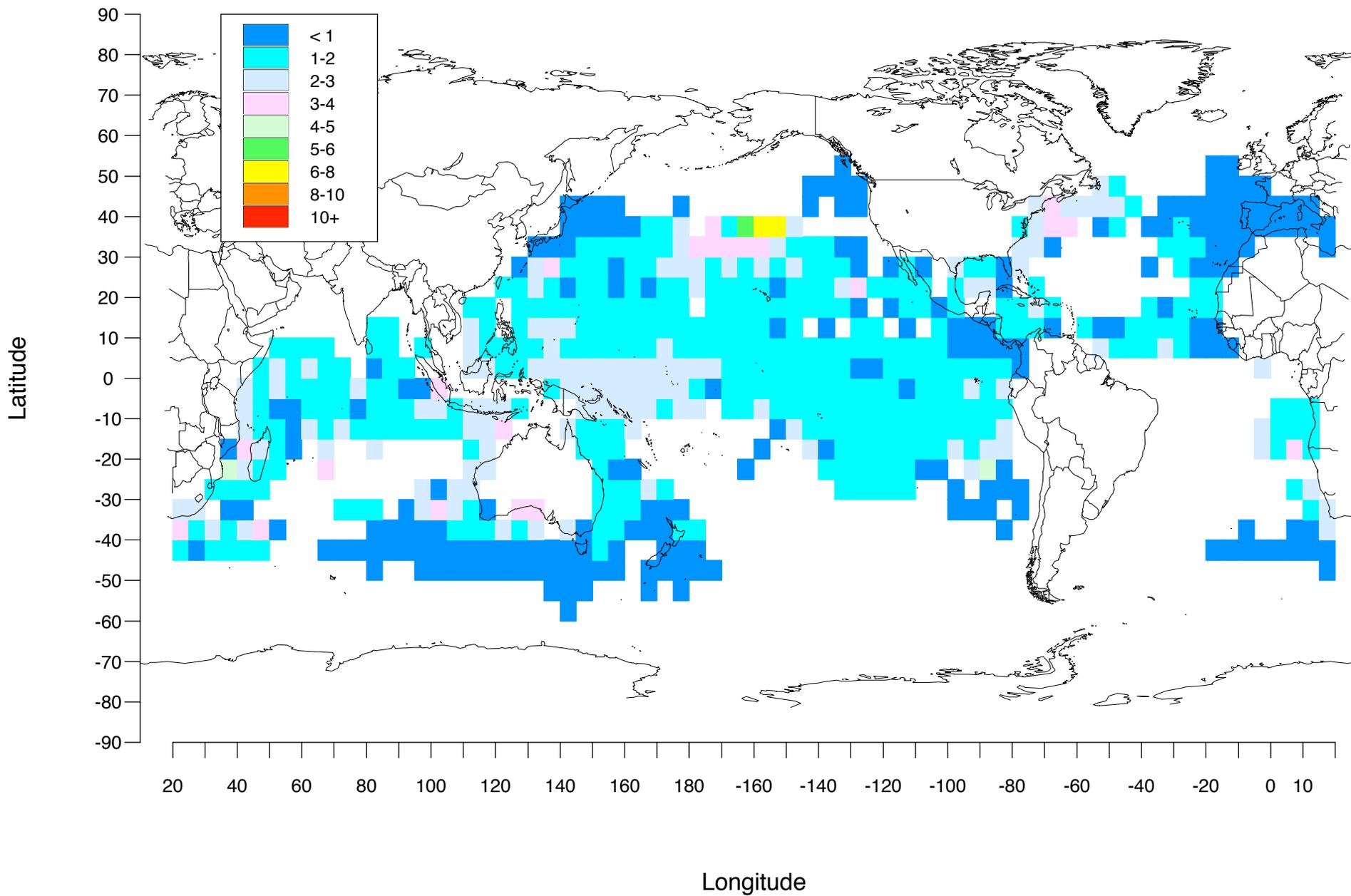
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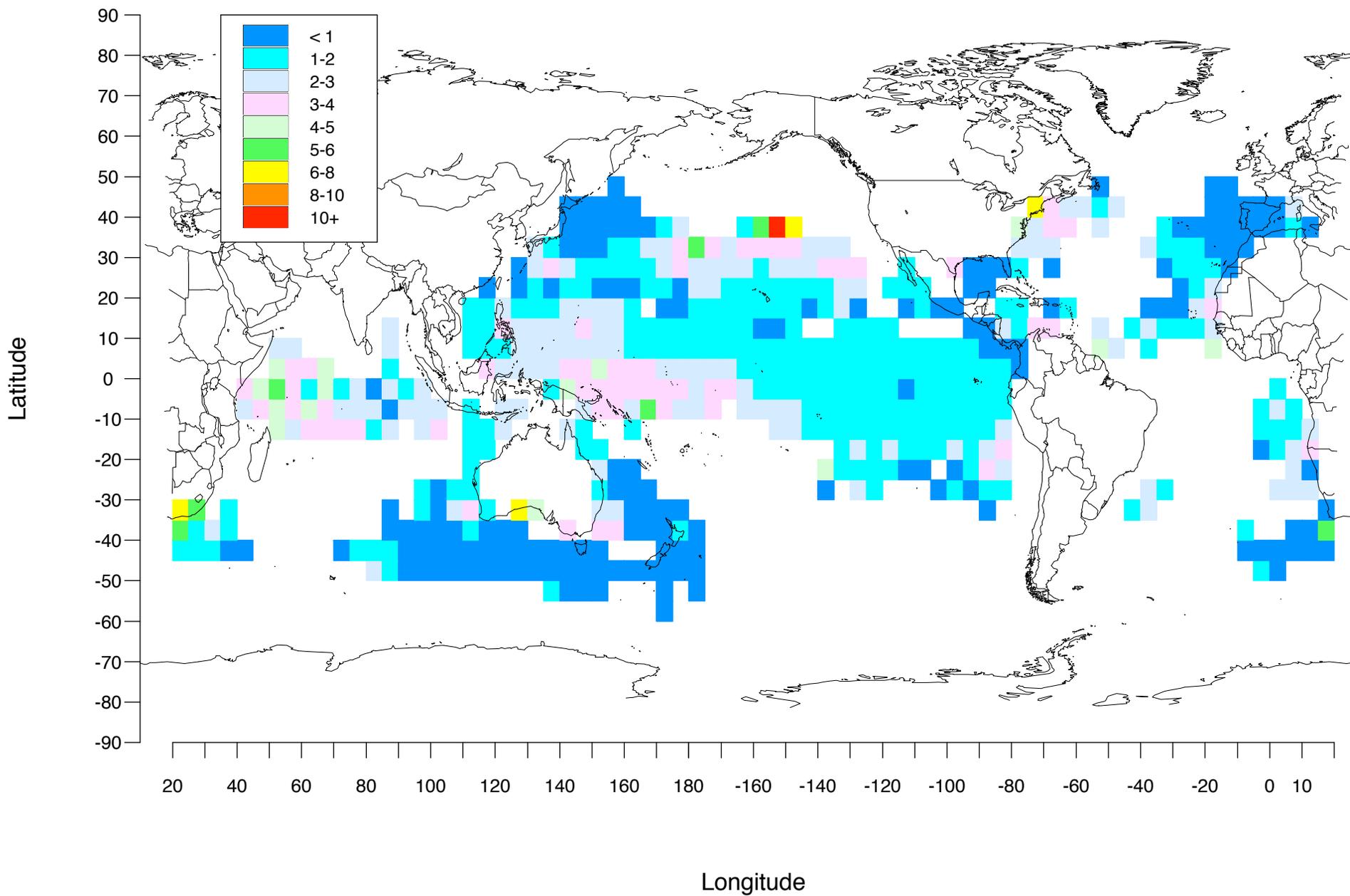
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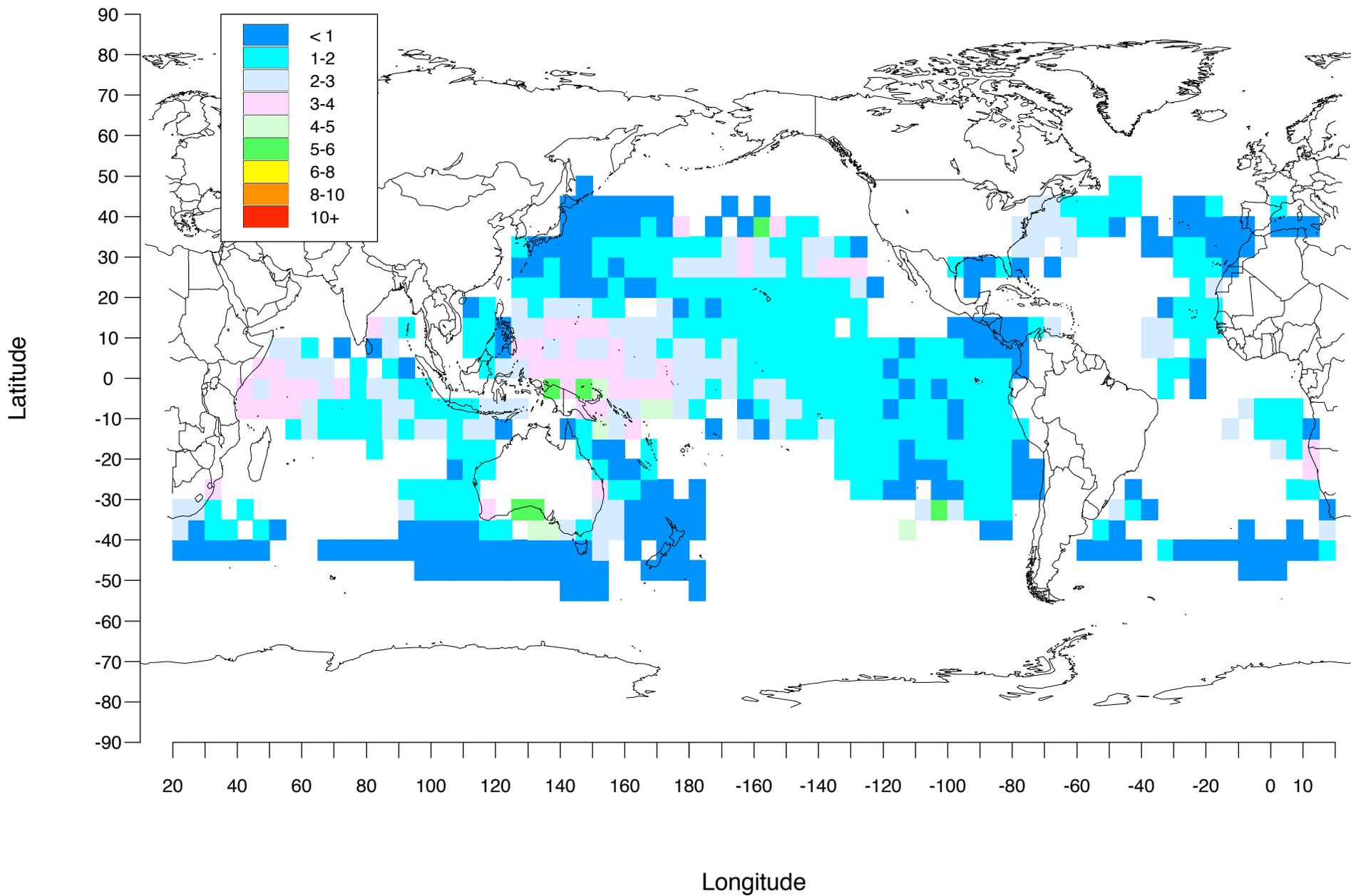
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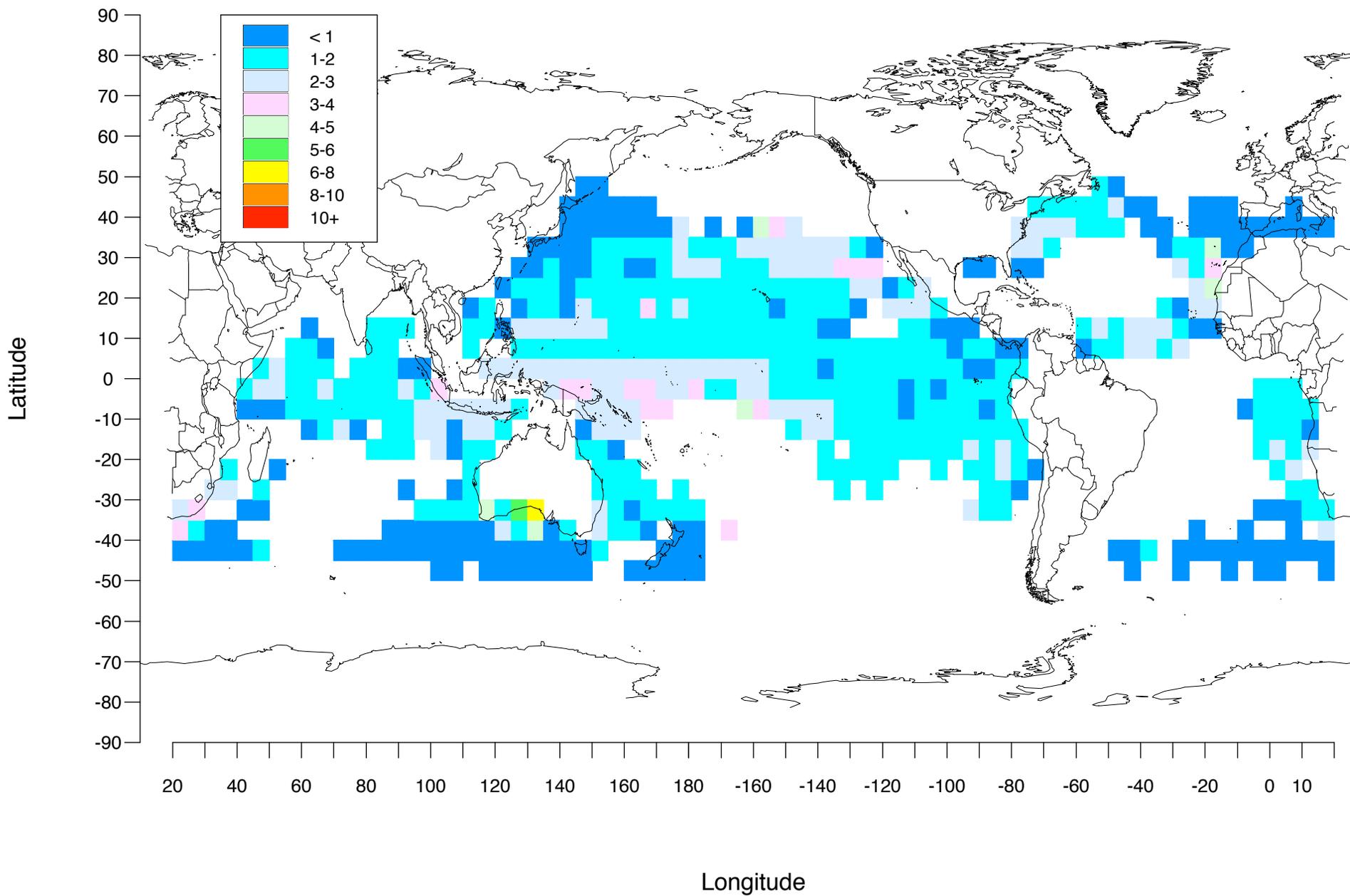
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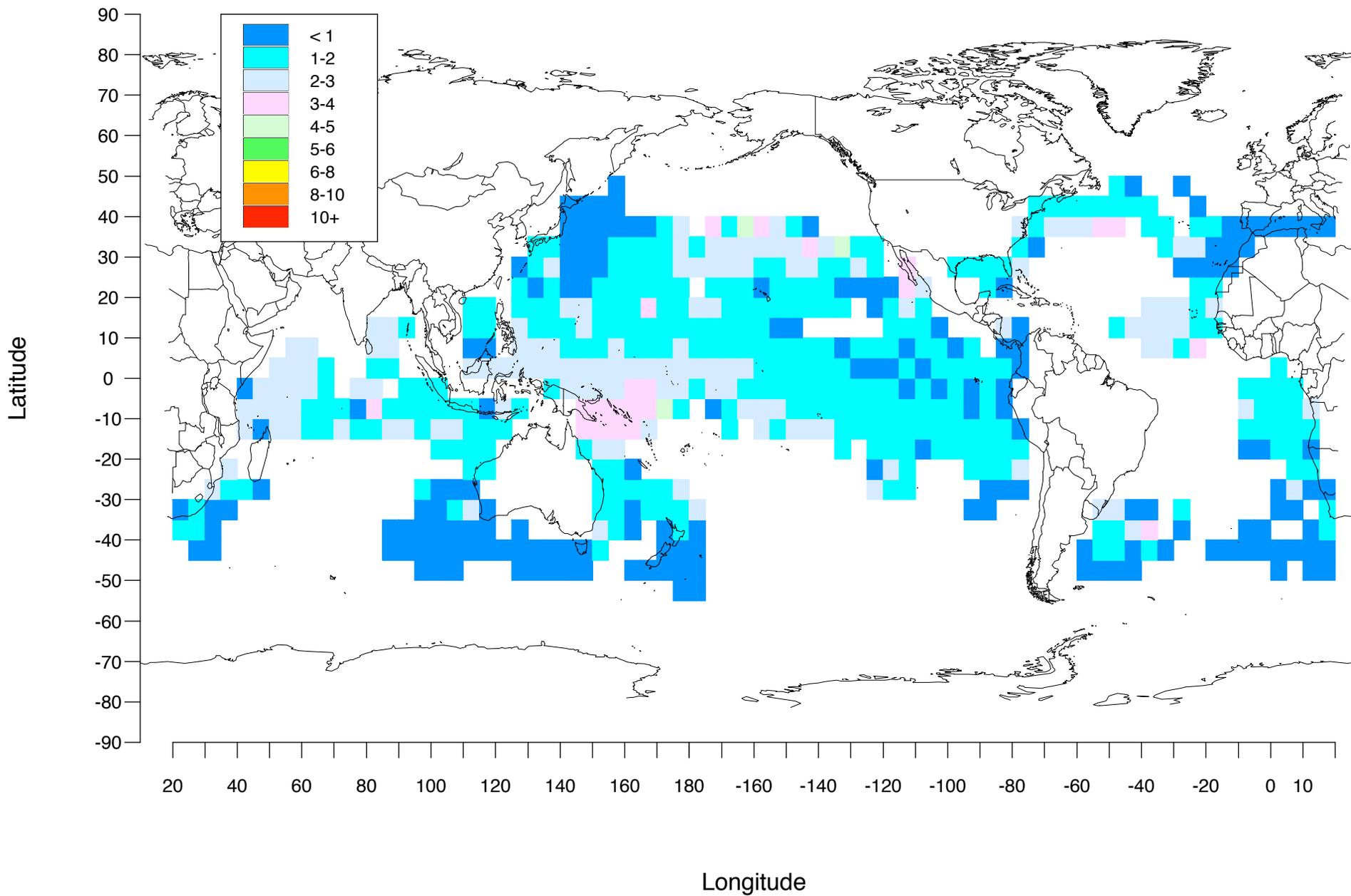
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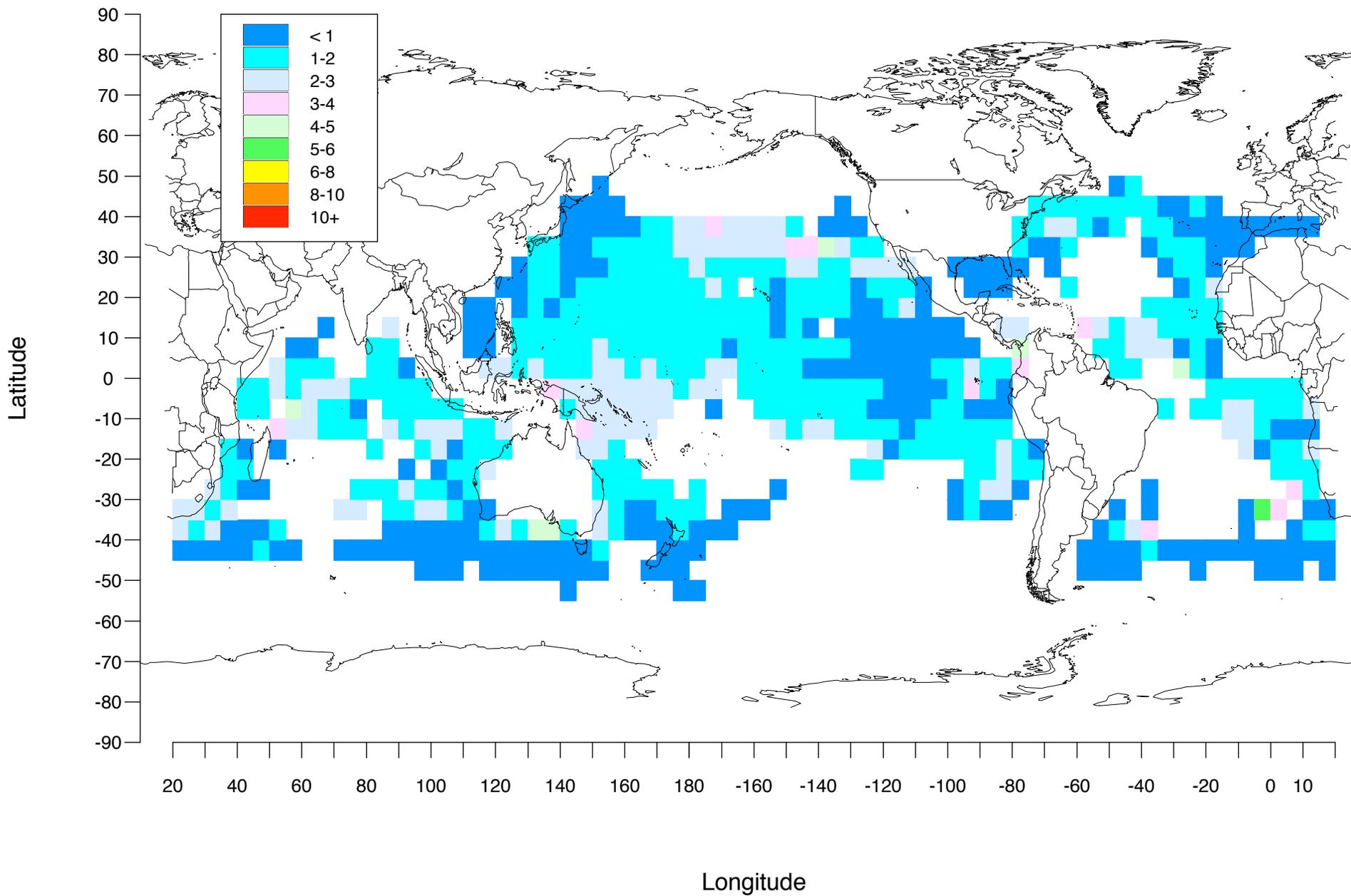
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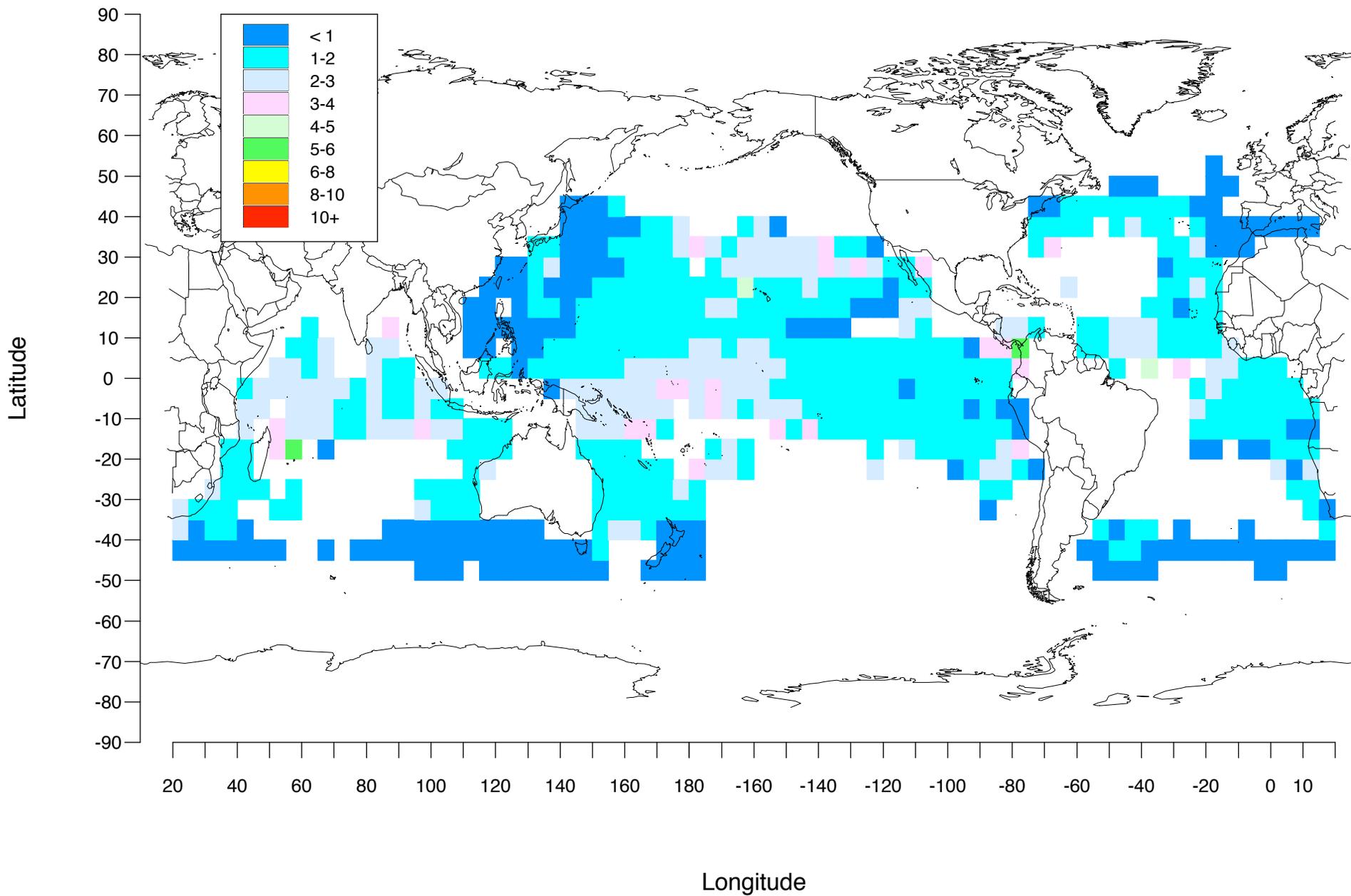
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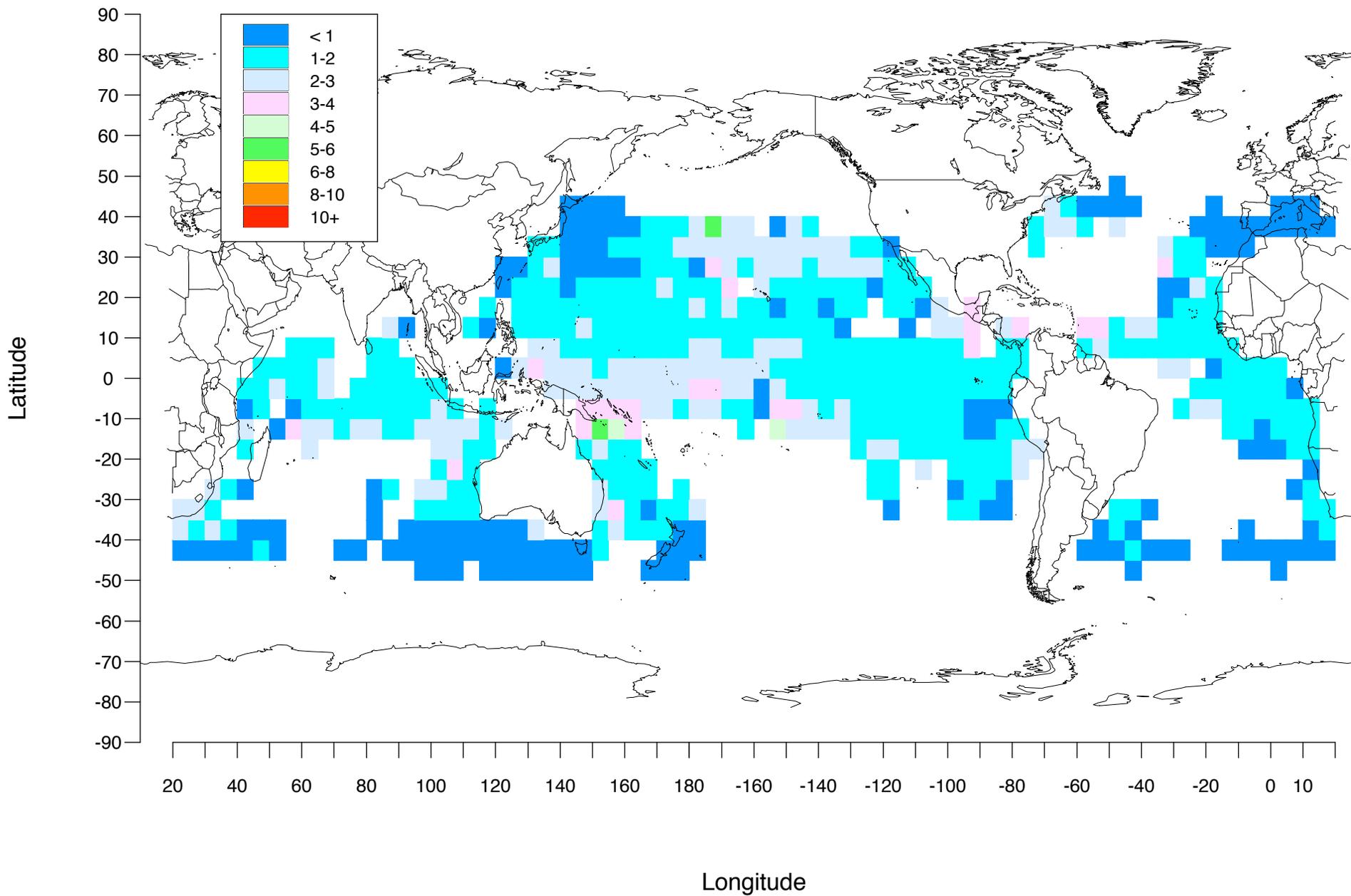
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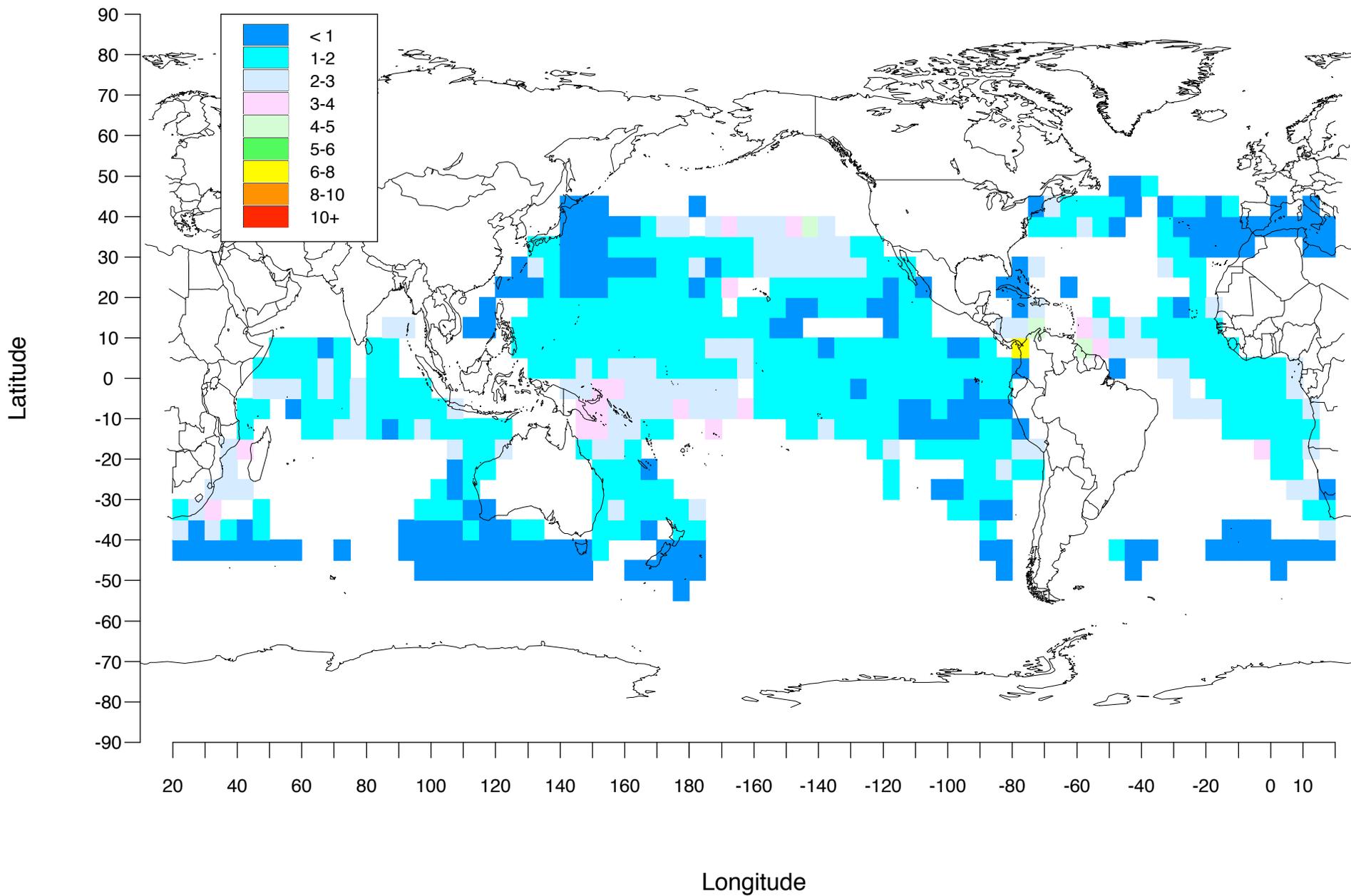
