Mangroves support an estimated annual abundance of over 700 billion juvenile fish and invertebrates

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Mangroves are a critical habitat that provide a suite of ecosystem services and support livelihoods. Here we undertook a global analysis to model the density and abundance of 37 commercially important juvenile fish and juvenile and resident invertebrates that are known to extensively use mangroves, by fitting expert-identified drivers of density to fish and invertebrate density data from published field studies. The numerical model predicted high densities throughout parts of Southeast and South Asia, the northern coast of South America, the Red Sea, and the Caribbean and Central America. Application of our model globally estimates that mangroves support an annual abundance of over 700 billion juvenile fish and invertebrates. While abundance at the early life-history stage does not directly equate to potential economic or biomass gains, this estimate indicates the critical role of mangroves globally in supporting fish and fisheries, and further builds the case for their conservation and restoration.

Food from the marine and coastal environment is a crucial source of protein and micronutrients for billions of people[1,2]. As the global human population and its requirement for food continues to increase, pressure for the marine and coastal environment to supply greater amounts of seafood will also increase[3,4]. In addition, marine fisheries support livelihoods for an estimated 260 million people, particularly in the Global South[5,6]. The production of marine and coastal food as well as the livelihoods supported are intrinsically linked to the condition of the environment, with healthy fish stocks dependent on the effective ecological functioning of freshwater, coastal and marine ecosystems[7]. Marine and coastal food production is therefore highly vulnerable to human driven environmental disturbance[7], including over-harvesting, which has already driven losses in productivity and the collapse

of some fisheries[8,9]. Coastal ecosystems have been highlighted as a critical driver of marine fisheries productivity[10]. In the face of widespread loss and degradation of these ecosystems, quantifying their role in marine fish and invertebrate production is key to help inform and support actions to sustainably manage these resources[11].

Mangrove forests are complex and highly productive ecosystems, thriving in sheltered intertidal areas of tropical, subtropical, and warm temperate coasts worldwide[12]. Their location, productivity, and structure provide critical habitat for several finfish and shellfish species, giving shelter, food, solid structure for settlement, and critical nursery grounds[13,14]. For millennia they have supported human communities who fished and foraged in their waters, and today there are an estimated 4.1 million mangrove-

associated fishers globally[15]. In addition to small-scale fisheries, mangrove-associated fisheries include some valuable export fisheries, notably of shrimp[16] and crab species[17]. Across all fishery sectors, the importance of these fisheries is likely to grow in times of stress such as financial, social or economic instability, or particular environmental or climatic impacts[18]. Well managed mangroves can support a relatively reliable and secure food supply enabling an important adaptive capacity for coastal communities. These fisheries benefits stand alongside other well-documented benefits such as carbon storage and sequestration[19], protecting coastlines from storms and flooding[20] and as habitat for birds, bats and other terrestrial species[21].

Studies have focused on the role of mangrove seascapes in enhancing fisheries[22] and the contribution of mangrove productivity to fish and shellfish biomass production[23]. Others have considered the role of mangroves in enhancing settlement and growth or hosting key life-history stages of individual species[24]. Despite these factors, there has been no attempt to derive a holistic global picture of fish/shellfish production associated with the world's mangrove forests[25]. Here, we produce a global analysis of the importance of mangroves to the density and abundance of commercially important fish and invertebrates that are known to utilise mangrove ecosystems extensively. This analysis gathered existing field data on the density of commercially important juvenile fish, and juvenile and resident invertebrates of those species in mangrove areas, and used the Delphi technique[26] to identify and weight expert knowledge on the biophysical drivers of the density of 37 mangrove-associated commercially exploited marine species[27], including species of fish, prawns, crabs and a bivalve. Geospatial data layers that describe the biophysical drivers were used to map the estimated density of each species for all locations where mangroves occur, and calculate the abundance associated with the world's mangrove forests. To evaluate the importance of mangrove fisheries for subsistence and income for local livelihoods, the correspondence between our fish and invertebrate abundance estimates and the number of mangrove small-scale fishers is assessed.

Results and discussion
Drivers of mangrove fish and invertebrate density
A literature search and expert elicitation resulted in 481 field measurements of juvenile fish, and juvenile and resident invertebrate density (standardized to individuals $100 \, m^{-2}$), across 37 commercially important mangrove-affiliated species (Supplementary Table 1). The included species were identified as being mangrove-affiliated and commercially important by zu Ermgassen et al.[27]. While many of these species have wide distributions, field data was geographically biased towards the Americas and to a lesser extent Asia and the east coast of Australia, with limited data from southern and East Africa and the Middle East, and none for West Africa (Supplementary Fig. 1a).

The 481 field measurements of juvenile fish and juvenile and resident invertebrate density were modelled against 12 environmental covariates (Table 1), with the covariates identified through an expert-driven Delphi approach[26]. The model structure was determined based on automated model selection[28], with the final model identified by averaging the top 30 candidate models. The top 30 candidate models fitted the data well, with R^2 values ranging between 71.6% and 72.4%. The final model contained the environmental variables, mangrove area (AREA), sea surface salinity (SSS), sea surface temperature (SST), tidal amplitude (TIDAL), edge length (EDGE), change in extent (CHANGE), and net primary productivity (NPP), as well as the categorical variables for geomorphic type (C_k), sampling method (G_j), and species (A_i) (Eq. 1; coefficient estimates available in Supplementary Table 2).

$$\begin{aligned} \log(\text{density}) = &\alpha + (\beta_1 * \text{AREA}) + (\beta_2 * \text{SSS}) + (\beta_3 * \text{SSS}^2) + (\beta_4 * \text{SST}) \\ &+ (\beta_5 * \text{SST}^2) + (\beta_6 * \text{TIDAL}) + (\beta_7 * \text{EDGE}) \\ &+ (\beta_8 * \text{CHANGE}) + (\beta_9 * \text{NPP}) + A_i + G_j + C_k \end{aligned} \quad (1)$$

The model predicted higher densities (individuals $100 \, m^{-2}$) of juvenile fish and juvenile and resident invertebrates with increasing sea surface salinity, tidal amplitude, net primary productivity, and in deltaic mangroves, with geomorphic setting having been identified as a key determinant of ecosystem function[29]. Based on the model, juvenile fish and juvenile and resident invertebrate densities were predicted to reduce with increasing mangrove area, sea surface temperature, edge length, and extent change. Mangrove edge length has been shown to be positively correlated with fish catches[22]; however, it was represented by a negative relationship in our model which may indicate a negative impact of mangrove fragmentation.