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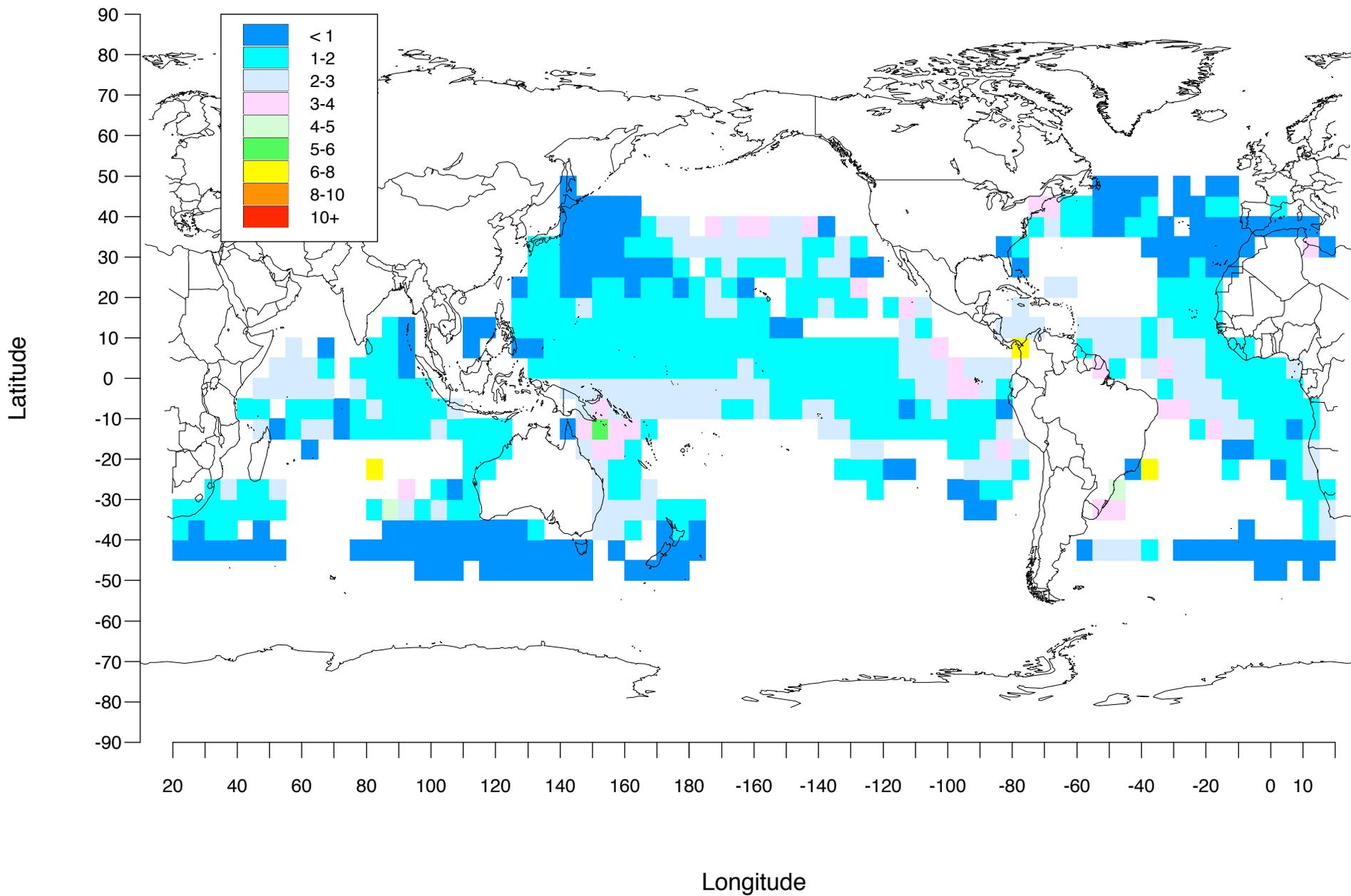
Catch Per Hundred Hooks, Year = 1983



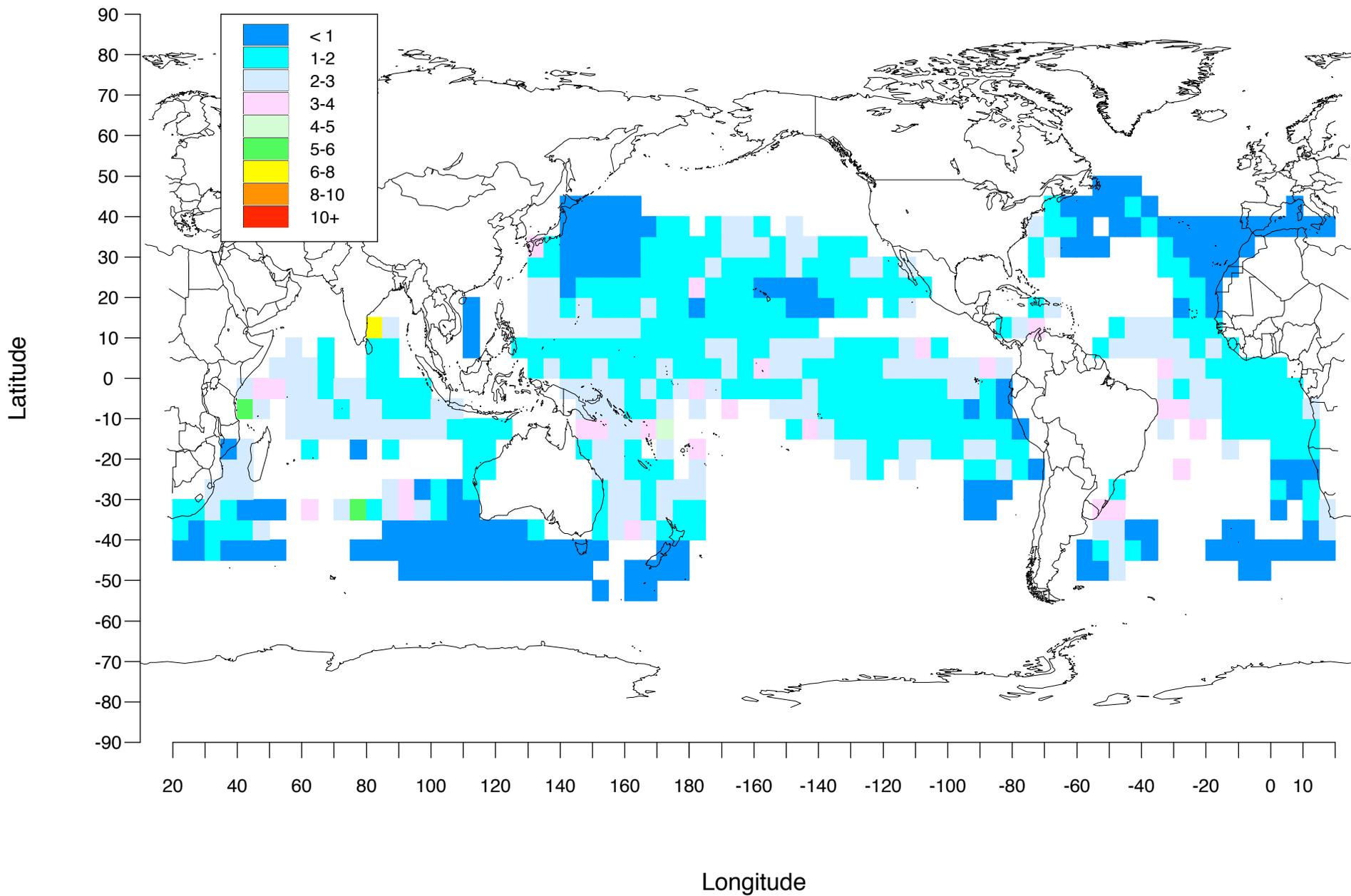
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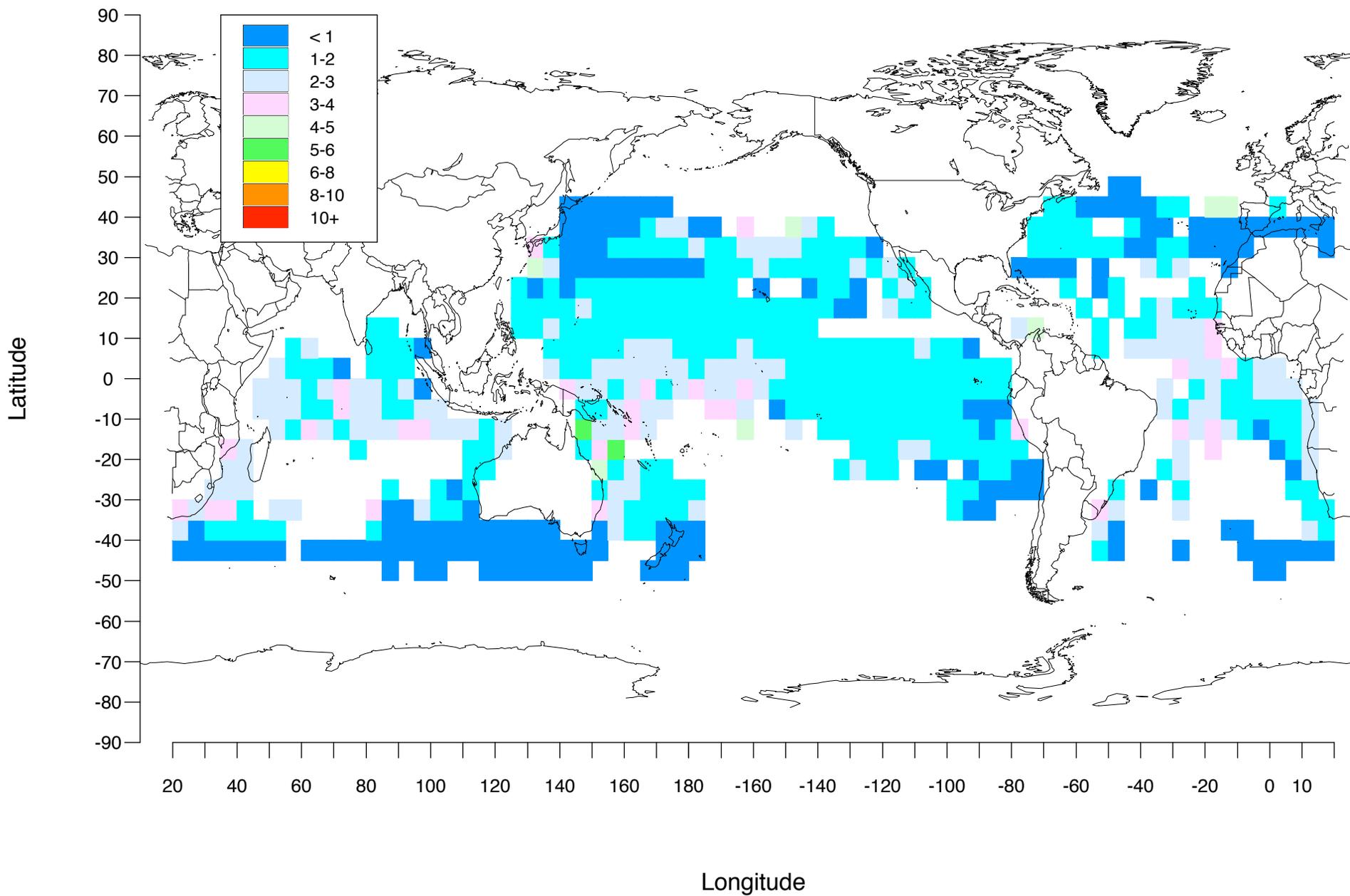
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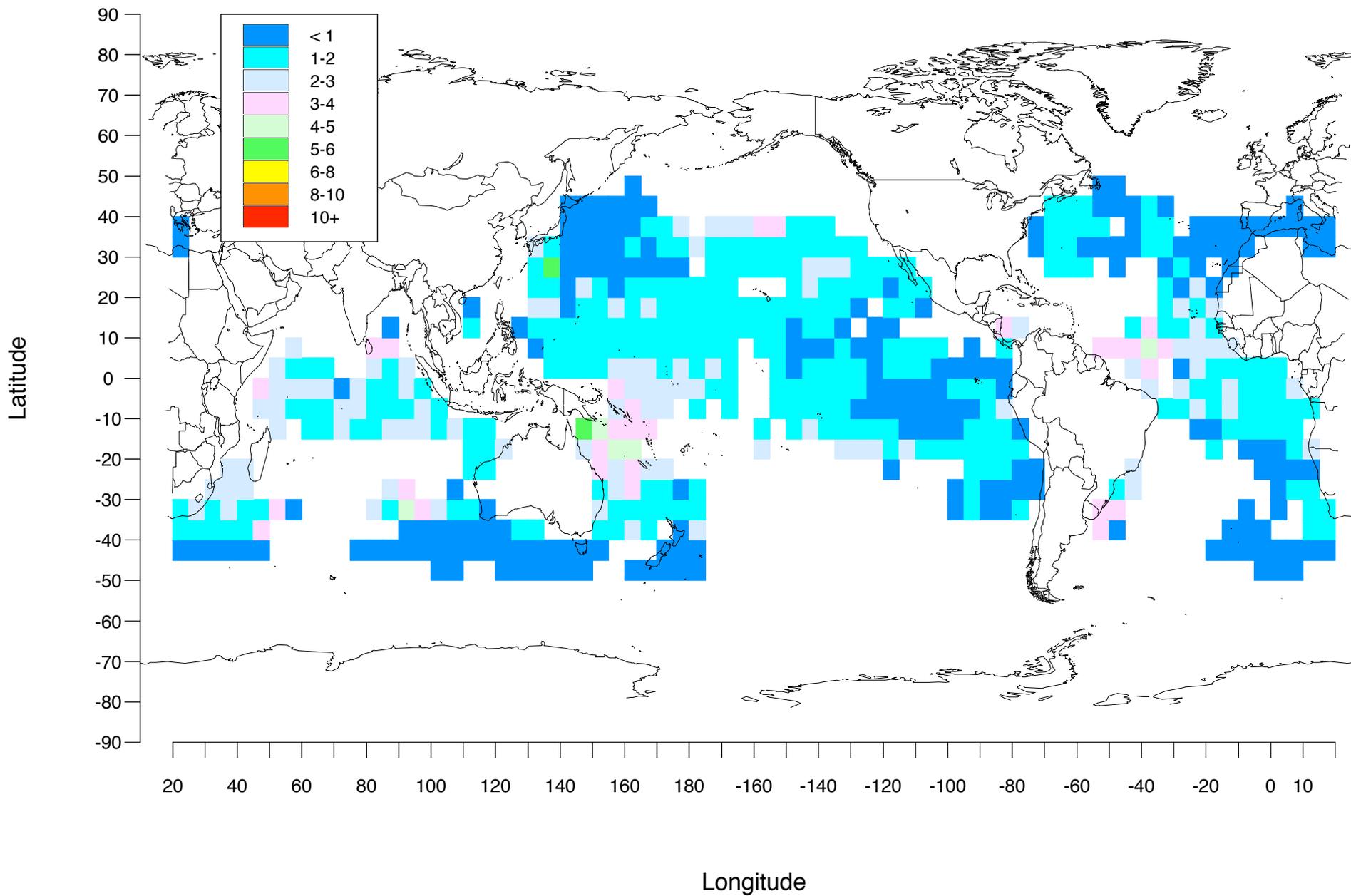
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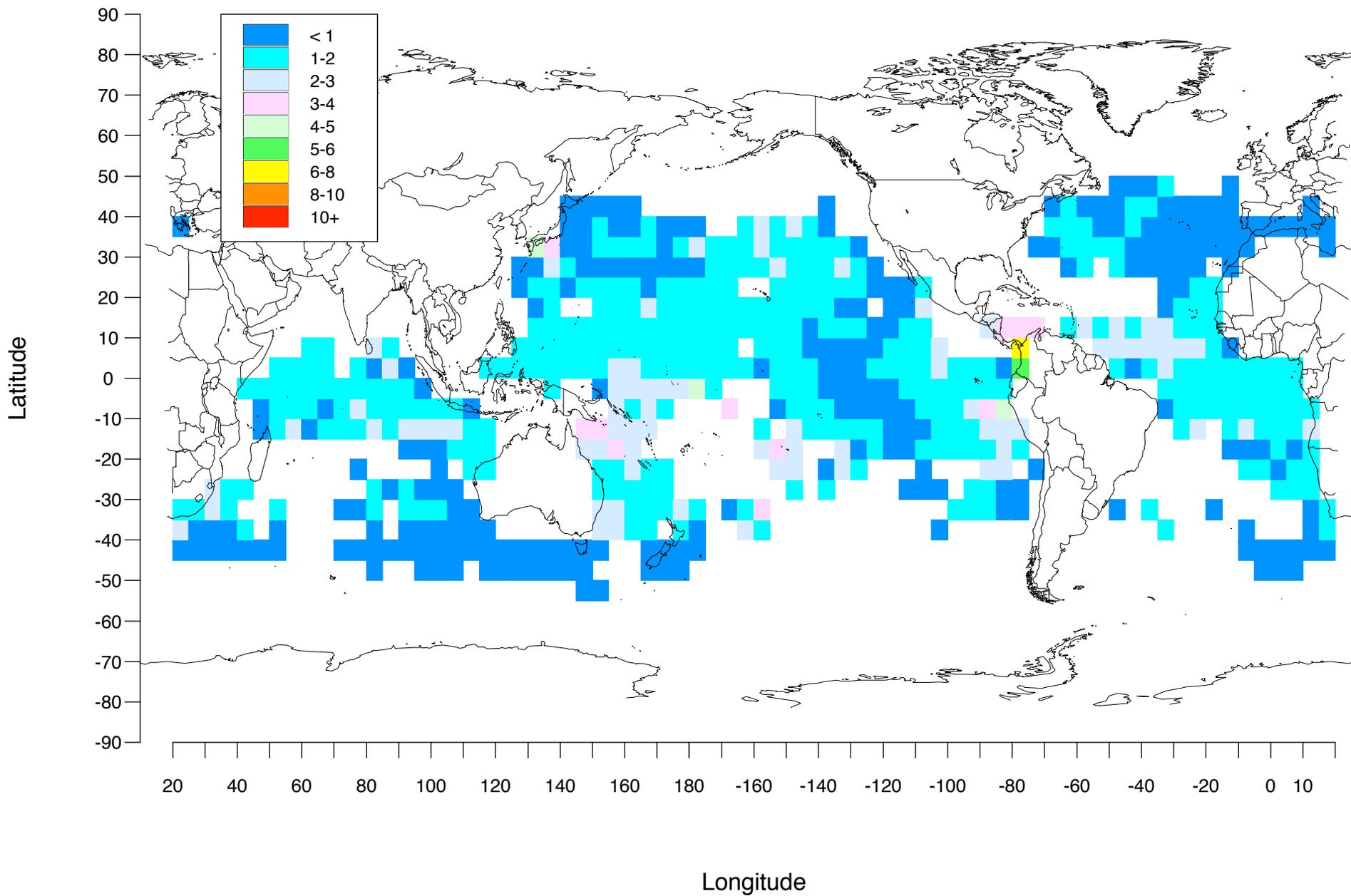
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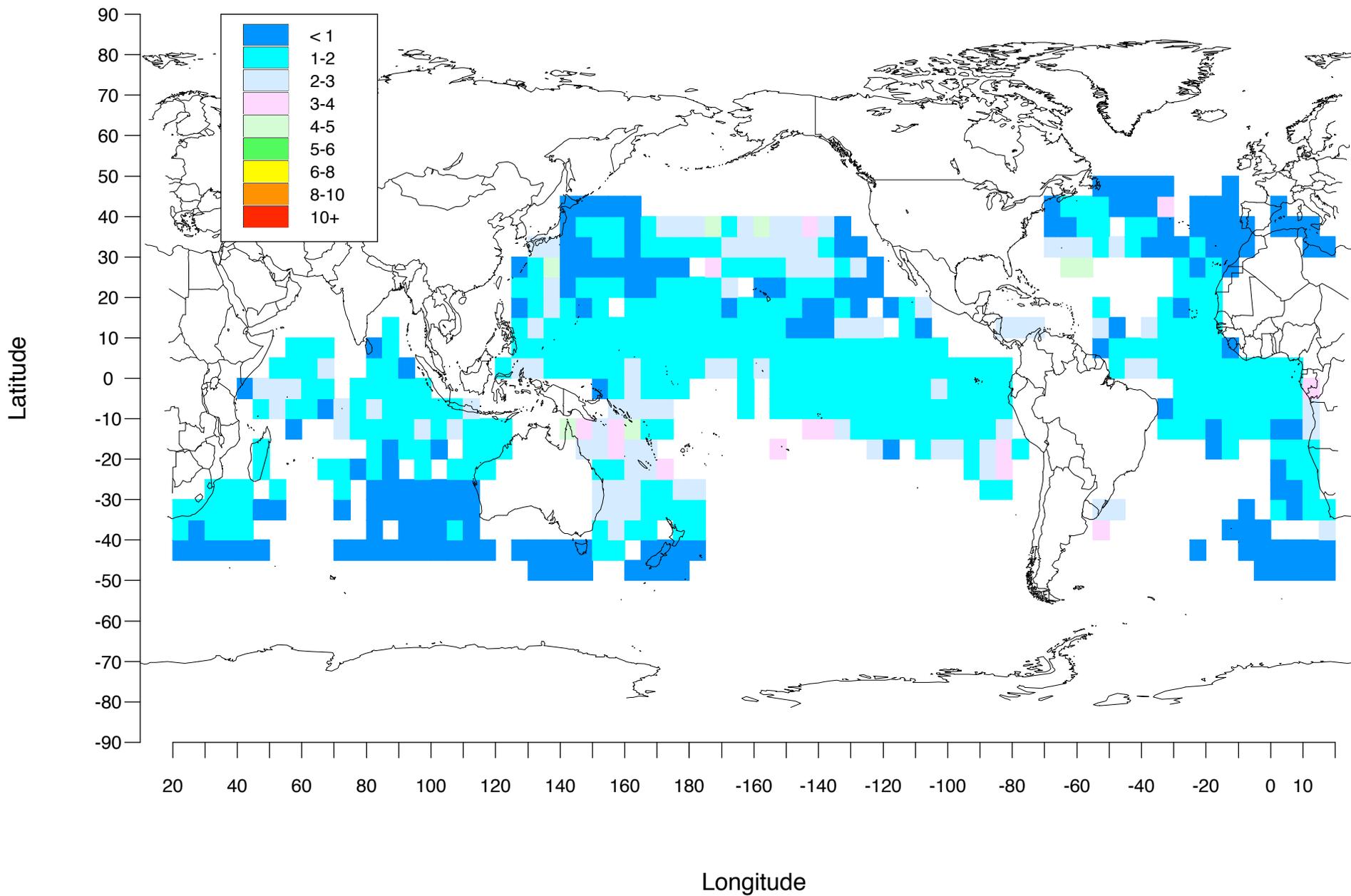
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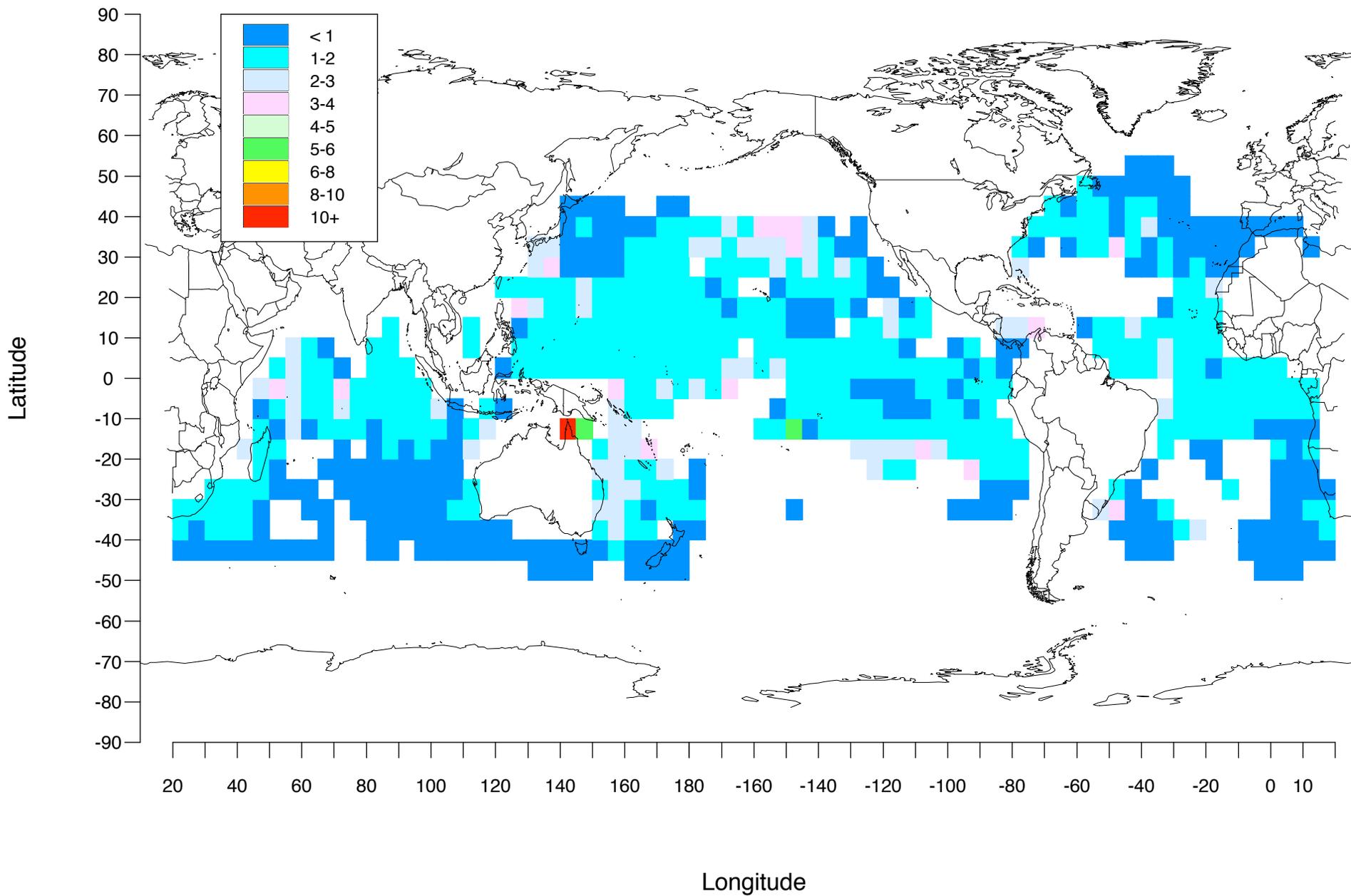
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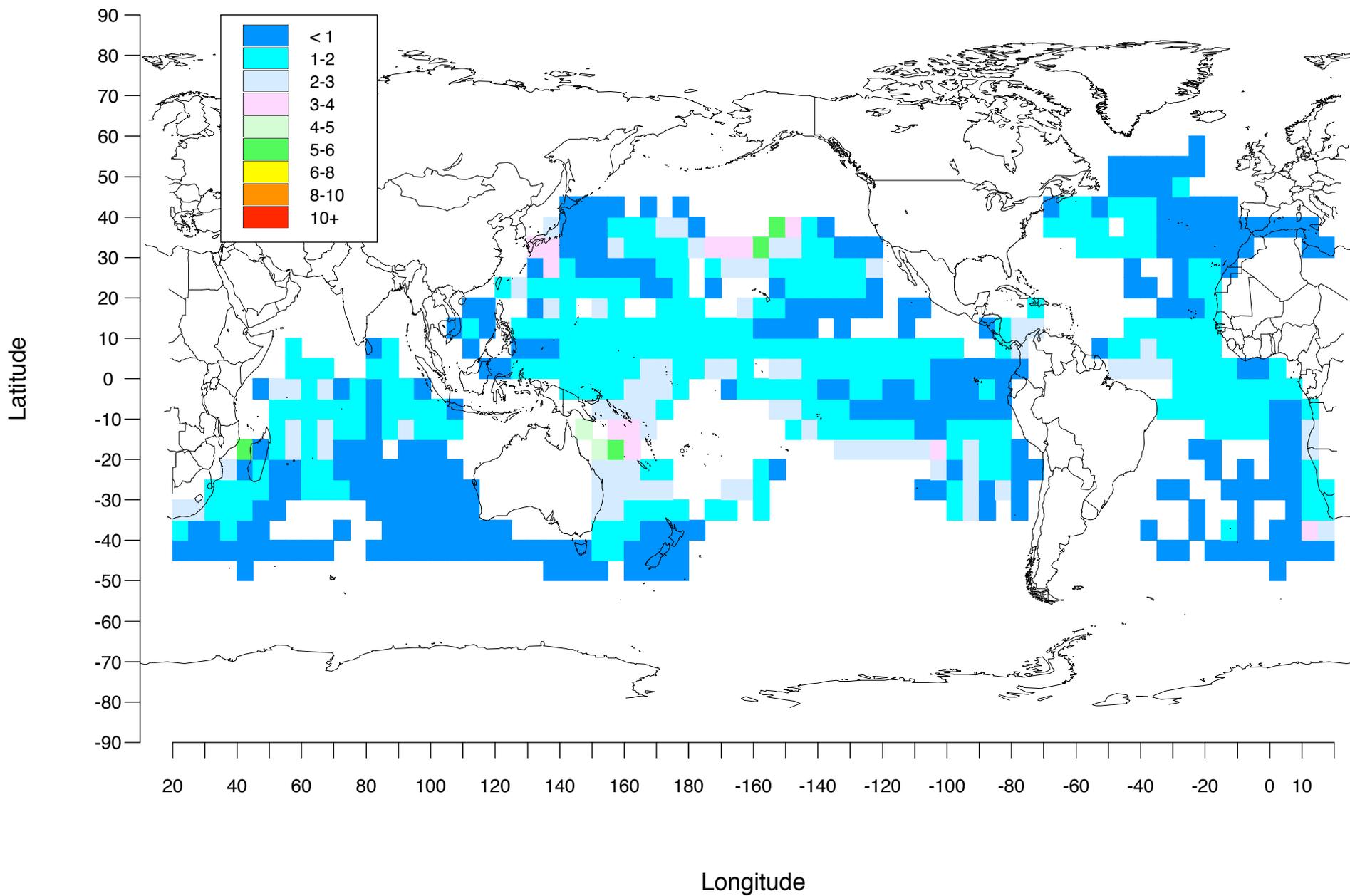
Catch Per Hundred Hooks, Year = 1990



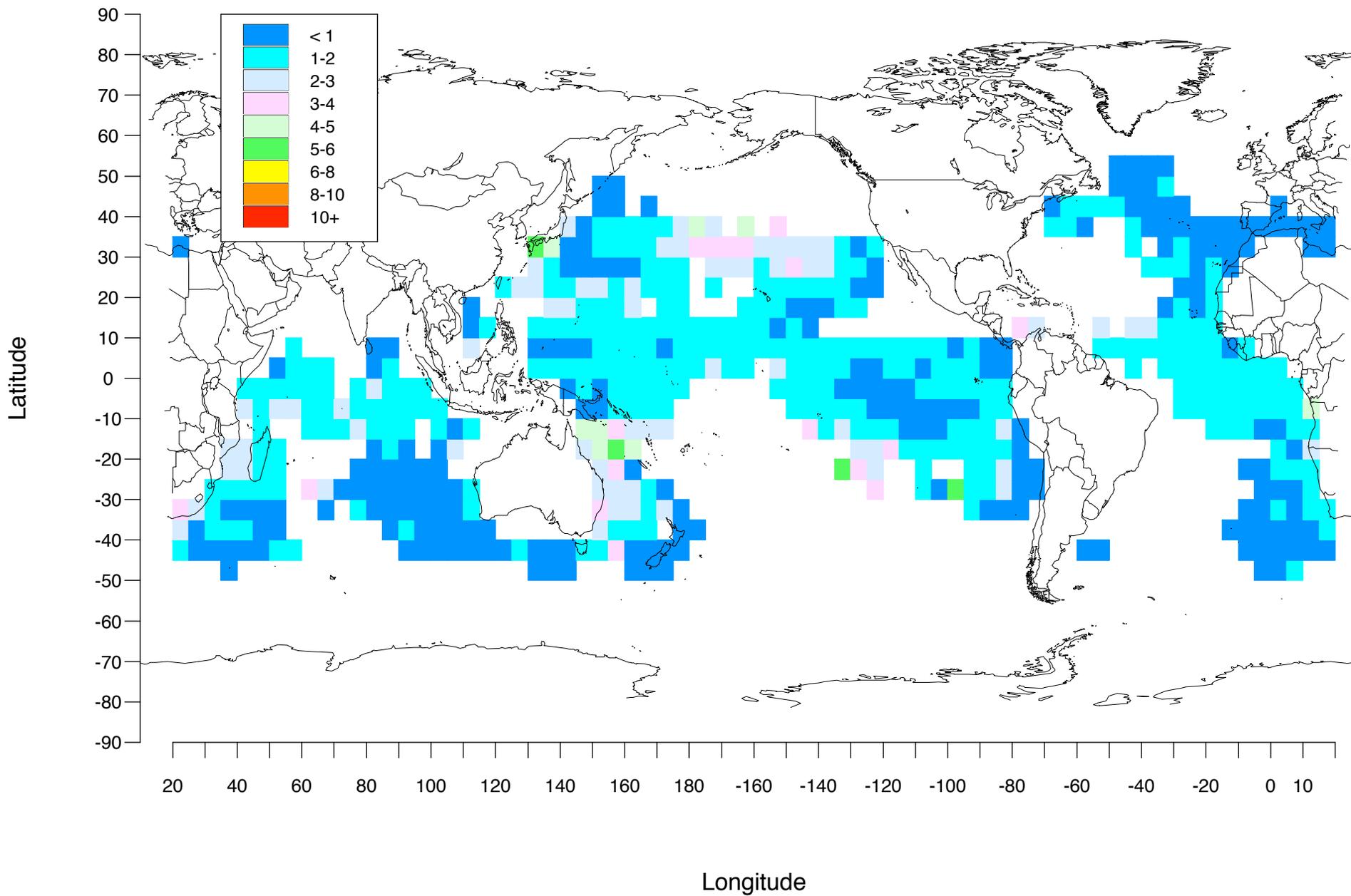
Catch Per Hundred Hooks, Year = 1991



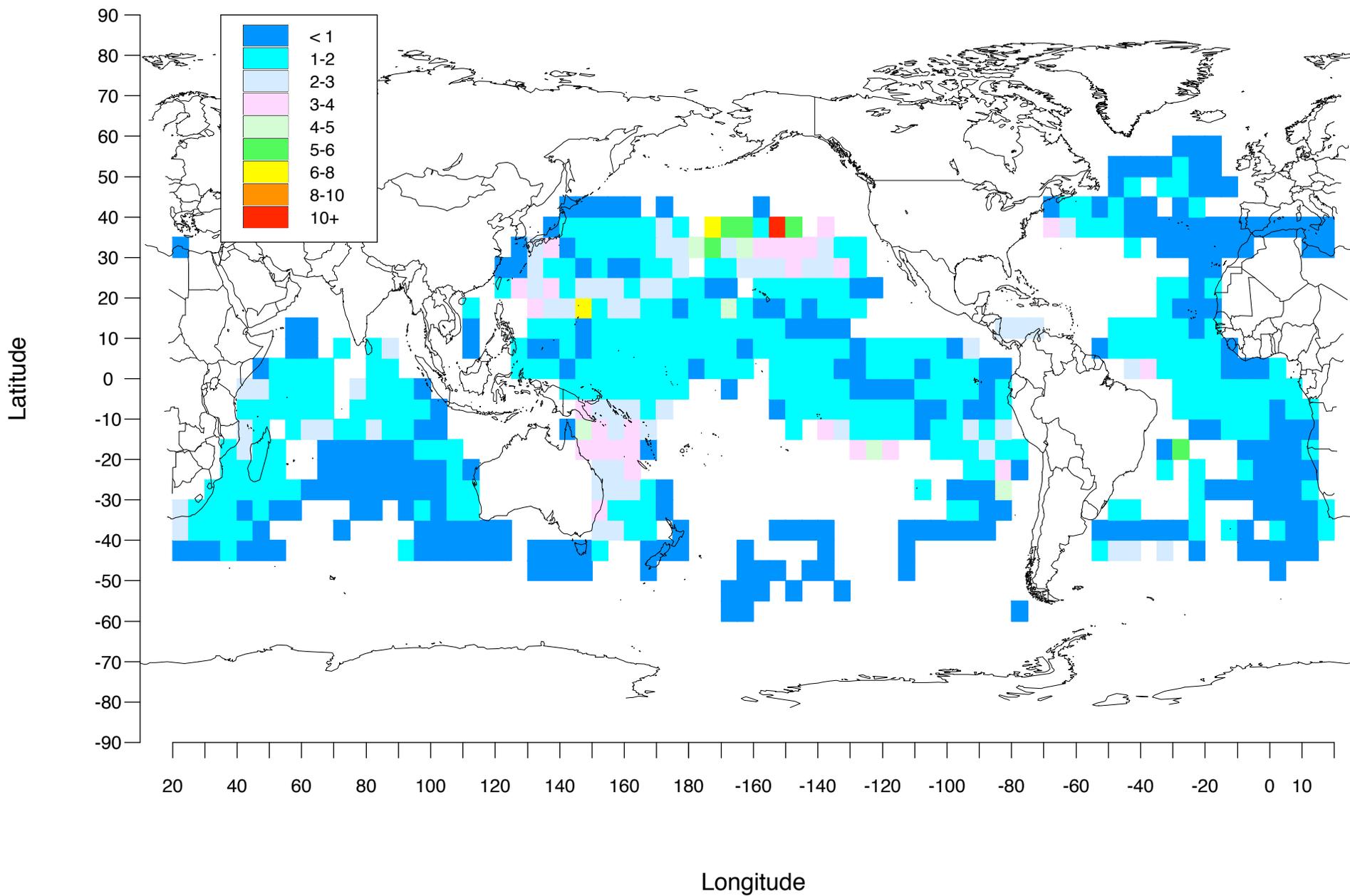
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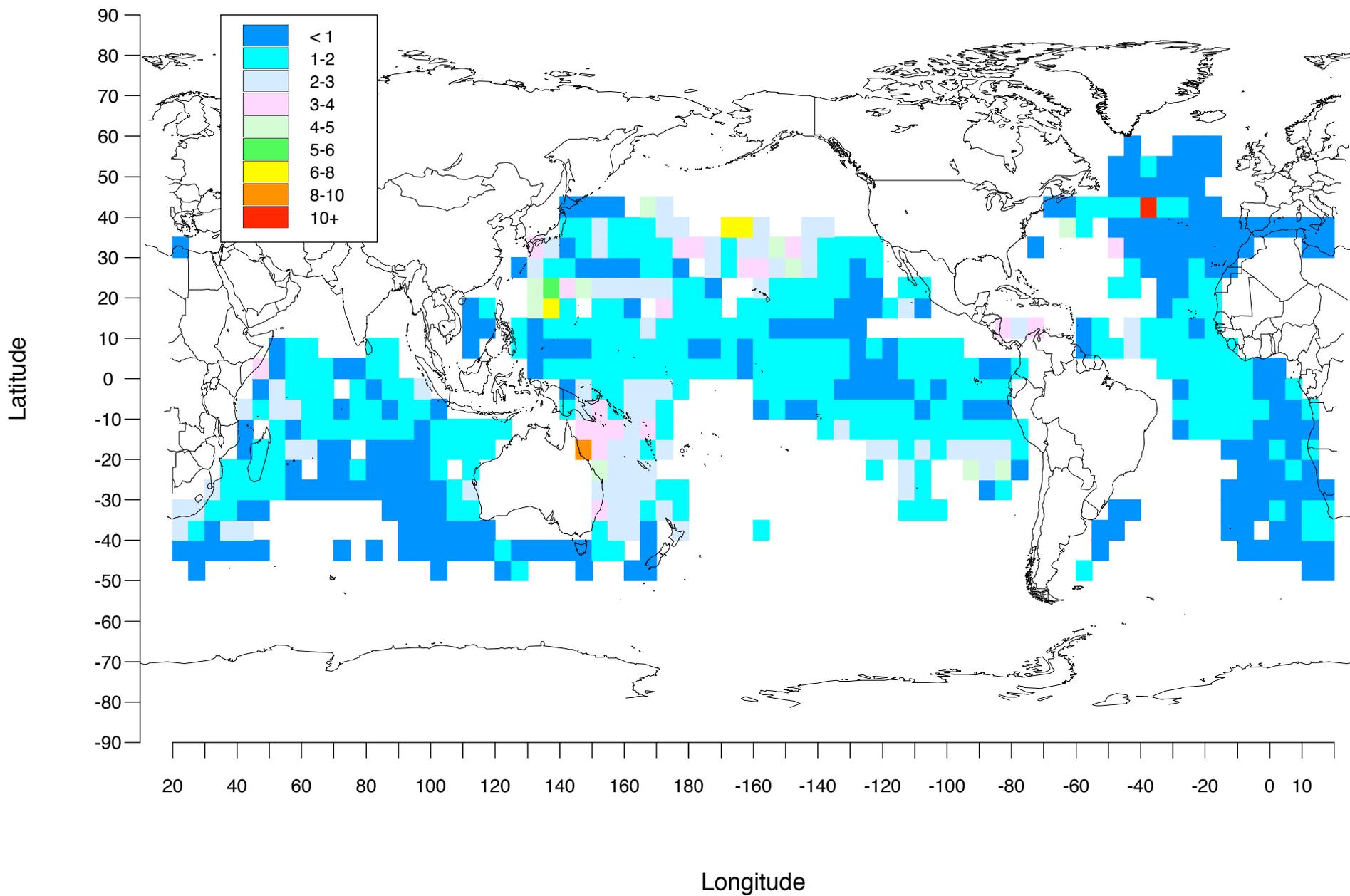
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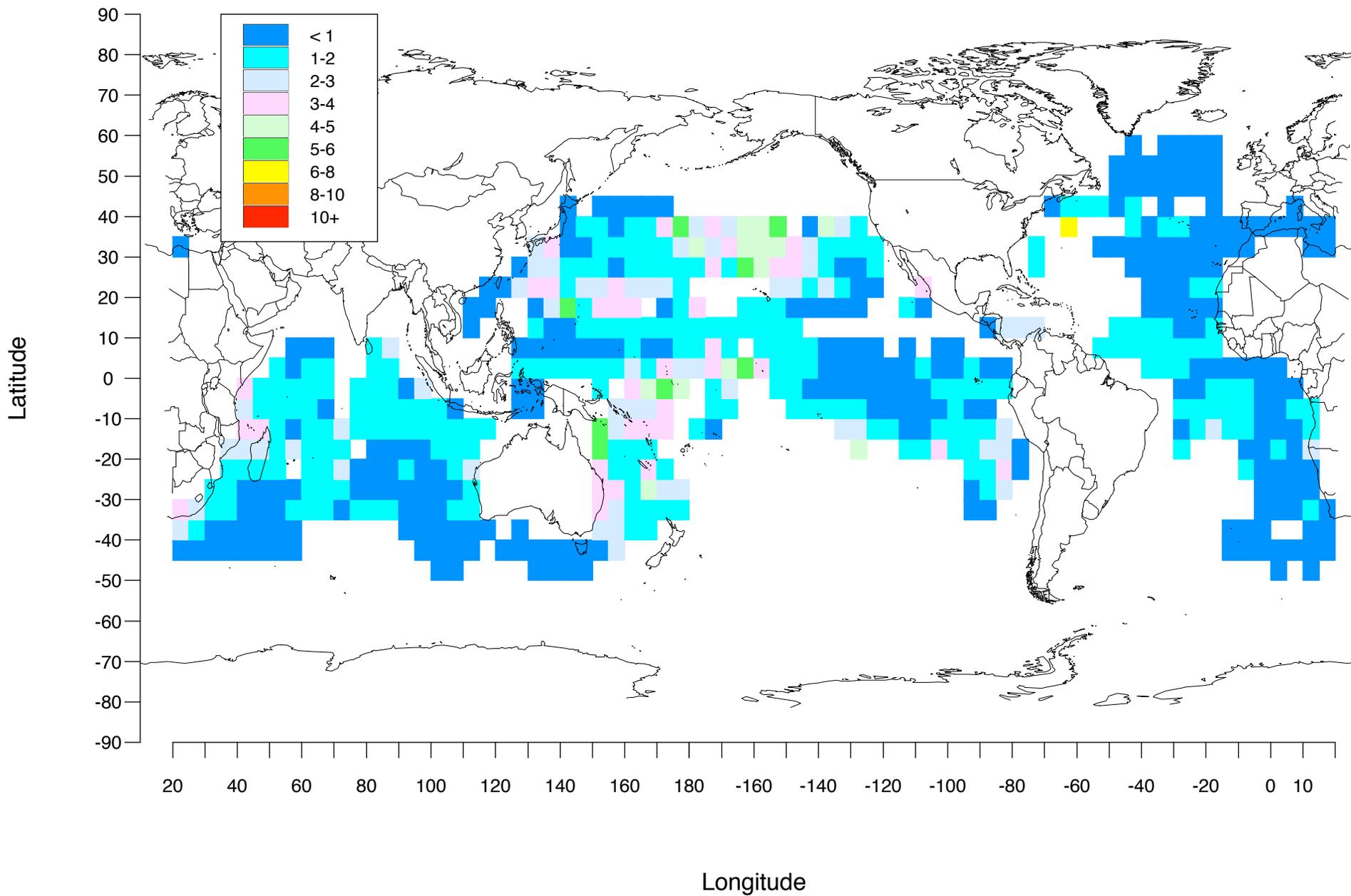
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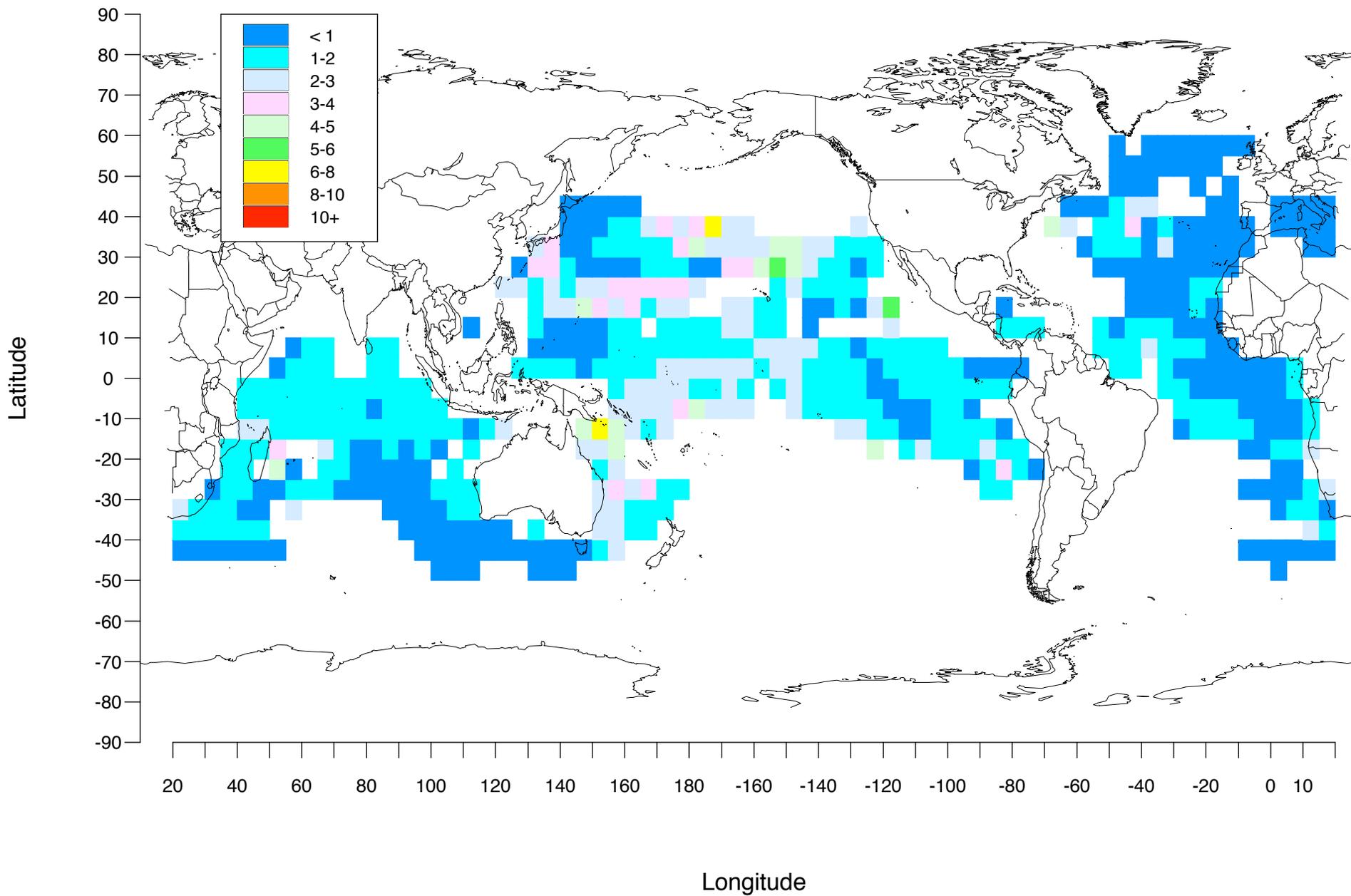
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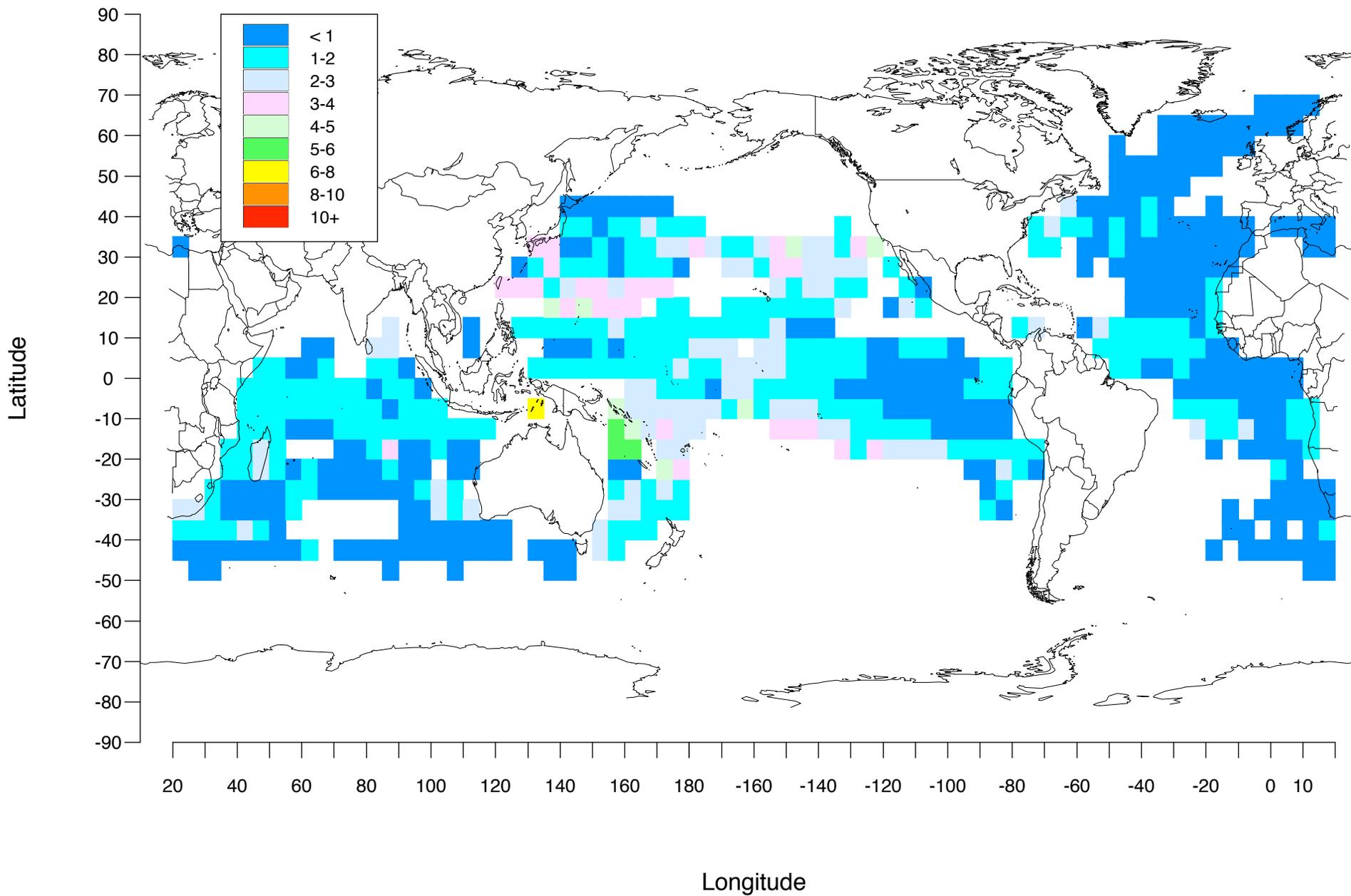
Catch Per Hundred Hooks, Year = 1996



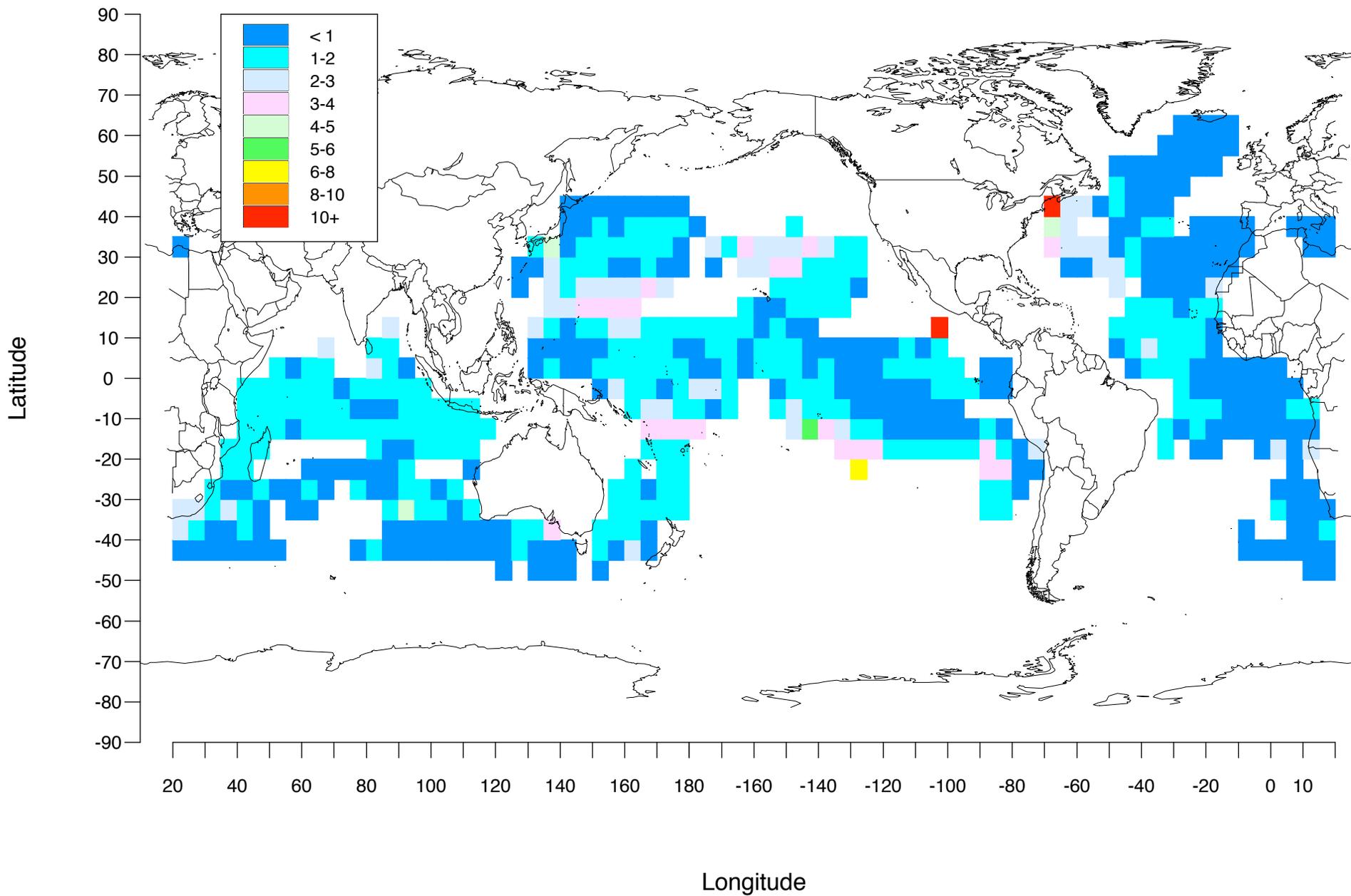
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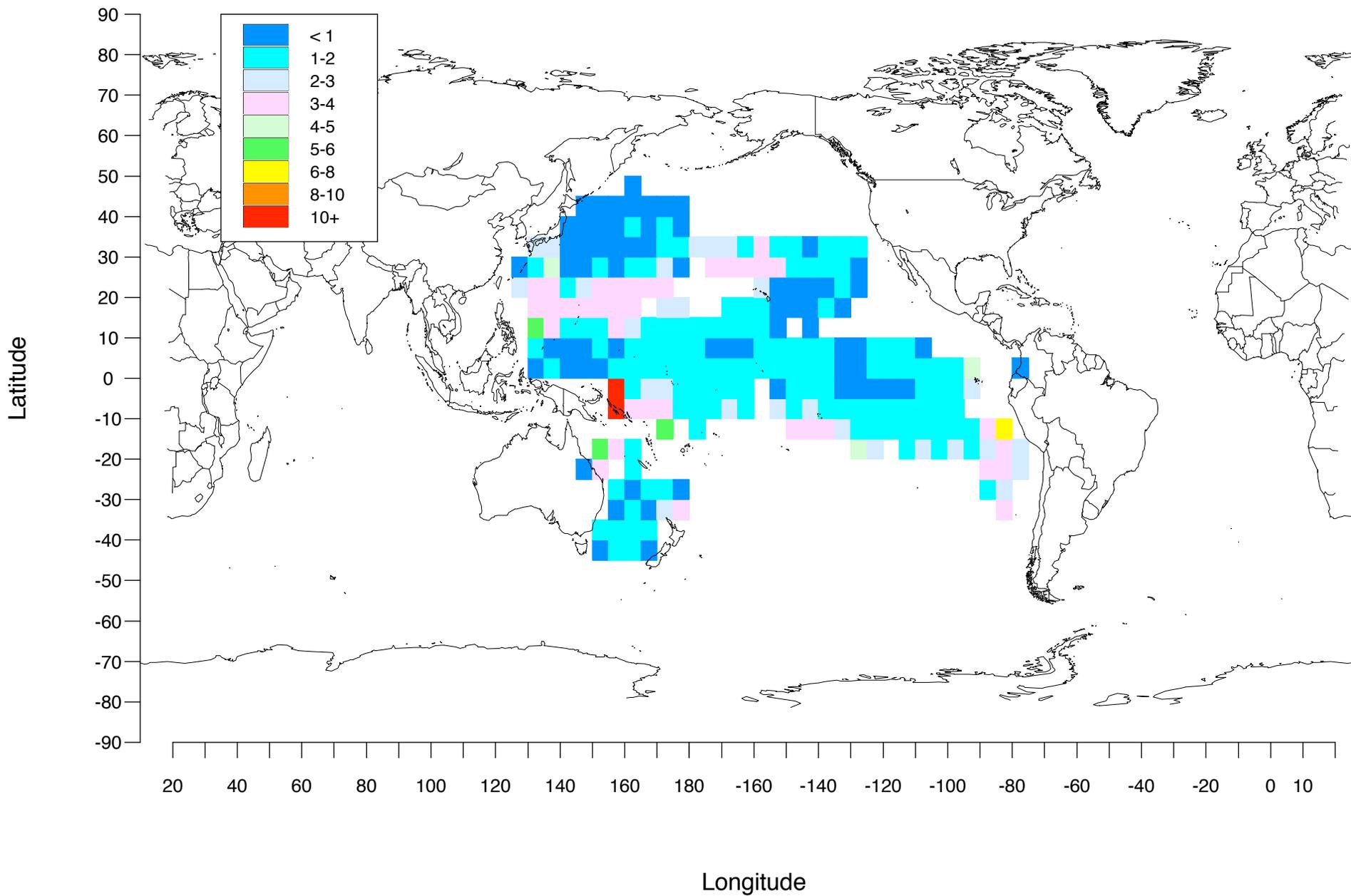
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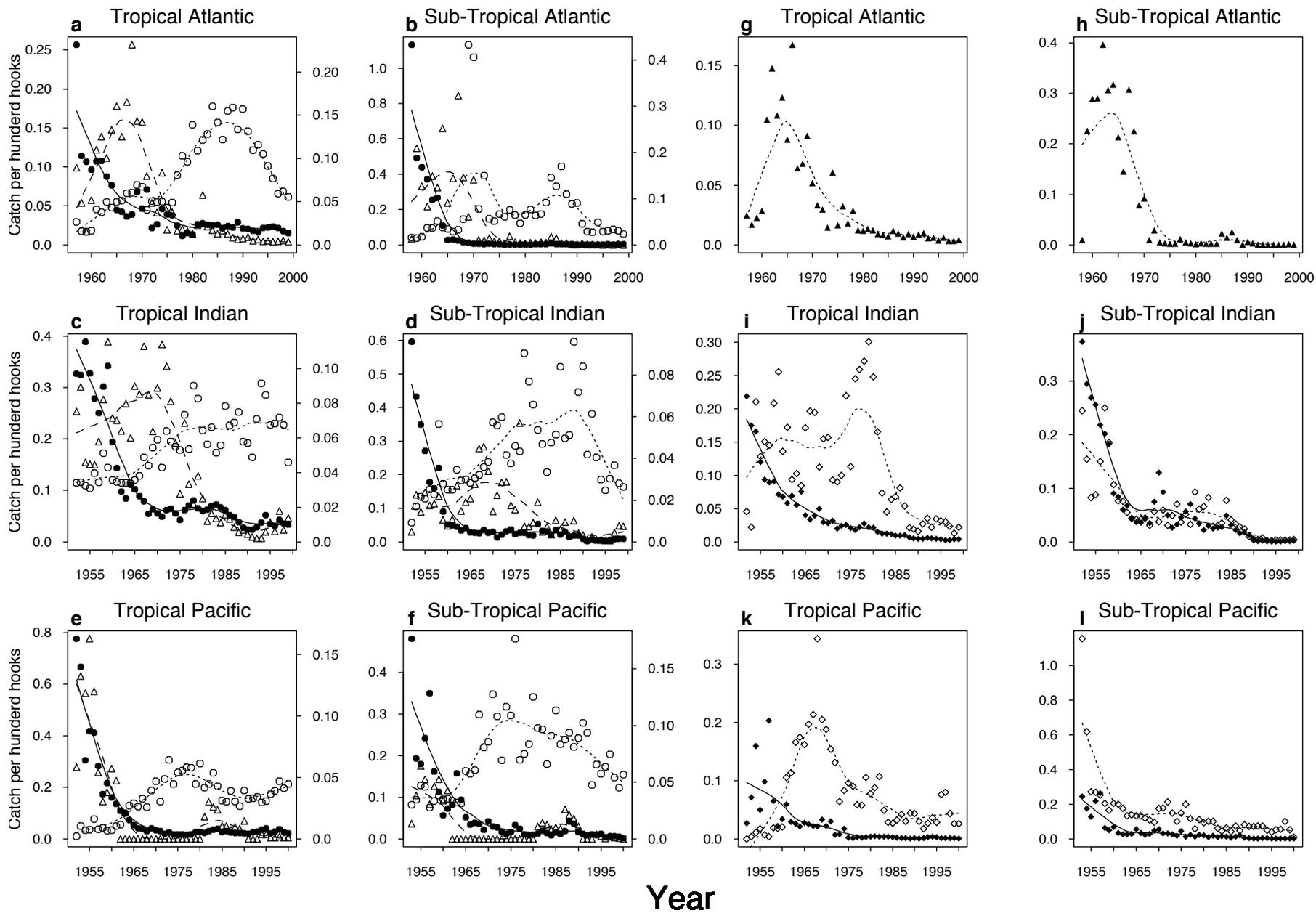


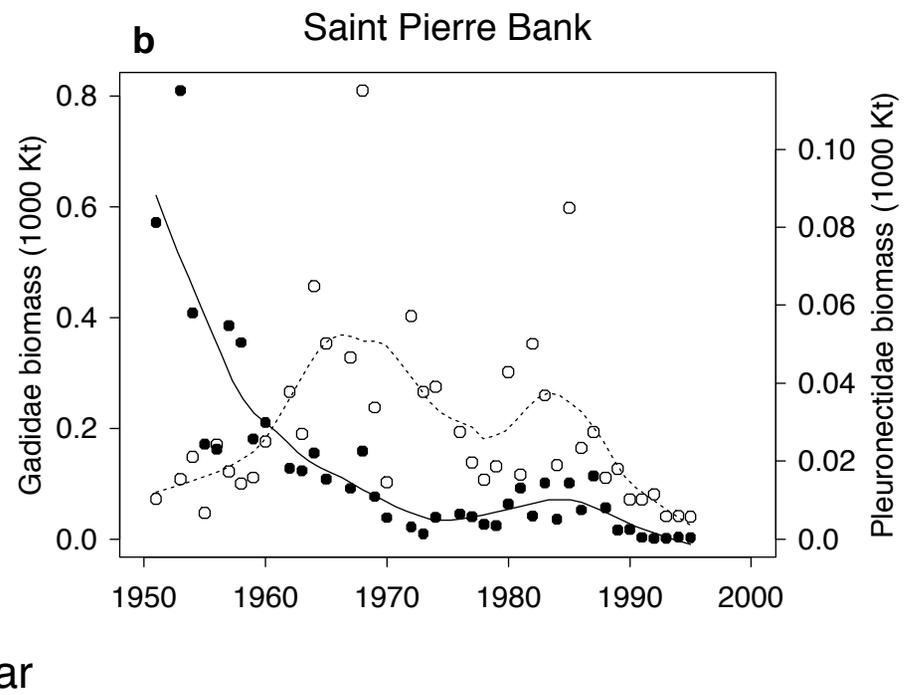
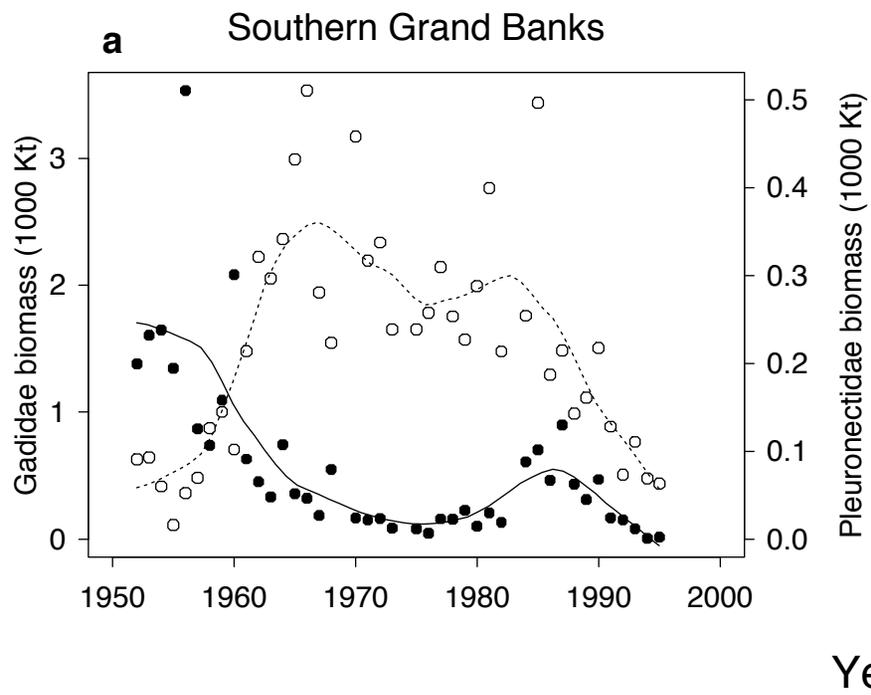
Catch Per Hundred Hooks, Year = 1999