The model was then extrapolated over a grid which consisted of cells with a spatial resolution of $1 \, km^2$ and encompassed the entire global distribution of mangroves in 2020[30]. Each grid cell had values for the 12 environmental covariates, while the values for sampling method and species were set to the reference categories. As such, the output represents the mangrove productivity potential based on biophysical factors and before accounting for variation between different species and their distributions. Linear model fits are typically expressed as values for a reference class, plus deviations from that reference model for other classes. The choice of reference model is arbitrary and does not change the resulting fit. The model predicted high densities of fish and invertebrates throughout parts of Southeast and South Asia, large extents of the northern coast of South America, the Red Sea, and parts of the Caribbean and Central America (Fig. 1). Lower densities of fish and invertebrates were predicted for much of the coast of east Asia, West and Southeast Africa and the coast of Australia (Fig. 1).

Regional patterns of mangrove fish and invertebrate density
The initial model was then predicted across the spatial grid using the species-specific density coefficients. To assure that the model did not predict species' densities outside their native ranges, we used Aquamaps[31] to constrain the predictions. However, it should be noted that the species-specific models extend to the full range of the 37 species, often far beyond the location of the field data from the literature. In addition, there is an uneven number of species per grid cell in different regions (Supplementary Fig. 1b–e). The greatest number of fish species was centred on south and central America and the Caribbean, with up to 26 species represented in some areas. Data on bivalves were limited to species of mangrove cockle *Anadara tuberculosa*, which are confined to the Pacific coast of the Americas, and as such our analysis does not include other commercially important and widely harvested bivalve species, e.g., *A. similis*, *Crassostrea* spp. and *Geloina* spp. In any one location there were up to two species of commercially important crabs, with richness centred in the Indian Ocean, while a maximum three species of penaeid prawns were distributed across the Indo-Pacific. However, no crustaceans could be modelled for the Atlantic-Eastern Pacific region.

The predicted densities of juvenile fish and juvenile and resident invertebrates ranged from 0.08 to 5971 individuals $100 \, m^{-2}$. These maps illustrate broad patterns in the predicted density of commercially important fish and invertebrates in mangroves globally, and heterogeneity in density estimates both within and between regions. They are useful for examining density patterns within regions (see below), but are not appropriate for making large inter-regional comparisons because they are based on combined species totals and there is considerable spatial variation in the numbers of species modelled at any given location.

Along the Atlantic coasts of the Americas where our models have the greatest richness of commercially exploited finfish species ($n = 26$), densities at the national level were highest for some islands of the Caribbean such as Sint Maarten (111 individuals $100 \, m^{-2}$, 95% CI: 49–278), as well as Venezuela (285 individuals $100 \, m^{-2}$, 95% CI: 90–944) and Brazil (190 individuals $100 \, m^{-2}$, 95% CI: 58–654) (Fig. 2a). Geomorphic setting is considered a key factor structuring mangrove fish assemblages across the Americas (G.A. Castellanos-Galindo pers. comm.) and in this region hotspots of finfish density include the extensive mangrove coastline of Brazil to the east of the Amazon, the Orinoco Delta, Venezuela, as well as the deltaic and lagoonal Caribbean coasts of Colombia (Ciénaga Grande de Santa Marta) and Mexico, all with commercial finfish densities over 400 individuals $100 \, m^{-2}$

Table 1 | The environmental covariates included in the global model of mangrove-affiliated fish and invertebrate densities

Variable	Rationale	Data Resolution	Model Fitting Data	Model Prediction Data	Refs.
Geomorphic Type	Coastal geomorphology is a key factor that structures the relationship between habitat and coastal fish communities[87]. For example, coastal mangroves and estuarine mangroves support a different suite and abundance of tropical prawn species[88]. Globally, mangrove areas have been assigned to a geomorphic class – deltaic, estuarine, lagoonal and open coast[72].	NA	1996, 2007–2010 and 2015–2020	1996 to 2020 Composite	72,73
Change in Extent	Mangrove forest habitat degradation can result in lower fish catch rates[36].	NA	Static Value	Static Value	30,63
Mangrove Area	Areal extent of mangroves is known to positively impact the abundance of mangrove-associated fish and invertebrate species across a range of geographies[89–91].	25 m	1996, 2007–2010 and 2015–2020	2020	30,63
Edge Length	Mangrove edge habitats are often found to harbour higher densities of fish than sites within mangroves and therefore likely play a disproportionately important role in total fish abundance[92,93].	25 m	1996, 2007–2010 and 2015–2020	2020	30,63
Tidal Amplitude	The amount of intertidal habitat available, which is a function in part of the tidal amplitude, is an important factor in explaining tropical prawn abundance[94].	~7 km²	Static Value	Static Value	80
Coastal Embayment Area	The size of the estuary associated with mangroves has been found to influence the abundance of fish and prawns.	NA	Static Value	Static Value	72
Fishing Pressure	Fish species richness and abundance is lower in areas with high fishing pressure[95].	1 km²	Static Value	Static Value	82
Proximity to Seagrass	Fish have been shown to utilise mangrove habitats near seagrass beds when the tide allows. There is therefore a positive synergistic effect between seagrasses and mangroves across the tidal cycle where they co-occur[96–98].	No data			
Duration of Inundation	Mangrove areas that are underwater for longer periods provide habitat to fish and aquatic invertebrate species for a greater proportion of the day[99].	No data			
Sea Surface Salinity	Sea surface salinity is often used in modelling large scale fish abundance[100,101].	25 km²	2011–2020	2020	74
Sea Surface Temperature	Sea surface temperature is commonly considered in large scale fisheries modelling as an important variable explaining fish abundance[102,103].	~5.55 km²	2001–2020	2020	75,76
Net Primary Productivity	Primary productivity explains variability in fish production in global and tropical seas[102,104].	~18 km²	2002–2002	2020	77,78

The environmental covariates were represented by two types, firstly variables whose value did not change over the period of the fisheries data (denoted by 'Static Value'), and secondly time series variables whose value could be more closely attributed to an individual fisheries survey year (denoted by the years of the available data).
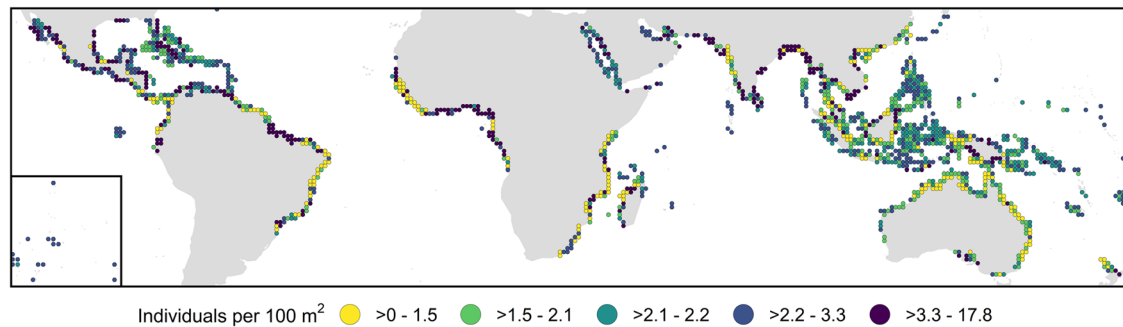
Fig. 1 | The density model output (individuals 100 m⁻²). Derived from the variables in Eq. 1: mangrove area, sea surface salinity, sea surface temperature, tidal amplitude, mangrove edge, change in extent, net primary productivity, and the categorical variables for sampling method (G_j) and mangrove geomorphic type (C_k). This output was visualised prior to applying individual species-specific density coefficients and their presence/absence, and as such represents the reference species group. Data summarised as the median value within 1° cells. Inset shows central Pacific islands including mangrove holding countries in Polynesia, Micronesia and Melanesia.
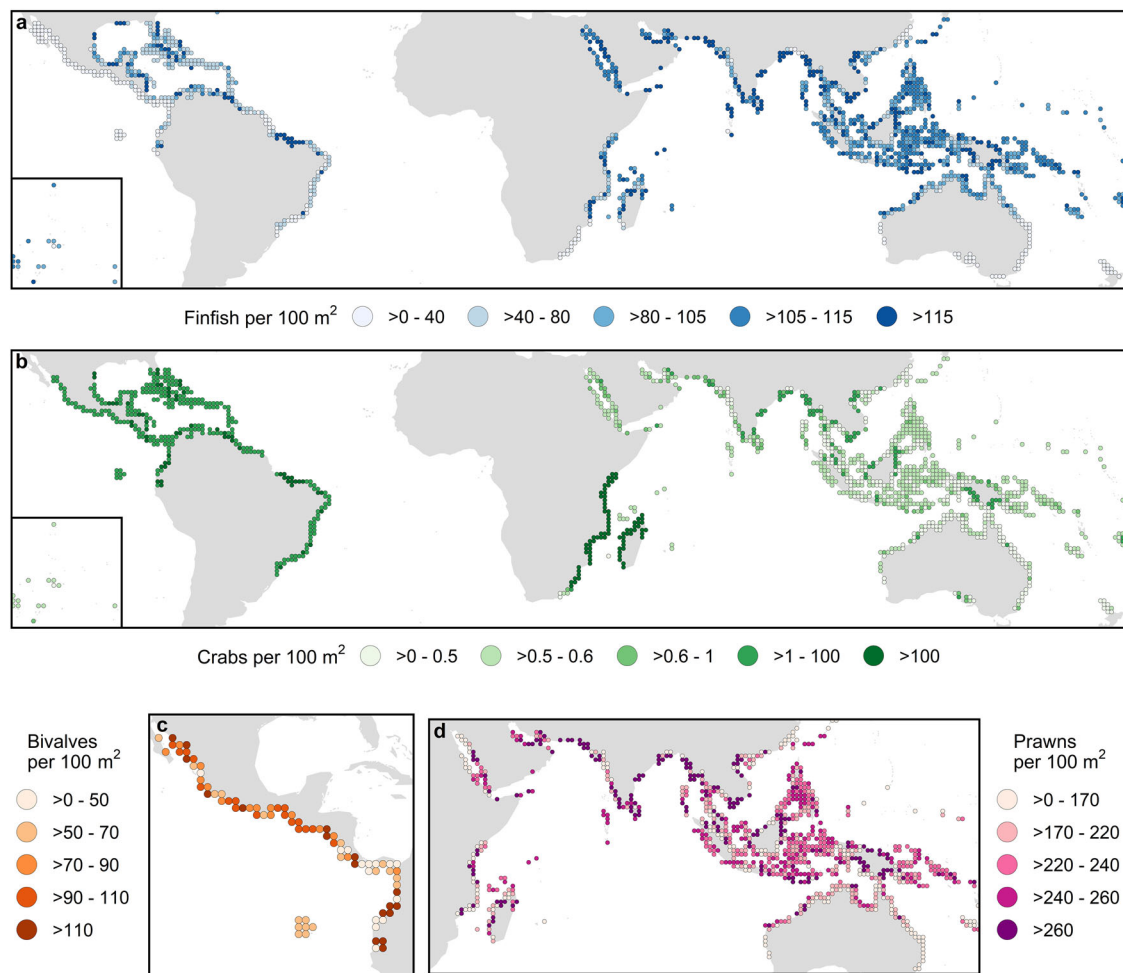
Fig. 2 | The modelled density of commercially important fish and invertebrate species due to the presence of mangrove ecosystems. Species grouped into **a** finfishes (n = 29), **b** crabs (n = 4), **c** bivalves (n = 1), and **d** prawns (n = 3). Although some species ranges also include West and Central Africa, predictions were removed for that region due to the lack of field data to inform the modelling process. Data summarised as the median value within 1° cells. Inset on (**a**, **b**) shows central Pacific islands including mangrove holding countries in Polynesia, Micronesia and Melanesia.

(Fig. 2a). The model's findings align with other observations that deltaic areas are characterised by high mangrove biomass and productivity[32], and that within South America they represent critical areas of finfish abundance supporting local artisanal fisheries[33–35].

Across the Indo-Pacific region there is a relatively even coverage of modelled finfish species and we see high predicted densities throughout the Red Sea and the Persian Gulf, as well as for countries such as Myanmar (548 individuals 100 m⁻², 95% CI: 122–2515) and Viet Nam (510 individuals 100 m⁻², 95% CI: 113–2350) (Fig. 2a). Within this region, finer scale patterns emerge with the deltaic coasts of Borneo, southern Viet Nam, and the south coasts of New Guinea among the areas supporting more than 400 finfish, and over 500 prawns, per 100 m² of mangroves. Given the extensive

areas of mangroves in many of these countries, the estimated overall abundance of commercial species is correspondingly high, and some of these mangroves have already been predicted to have a critical role in supporting large numbers of small-scale mangrove-associated fishers[15]. Elsewhere, areas which have already lost substantial areas of mangroves, such as across Java and much of the Philippines, have likely also lost a large proportion of these benefits[36]. The high finfish densities in this region are supported by the presence of *Atherinomorus lacunosus*, a small schooling species that had the highest predicted densities of any commercial finfish species in our model.