Catch Per Hundred Hooks, Year = 2000







Rapid worldwide depletion of predatory fish communities

Ransom A. Myers & Boris Worm

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 abundance¹. 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 structure³⁻⁵. The only clear cases where the magnitude of the CPUE trends are not reconcilable with age-structured models concern yellowfin tuna⁶, 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 gear⁶, 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 abundance⁶.

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 marlin¹². However, recent work has shown that this objection is not valid because of the unusual pattern of growth of the marlins⁵.

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 tuna¹³. 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 targeted²⁰ and bycatch fisheries²¹. 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 areas²². 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 statistics²⁵), 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 Atlantic²⁶. 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		
		Pacific	Indian	Atlantic
Japanese longlining				
Albacore tuna	<i>Thunnus alalunga</i>	Y	Y	Y
Atlantic blue marlin	<i>Makaira nigricans</i>			Y
Atlantic bluefin tuna	<i>Thunnus thynnus</i>			Y
Bigeye tuna	<i>Thunnus obesus</i>	Y	Y	Y
Black marlin	<i>Makaira indica</i>	Y	Y	Y
Broadbill swordfish	<i>Xiphias gladius</i>	Y	Y	Y
Indo-Pacific blue marlin	<i>Makaira mazara</i>	Y	Y	
Longbill spearfish	<i>Tetrapturus pfluegeri</i>			Y
Pacific bluefin tuna	<i>Thunnus orientalis</i>	Y		
Sailfish	<i>Istiophorus platypterus</i>	Y	Y	Y