For crabs, density is high and quite consistent across the Atlantic and Pacific coasts of the Americas, with the inclusion in our model of the two species from the genus *Ucides*, with the highest predicted densities in Venezuela (257 individuals 100 m^{-2}, 95% CI: 91–727), Brazil (198 individuals 100 m^{-2}, 95% CI: 70–563), Ecuador (151 individuals 100 m^{-2}, 95% CI: 23–985) and Colombia (145 individuals 100 m^{-2}, 95% CI: 37–687) (Fig. 2b). The two species, *U. cordatus* and *U. occidentalis*, are commercially, ecologically and culturally important and a key part of the diet for coastal communities in the region[37,38], with densities driven by factors such as tidal influence, mangrove condition and fishing pressure operating at a range of spatial scales[39,40]. By contrast, across the Indo-Pacific, crab density (species *Scylla serrata* and *Neosarmatium africanum*) appears to be highly heterogeneous and lower than in the Americas. High densities in the Western Indian Ocean, including Mozambique (927 individuals 100 m^{-2}, 95% CI: 209–4124), Tanzania (858 individuals 100 m^{-2}, 95% CI: 200–3713), Madagascar (815 individuals 100 m^{-2}, 95% CI: 189–3544), and Kenya (334 individuals 100 m^{-2}, 95% CI: 85–1320), are driven by the inclusion of an additional species in the model, *N. africanum*, that is restricted to this region (Supplementary Fig. 1c).

Three species of penaeid prawns were included, with ranges covering much of the Indo-Pacific (Supplementary Fig. 1d). Several studies have highlighted a correlation between the area or linear extent of mangrove habitat, as well as factors such as sea surface temperature and latitude, and the commercial catches of penaeid prawns, with mangroves acting as a nursery habitat for post-larval prawns[16,41,42]. Within the model the penaeid prawns were predicted to have some of the highest densities of any species. This high abundance coupled with a high market value means that penaeid prawns are an economically important mangrove-associated fisheries commodity[41]. High densities of prawns are modelled for South Asia (for example Pakistan (1378 individuals 100 m^{-2}, 95% CI: 260–7313) and India (658 individuals 100 m^{-2}, 95% CI: 123–3530)) and Southeast Asia (Myanmar (1169 individuals 100 m^{-2}, 95% CI: 220–6212) and Viet Nam (1127 individuals 100 m^{-2}, 95% CI: 212–5995)) (Fig. 2d), driven by the presence of all three species in the model. The species *Penaeus merguiensis* and *P. indicus* are highly dependent on mangrove ecosystems to complete their life history, being observed almost exclusively in mangrove creeks[16].

On the Pacific coasts of the Americas the model includes few finfish and no prawns (Supplementary Fig. 1). However, this region comprises the only bivalve species *Anadara tuberculosa* in our model. *A. tuberculosa* is distributed across ten countries of the Pacific seaboard of the Americas and showed the highest densities in Ecuador (284 individuals 100 m^{-2}, 95% CI: 96–838) and Costa Rica (141 individuals 100 m^{-2}, 95% CI: 48–416) (Fig. 2c), where they represented nearly 60% of the total density of individuals. *A. tuberculosa* is associated with the root system of red mangrove (*Rhizophora mangle*) and represents one of the commercially most important species in the region[43]. Other commercially important bivalve species, e.g., *A. similis*, *Crassostrea* spp. and *Geloina* spp. are widely harvested from mangroves around the world, but could not be incorporated into our model due to a lack of species specific density data.

The results highlight the role of mangroves in supporting a range of commercially important fish and invertebrate species; however, the underlying model contains some key assumptions and limitations. Firstly, as highlighted above, the distribution of field density data was geographically biased (Supplementary Fig. 1a), which resulted in an imbalance in the number of species modelled in different parts of the world (Supplementary

Fig. 1b–e). In addition, our model assumes that there is a linear relationship between the environmental covariates and the density of the fish and invertebrate species. Other studies have highlighted non-linear associations between richness and community structure in coral-reef fishes, and mangrove attributes such as extent and perimeter; this suggests the potential for thresholds above which density dependence limits further benefits[44,45].

Fish and invertebrate abundance from mangroves

Application of our model onto the 2020 global mangrove extent[30] estimates that the presence of mangroves supports an annual abundance of nearly 735 billion (95% confidence intervals (CI): 160–3500 billion) juvenile fishes, prawns and bivalves, and adult crabs from across the commercially important species considered here. It should be noted that abundance at the early life-history stage, and across a range of species with very different life-history parameters does not directly equate to potential economic or biomass gains. Furthermore, such numbers represent a substantial underestimate of the commercial importance of mangroves across all commercial species, focusing only on a subset of species targeted by fisheries, and with no data at all for abundance from West and Central African mangroves. Of the global 735 billion total, the three species of the genus *Penaeus* represented over half (51.0%) the total, with the 29 species of finfish contributing a further 31.7%. The remaining amount was split between four species of crabs (15.6%) and the single bivalve, *A. tuberculosa*, (1.8%).

The contribution of different groups to the total abundance world-wide is affected by species data availability. For example, prawn species are an important component of both mangrove ecosystems and fisheries catches across the Americas[46,47], and their inclusion would greatly increase numbers in this region; however, penaeids quite strongly influence the model numbers across much of the Indo-Pacific where available data met the requirements for inclusion in the model. By contrast, crabs make up a larger proportion of total numbers in the Americas and in east and southern Africa (Fig. 2b), while included bivalves are restricted to the Pacific coast of the Americas. Given this regional variation in data availability, the description and exploration of the model and its predicted patterns focuses at regional (or finer) scales where there are similar taxa and comparable species richness within the model.

Southeast Asia supports some of the highest abundance of fish and invertebrates, with nearly half of the global numbers predicted by our model, which includes 49.7% of the global finfish and 66.6% of the global prawn numbers. Three species of prawns account for over two thirds of the total numbers in Southeast Asia, but fish are also a large component with *Atherinomorus lacunosus*, and *Gerres filamentosus* being among the most numerous. In addition to these highly abundant species, the model also contains species such as the mangrove red snapper (*Lutjanus argentimaculatus*) that, although making up only a small proportion of the total numbers, represents a particularly high-value species important across the region[48]. Given its extensive mangrove habitat, Indonesia has the highest totals, with this abundance shown to support livelihoods for communities across the country[49,50] and to have a critical role in food security and nutrition[51]. Similarly high abundance of commercially important mangrove-associated fish and invertebrate occurs in Myanmar, Malaysia, and Papua New Guinea (Table 2).

Among the modelled species, crab abundance is high across the mangrove coasts of the Americas, underpinned by the high-densities of *U. cordatus* and *U. occidentalis*. Multiple studies have highlighted the socio-economic importance of crab and bivalve fisheries for local use across Central and South America[40,52,53]. In the western Indian Ocean, total abundance is dominated by two crab species (*S. serrata* and *N. africanum*) (59.1%). This includes one crab species, *N. africanum*, that is restricted to this region and has the highest modelled density of any species in our models. Crabs are highly important species here, not only for local consumption. In Madagascar, small-scale subsistence *S. serrata* fisheries have shifted to market driven exports, resulting in a fivefold increase in their price[54]. In addition, crabs and other invertebrate species may fulfil important ecosystem engineering functions due to their low functional redundancy[55].

Table 2 | Top 10 countries for mangrove commercially-harvested marine species abundance

Rank	All Species		Prawns		Finfish		Crabs		Bivalves	
1	Indonesia	185 (37–953)	Indonesia	126 (23–686)	Indonesia	58 (13–266)	Mozambique	26 (6–118)	Ecuador	4 (1–13)
2	Myanmar	83 (16–427)	Myanmar	56 (10–304)	Myanmar	26 (6–122)	Brazil	23 (8–65)	Colombia	4 (1–11)
3	Malaysia	56 (11–288)	Malaysia	38 (7–205)	Brazil	22 (6–77)	Madagascar	22 (5–97)	Mexico	2 (1–6)
4	Brazil	45 (15–142)	India	29 (5–160)	Malaysia	18 (4–83)	Tanzania	11 (2–49)	Nicaragua	1 (0–3)
5	India	42 (8–221)	Papua New Guinea	28 (5–151)	Papua New Guinea	14 (3–62)	Mexico	8 (3–29)	Costa Rica	1 (0–2)
6	Papua New Guinea	42 (8–214)	Viet Nam	19 (3–102)	India	13 (3–61)	Venezuela	7 (2–20)	Honduras	1 (0–2)
7	Madagascar	39 (8–186)	Australia	16 (3–90)	Mexico	9 (3–28)	Colombia	4 (1–19)	Panama	0.5 (0–1)
8	Mozambique	39 (8–181)	Bangladesh	13 (2–70)	Viet Nam	8 (2–39)	Cuba	3 (1–7)	El Salvador	0.2 (0–1)
9	Viet Nam	27 (5–140)	Madagascar	12 (2–65)	Venezuela	8 (2–27)	Ecuador	2 (0–16)	Guatemala	0.2 (0–1)
10	Australia	24 (5–122)	Pakistan	10 (2–53)	Bangladesh	8 (2–37)	United States	2 (1–4)	Peru	0.02 (0–0)

Different groups of species in billions per year, number in parentheses is the 95% confidence interval.
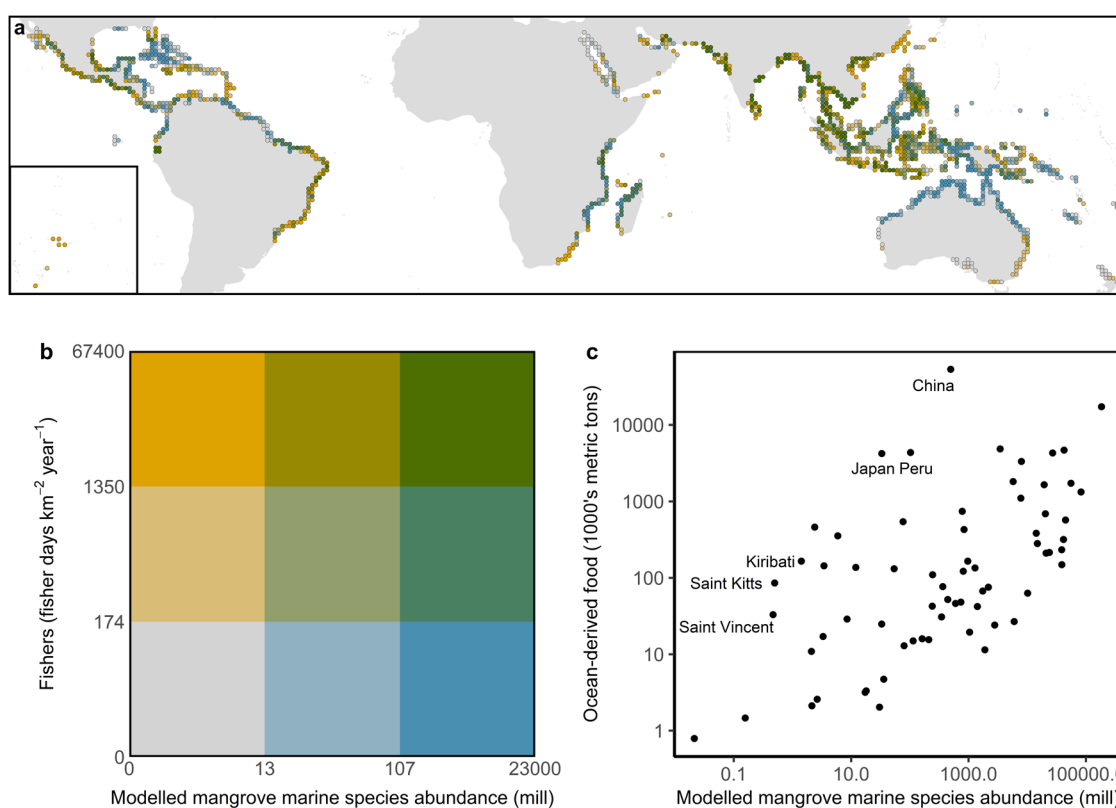
Fig. 3 | Mangroves' contribution to livelihoods and global food security. a The correspondence between modelled mangrove commercially-harvested marine species abundance and the number of fishers participating in in-mangrove, near-shore subsistence and artisanal and near-shore commercial fisheries[15]. Data summarised within 1° cells, inset shows central Pacific islands, **b** key to colours in panel (a) showing the breakpoints in terms of modelled mangrove fish and invertebrate abundance and fishers for the different categories, and **c** the relationship between a country's mangrove commercial fish and invertebrate abundance (this model) and its total ocean-derived food production. Countries highlighted in the text are labelled.

In contrast to other regions, total abundance of commercially important mangrove-associated fish and invertebrates for large parts of the Middle East remains low. Although the models predict high density per unit area, mangroves in much of this region are limited in total extent. Moving across South Asia, the pattern changes, with highly heterogeneous numbers, including very high numbers in low-lying coastal areas around rivers with extensive mangroves. Data gaps for many key species reduce regional and global totals, and constrain use in broad regional comparisons; however, the patterns that our model highlights are important for a better understanding of the value of mangrove ecosystems. Indeed, many of the species we were unable to model or map likely follow similar patterns to those modelled.

Mangroves' contribution to livelihoods and global food security

Mangrove fisheries provide important contributions to the provision of dietary protein[56] as well as subsistence, recreation, and employment in commercial fisheries[15,57], known to involve numerous stakeholders between fishers and markets[58]. The correspondence between our abundance

estimates and the number of fishers participating in in-mangrove, near-shore subsistence and artisanal and near-shore commercial fisheries[15] (hereafter referred to as small-scale fishers) showed considerable heterogeneity, but with some distinct regional variation (Fig. 3a). Areas predicted to support high fish and invertebrate abundance, and large numbers of small-scale fishers[15] were centred on South and Southeast Asia, particularly in highly populated areas such as the Mekong delta. Conversely, relatively low values of those two variables were apparent in the Caribbean, northern Red Sea and parts of Australia. Areas that had relatively low fish and invertebrate abundance but still supported high numbers of small-scale fishers were evenly distributed across the world (Fig. 3a). By contrast, areas of high abundance and low numbers of small-scale fishers can be seen across much of tropical Australia, Southern Papua (Indonesia and Papua New Guinea) as well as the Western Caribbean (Cuba, Bahamas, South Florida), although it should be noted that in certain regions such as the Western Caribbean and Northern Australia this abundance supports high value recreational fisheries[57].