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	Y	Y	
Skipjack tuna	<i>Katsuwonus pelamis</i>	Y	Y	Y
Southern bluefin tuna	<i>Thunnus maccoyii</i>	Y	Y	Y
Striped marlin	<i>Tetrapturus audax</i>	Y	Y	
White marlin	<i>Tetrapturus albidus</i>			Y
Yellowfin tuna	<i>Thunnus albacares</i>	Y	Y	Y
Gulf of Thailand trawl survey				
Bigeye	<i>Priacanthus</i> sp.		Y	
Cutlassfishes	Trichiuridae		Y	
Drums and croakers	Sciaenidae		Y	
Emperors	Lethrinidae		Y	
False trevally	<i>Lactarius lactarius</i>		Y	
Goatfishes	Mullidae		Y	
Groupers	Serranidae		Y	
Grunts	<i>Pomadasys</i> sp.		Y	
Indian spiny turbot	<i>Psettodes erumei</i>		Y	
Jacks and pompanos	Carangidae		Y	
Lizardfish	<i>Saurida</i> sp.		Y	
Pike conger	<i>Muraenesox</i> sp.		Y	
Rays	Rajidae		Y	
Sea catfishes	Ariidae		Y	
Sharks	Chondrichthyes		Y	
Snappers	Lutjanidae		Y	