The national fish and invertebrate abundance from mangrove ecosystems predicted by our model was highly positively correlated with a country's total ocean-derived food production[59] ($t_{66} = 5.6$, $P < 0.001$, $r^2 = 0.564$; Fig. 3c). Outliers within this trend were Peru, Japan, and China, as well as smaller island nations such as Kiribati, Saint Kitts and Nevis, and Saint Vincent and the Grenadines. These countries have high total ocean-derived food production, but only small mangrove areas and thus relatively less mangrove-associated fish and invertebrate abundance. To date, the relationship between mangrove ecosystems and enhanced coastal and inshore fisheries has largely been assumed, with empirical relationships between mangrove descriptors e.g., area or edge length, and fish catches based on certain species or countries[23]. Despite their relatively small area, mangrove-associated fish and invertebrate species can contribute substantially to fisheries catches[14,41]. For example, mangrove-affiliated fish and crab species represent 32% of the landings of small-scale fishers in the Gulf of California, Mexico[22], while in small island developing countries as much as 50–80% of both subsistence and commercial species exploited by people rely on mangroves for some part of their life-history[60]. The overall pattern found in this study supports the inference that mangroves play a relatively consistent and important role in global fisheries and as such adds another supporting argument for their conservation and restoration, alongside other quantified benefits such as carbon storage or coastal flood protection.

Conclusions

Mangrove forests are known to provide important nursery areas for finfish and invertebrate species of commercial importance[13,14]. While a number of studies have attempted to quantify the enhancement role of mangroves for commercially important species, there is insufficient data to measure such enhancement at the global scale for all commercial species. The current work thus focuses on a subset of commercially important fish and invertebrate species for which data are available and which are known to have a high dependency on mangroves, and then models the likely density within the mangroves. The model outputs confirm the high densities of commercially important fish and invertebrate species in many mangrove areas world-wide. Within particular regions where the model includes a consistent set of modelled species, the generated maps enable within-region comparison. Our study highlights the particular role of deltaic coasts in Southeast Asia and the Americas, and also arid coastlines of the Middle East in supporting high densities of commercial species per unit area. Clearly, overall abundance of commercially important fish and invertebrate species is strongly influenced by overall mangrove extent, and in this regard, the mangroves of Indonesia support the greatest abundance of commercial fish and invertebrates of any single country in the Indo-Pacific, with Brazil and Mexico dominating total abundance in the Americas. Particular attention can also be drawn to important ecological and geomorphological features which are promoting high numbers of commercial species, such as the deltaic coastlines of the Sundarbans, southern New Guinea, north-east Borneo, and the northern coasts of South America.

The importance of commercial mangrove fish and invertebrates to small-scale and local fishers has been emphasised in other work[15], but overlapping such information with models of abundance highlights areas where fishing pressure and fish abundance may be interacting, with areas of low commercial fish abundance and high apparent fishing effort being areas in need of particular attention from a sustainability and fisheries management perspective. A close correlation between the estimated abundance of fish supported by mangroves from our models and total fisheries dependence at the national level highlights the critical importance of mangroves to fisheries and food security world-wide.

Methods

Fish and invertebrate density data

A literature search was undertaken on 20th September 2016 in Scopus using the following search terms to search for relevant titles, abstracts or keywords ((mangrove*) AND (densit*) AND (*fish* OR invertebrate* OR crab* OR mollusc* OR shrimp* OR mussel*)) to identify papers containing species-specific fish and invertebrate data from field studies undertaken in mangroves ($n = 520$). Additionally, participating experts were asked to contribute published datasets, and relevant references were searched for mention of other possibly relevant publications in a snowball approach.

The abstracts of all identified papers were screened to assess whether they were likely to contain field measurements of fish or invertebrate abundance in mangroves. Relevant papers were then searched for species-specific juvenile commercial fish and juvenile and resident bivalve and crustacean data. Density data sampled within or adjacent to mangrove areas were extracted, with values standardised to represent the number of individuals per 100 m². Only sampling methods that provided information as to the spatial area of sampling were included, therefore sampling methods focussed on catch per unit effort were excluded. Sampling methods included trawl, quadrat, mark-recapture, visual survey, block net, seine net, and lift net. Mark-recapture data were included from a single study[61] in which the authors converted the data to abundance via the Chao model[62]. Sampling method and standard error were also extracted into the dataset. Where standard deviation was provided, this was transformed into standard error. To avoid pseudoreplication within the dataset all samples from the same estuary, or fewer than 5 km apart, were aggregated to a single mean value. Similarly, where papers had recorded data at multiple timepoints, annual averages were derived when possible, with each annual average included as a separate datapoint. Papers providing data from areas outside of the native range of mangroves (e.g., Hawaii), were excluded.

In total 481 data points with density data on juvenile commercial fish and juvenile and resident bivalve and crustacean species were extracted. The data covered 37 species, with the number of data points per species ranging between three and 79, with a median value of nine (Supplementary Table 1).

Spatial data

A grid with a spatial resolution of 1 km² was created for the entire world. Grid cells ($n = 488,097$) that contained mangroves between the years 1996 and 2020 from the Global Mangrove Watch (GMW; v3.14) time series[30,63] were identified, and formed the spatial framework of the analysis.

To estimate the fish and invertebrate density within mangroves, a statistical model that linked the fish and invertebrate density data to environmental covariates was created. The environmental covariates were identified through a Delphi approach conducted over a two-month time frame (May 19–July 20, 2016). The Delphi technique is an iterative and anonymous approach to achieving consensus on complex issues or addressing data gaps[26]. Seventeen mangrove fish and/or invertebrate experts from academia across the globe, with a mean 17 years experience with mangroves and field experience in 39 countries and territories were asked to determine which abiotic and human factors most influenced the density of mangrove-affiliated fish and invertebrates. The countries in which experts had the most experience included Australia ($n = 7$), Papua New Guinea (4), Singapore (4), Fiji (3), Malaysia (3), New Caledonia (3), Tanzania (3) and

Thailand (3), with three experts identifying the Caribbean, Central America, and South America as their regions of expertise. Fourteen of the experts identified themselves as having expertise in fish and/or invertebrate ecology, with the remaining three identifying their expertise as fisheries (catch), food-webs and spatial ecology. The experts were asked via a questionnaire distributed by email, to provide insight on three aspects of mangrove fisheries: (1) parameters that might influence fish and invertebrate density, (2) the direction of the relationship between the parameter and fish and invertebrate density, and (3) the geographic scale at which the parameter might exert the strongest influence. Experts were asked to score 36 parameters identified as being potentially important on a Likert scale of 1–5[64]. After each round, experts were provided with a summary report detailing the frequency of each response for each parameter. Experts were asked to review parameters for which more than 75% of experts scored the factors as 4 or 5 on the Likert scale, and confirm that they agreed with the consensus that these were important in determining fish and invertebrate density in mangrove systems and should be considered for inclusion in the global model of mangrove-affiliated fish and invertebrate densities.

Following two rounds of the Delphi technique, consensus was reached on ten of the initial 45 proposed factors (see Supplementary Table 3): mangrove extent, mangrove geomorphic type, duration of inundation, fish and invertebrate species mangrove-dependency, mangrove condition, proximity to seagrass (where co-occurring), fishing pressure, mangrove edge length, extent of estuary/embayment proximate to the mangrove, and fish and invertebrate species probability of occurrence. Global geospatial datasets representing these factors were sought (Table 1); however, suitable datasets representing duration of inundation or proximity to seagrass were not available on a global scale. While consensus was not reached on the importance of sea surface temperature, salinity, and net primary productivity to fish and invertebrate density within mangroves specifically, they are known to influence fish abundance at a large spatial scale[65,66], and were therefore retained as covariates for the model fitting.

The environmental covariates were represented by two types, firstly static variables whose value did not change over the period of the fish and invertebrate density data, and time series variables whose value could be more closely attributed to an individual survey year (Table 1). To assign the environmental covariates to the fish and invertebrate density data, we used the covariate values from the closest grid cell. Nearly two-thirds (73%) of fish and invertebrate density datapoints fell within the grid that formed the spatial framework of the analysis and all were <10 km from a grid cell. For static variables the single value was used both for model fitting and predictions. For the time series variables, the value used for model fitting was from the year closest in time to the collection year of each fish survey data point, with the model predictions using the 2020 data to match the most recent global mangrove extent. For each cell of the spatial grid, the value for the 12 environmental covariates was determined. For raster datasets, to identify the environmental covariate value for each grid cell, the centroid was used. The raster value closest to the grid cell centroid for the variables sea surface salinity (SSS), sea surface temperature (SST), tidal amplitude and net primary productivity (NPP) was identified. For the other environmental covariates, covariate specific procedures were followed (see below). The spatial data processing was carried out in ArcGIS, and R[67] using the packages sp[68], raster[69], ncdf4[70] and rgdal[71].

Geomorphic type and change in extent. The geomorphic type of the mangroves in each 1 km^2 cell was derived from a mangrove biophysical typology[72]. This typology was developed for a different mangrove extent, therefore it was updated to match the spatial extent of GMW v3.14[73]. The typology assigns areas of mangroves into 'units' based on their proximity to macroscale coastal features which determines their geomorphic class – deltaic, estuarine, lagoonal and open coast. For cells that intersect multiple mangrove typological units, the geomorphic type of the unit covering the largest proportion in a cell was used. The change in extent of mangroves in a cell was assessed at the scale of the typological units. The

dominant (i.e., the unit covering the largest proportion of a cell) typological unit within a cell was identified, with change in extent the percentage change in mangrove area of that unit between 1996 and 2020. For those units with an infinite percentage increase in area i.e., those with area = 0 in 1996 and area >0 in 2020, the value was set to the maximum percentage from the other units.

Mangrove area. The area of mangrove within each of the 488,097 cells was calculated for all years (1996, 2007–2010 and 2015–2020) within the GMW v3.14 dataset[30,63]. Given the mis-registration identified in the Japan Aerospace Exploration Agency Synthetic Aperture Radar mosaics that result in inflated change statistics for the GMW dataset, we calculated the adjusted area based on equation three and the commission and omission values from Table 10 in Bunting et al.[30]. Model predictions were mapped onto the cells that intersect with the 2020 extent (n = 477,199).

Mangrove edge length. The edge length was derived by converting the mangrove extent polygons (1996, 2007–2010 and 2015–2020) of the GMW v3.14 dataset[30,63] to polylines. The length of mangrove edge (in metres) within a 2 km buffer of each 1 km grid cell was calculated. For estuarine deltaic, and lagoonal mangroves, the length of all edges within 2 km was used; however, for open coast mangroves, this approach included a disproportionate amount of landward mangrove edge that would have no mangrove fisheries density value. Therefore, for open coast mangroves, only the mangrove edge lengths that fell within a 100 m landward buffer from the shoreline (derived from Database of Global Administrative Areas v3.6, https://gadm.org/index.html) were used. While the mangrove extent data are available at moderate resolutions (25 m), it likely underestimates the extent of small watercourses within the mangroves. Model predictions used the 2020 mangrove extent to quantify edge length.

Sea surface salinity. Data from the European Space Agency's Sea Surface Salinity Climate Change Initiative[74] were accessed. Monthly mean data centred on the 1st and 15th day of each month covering the full assessment period, January 1st 2011 to September 15th 2020, were used. The 234 netCDF-4 were imported into R, and the coordinate system was converted from the Equal Area Scalable Earth grid to rasters with a World Geodetic System 1984 coordinate system. Ten mean annual SSS composites were created and linked temporally to the fish density data, with the predictions mapped onto the 2020 composite.

Sea surface temperature. Daily average ocean surface temperature adjusted to a standard depth of 20 cm were accessed from the Copernicus Climate Change Service[75,76]. Data were Level 4 spatially complete global sea surface temperature based on measurement from multiple sensors. Daily data in netCDF-4 form for the 1st and 15th of each month between 2001 and 2020 (n = 480) were downloaded and imported into R. Twenty mean annual average SST composites were created, with the predictions mapped onto the 2020 composite.

Net primary productivity. Net primary productivity data based on the Vertically Generalised Production Model (VGPM)[77,78] were downloaded. The VGPM model provides an estimate of NPP, based on chlorophyll from MODIS data, available light and photosynthetic efficiency. Two hundred and twenty monthly files covering 2002 to 2020 in .xyz format were imported into R and converted to rasters. Nineteen mean annual NPP composites were created, with the predictions mapped onto the 2020 composite.

Tidal amplitude. Tidal amplitude data were based on the Finite Element Solution tide model, FES2014. FES2014 integrates altimeter data from multiple satellites into a 2/3-D ocean hydrodynamics model[79]. A previous iteration (FES2012) was assessed as being one of the most accurate tide models for shallow coastal areas[79], with substantial improvements in

predictions for those areas identified in FES2014[80]. For the analysis the principal lunar semi-diurnal or M2 tidal amplitude was used, as in most locations this is the most dominant tidal constituent[81]. The tidal amplitude raster with a pixel resolution of 1/16° (~7 km² at the equator) was downloaded. This static data layer was used for both model fitting and model predictions.