Sweetlips	<i>Plectorhinchus</i> sp.		Y	
South Georgia trawl survey				
Green notothenia	<i>Gobionotothen gibberifrons</i>		Y	
Mackerel icefish	<i>Champscephalus gunnari</i>		Y	

Marbled notothenia	<i>Notothenia rossii</i>		Y
Scotia Sea icefish	<i>Champscephalus aceratus</i>		Y
South Georgia icefish	<i>Pseudochaenichthys georgianus</i>		Y
NW Atlantic trawl surveys			
		Grand Banks	St. Pierre Bank
American plaice	<i>Hippoglossoides platessoides</i>	Y	Y
Atlantic Cod	<i>Gadus morhua</i>	Y	Y
Atlantic halibut	<i>Hippoglossus hippoglossus</i>	Y	Y
Barndoor skate	<i>Raja laevis</i>	Y	Y
Broadhead wolffish	<i>Anarhichas denticulatus</i>	Y	Y
Haddock	<i>Melanogrammus aeglefinus</i>	Y	Y
Longfin Hake	<i>Urophycis chesteri</i>	Y	Y
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>	Y	Y
Mailed sculpin	<i>Triglops sp.</i>	Y	
Marlin-spike	<i>Nezumia bairdi</i>		Y
Monkfish	<i>Lophius americanus</i>	Y	Y
Pollock	<i>Pollachius virens</i>		Y
Redfish	<i>Sebastes sp.</i>	Y	Y
Sea raven	<i>Hemitripterus americanus</i>	Y	Y
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>	Y	Y
Silver hake	<i>Merluccius bilinearis</i>	Y	Y
Smooth skate	<i>Raja senta</i>	Y	Y
Spotted wolffish	<i>Anarhichas minor</i>	Y	Y
Striped wolffish	<i>Anarhichas lupus</i>	Y	Y
Thorny skate	<i>Raja radiata</i>	Y	Y
White hake	<i>Urophycis tenuis</i>	Y	Y
Winter skate	<i>Raja ocellata</i>		Y
Witch flounder	<i>Glyptocephalus cynoglossus</i>	Y	Y
Yellowtail flounder	<i>Limanda ferruginea</i>	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 line in **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 species²⁸. 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.