Coastal embayment area. Coastal embayment area was assessed based on spatial polygons representing geomorphic features along the coastline. These spatial polygons were the framework for the mangrove typology (see Worthington et al.[72] for full details) and identified based on rapid change in direction of a high-resolution coastline. These polygons represent individual riverine estuaries and deltas, or coastal lagoons and bays. The area of coastal embayment polygons within a 2 km buffer of each grid cell was calculated.

Fishing pressure. Spatial data from published research on fishing effort (boat-metres per km²) within the coastal zone was used[82], and sourced from the study co-authors. Fishing effort data (number of boats, the length of boats, and the spatial boundary of the fishery) was extracted from FAO country profiles, published and grey literature and distributed across the coastal zone using contextual information on the distance from shore, distance from port, and the depth of the fishery. Six regional raster datasets (pixel resolution 1 km²) were combined and the raster value closest to the grid cell centroid was calculated. Owing to missing data in certain regions, distances between the grid cells and the fishing effort layer could be extremely large. Therefore, any grid cell >100 km from the fishing effort dataset had its value set to 0.

Data analysis

A linear model using generalised least squares from the package nlme[83] was fitted to the fish and invertebrate density data in R[67]. The density data was log transformed to reduce the impact of extreme values. An initial model was fitted to 14 explanatory variables. This consisted of continuous variables: sea surface salinity, sea surface temperature, net primary productivity, change in extent, mangrove area, edge length, tidal amplitude, coastal embayment area and fishing pressure. In addition, to reduce extreme density predictions at high values of sea surface salinity and sea surface temperature, the square of these variables was included. Sampling method, geomorphic type, and species were included as factor variables. In the case of sampling method, in initial exploratory analysis all pairwise sampling method comparisons were considered and sampling method types not significantly different from one another were merged.

There was also a difference in the number of field density data points per species, with some having far fewer than others (Supplementary Table 1). Due to the lack of data for some species, we fitted a single global model that assumes all species are affected by the same set of environmental covariates and the direction of relationship between the covariates and density is the same for each species.

Examination of the residuals of the initial model suggested that it violated the assumption of homogeneity of variance, and therefore the inclusion of different variance structures was tested[84]. A structure that allows different variances per stratum of the variable geomorphic type produced the lowest Akaike Information Criterion (AIC); however, there was also an indication of a difference in variance across values of mangrove edge. Therefore, a combined structure that allows different variances per stratum of geomorphic type and power of the variance covariate for mangrove edge was used. When comparing models with different variance structures, restricted maximum likelihood estimation was used[84].

Once the optimal random structure had been determined, the fixed structure i.e., the explanatory variables to be included in the model, was identified using automated model selection. The 'dredge' function from the R package MuMIn[28] was used to fit all potential combinations of the initial model containing the full set of 14 explanatory variables. However, within our model specification, potential combinations were constrained to ensure the

categorical variables sampling method, geomorphic type, and species were included, resulting in a candidate set of 2048 models. The candidate models were ranked using small-sample corrected Akaike Information Criterion (AICc). When comparing models with different fixed structures, models were fitted using maximum likelihood estimation[84]. Since the top ranked model had a very similar AICc to several other candidate models, model averaging was used. We retained models ($n = 30$) with AICc ≤2 of the top model, and refitted them using restricted maximum likelihood estimation. A goodness-of-fit statistic, Nagelkerke's adjusted R^2 statistic, was computed for the 30 retained models. The final model coefficients (Supplementary Table 2) were estimated using the 'model.avg' function in MuMIn[28], with the 'full average' of the coefficients used as these are less likely to bias the value away from zero. The final average model contained the variables mangrove area, change in extent, edge length, sea surface salinity, sea surface temperature, net primary productivity, and tidal amplitude, as well as the categorical variables for sampling method, geomorphic type, and species.

The model was then predicted over the spatial data framework for the cells within the grid which contained mangrove in 2020 ($n = 477,199$), using the cell values for the retained variables. For the predictions the coefficient value for sampling method was set to 1. For certain areas the combination of covariates resulted in density predictions for this predictive surface greatly above those based on the covariate values represented within the input fish and invertebrate density field data. Therefore, any cells with predictions greater than the maximum prediction of the fisheries model were removed ($n = 2904$). In addition, a further 285 cells from Hawaii and French Polynesia where mangroves have been introduced were removed. Ninety-five percent confidence intervals were created for all predictions using 1.96 * standard error of the model fit.

The model output was predicted densities (individuals 100 m⁻²) for each of the 37 species across the 474,010 grid cells. To assure that the model did not predict species' densities outside their native ranges we used Aquamaps[31] to constrain species predictions. The current distribution for the 37 species were downloaded and converted to presence/absence maps using a threshold 0.01, representing all areas in which any given species was predicted to be present. These presence/absence maps were then multiplied by the density values to remove density predictions outside the species' native range. Aquamaps was used for all species apart from the recently described *N. africanum*. For *N. africanum* the range was set as the east coast of Africa from KwaZulu-Natal in South Africa to the middle of Somalia, and the whole of Madagascar[85]. Owing to the lack of fish and invertebrate density data from West and Central Africa (Supplementary Fig. 1a), this region was removed from this analysis.

To examine differences between types of fish and invertebrates, the 37 species were grouped into fish, crab, bivalves and prawns. To calculate the abundance of the 37 species in mangrove areas, the cell species densities (individuals 100 m⁻²) were multiplied by the area of mangroves within each cell in 2020. To evaluate mangrove contribution to employment, the correspondence between the fish and invertebrate abundance value of mangroves, and the number of fishers participating in in-mangrove, near-shore subsistence and artisanal and near-shore commercial fisheries (small-scale fishers) was assessed. As such, a separate data source on fishing pressure than that included in the fish and invertebrate model (see above) was used. Data on the intensity of small-scale fishing (fisher days km⁻² year⁻¹) from zu Ermgassen et al.[15] was spatially matched to our grid cells ($n = 397,187$). Data was summarised to 1° cells and the R package biscale[86] was used to split the data into nine groups representing combinations of low, moderate and high values of total fish and invertebrate abundance, and small-scale fishers. To assess the contribution of mangroves to overall ocean-sourced food, we correlated our estimates of the national fish and invertebrate abundance value of mangroves with data on total ocean derived food production using data from the Food Balance Sheets produced by the Food and Agriculture Organization of the United Nations[59]. Data were available for 67 countries.

Data availability

The raw fish density data, and species and species group predictions are available on Zenodo (https://doi.org/10.5281/zenodo.14965669).

Code availability

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Acknowledgements

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Competing interests

The authors declare no competing interests.

Ethics statement

Data used in the article was collected following relevant ethical guidelines. The protocol relating to expert participation in the Delphi approach was approved by University of Cambridge's Department of Geography Research Ethics Review Group. We obtained informed consent from all participants.

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