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Dependence on seagrass fisheries governed by household income and adaptive capacity

Benjamin L.H. Jones [a,b,*], Richard K.F. Unsworth [b,c], Lina M. Nordlund [d], Johan S. Eklöf [a], Rohani Ambo-Rappe [e], Filipo Carly [f], Narriman S. Jiddawi [g], Yayu A. La Nafie [e], Susantha Udagedara [h], Leanne C. Cullen-Unsworth [b,c]

[a] Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden
[b] Project Seagrass, Bridgend, UK
[c] Seagrass Ecosystem Research Group, Department of Biosciences, Swansea University, UK
[d] Department of Earth Sciences, Natural Resources and Sustainable Development, Uppsala University, Sweden
[e] Faculty of Marine Science and Fisheries, Hasanuddin University, Indonesia
[f] Fauna and Flora International (FFI), Myeik City, Myanmar
[g] Zanzi Marine and Coastal Solutions Ltd, Zanzibar, Tanzania
[h] Blue Resources Trust, Colombo, Sri Lanka

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ABSTRACT

Seagrass meadows, like other tropical coastal ecosystems, are highly productive and sustain millions of people worldwide. However, the factors that govern the use of seagrass as a fishing habitat over other habitats are largely unknown, especially at the household scale. Using socioeconomic factors from 147 villages across four countries within the Indo-Pacific, we examined the drivers of household dependence on seagrass. We revealed that seagrass was the most common habitat used for fishing across villages in all the countries studied, being preferred over other habitats for reliability. Using structural equation modelling, we exposed how household income and adaptive capacity appears to govern dependence on seagrass. Poorer households were less likely to own motorboats and dependent on seagrass as they were unable to fish elsewhere, whereas wealthier households were more likely to invest in certain fishing gears that incentivised them to use seagrass habitats due to high rewards and low effort requirements. Our findings accentuate the complexity of seagrass social-ecological systems and the need for empirical household scale data for effective management. Safeguarding seagrass is vital to ensure that vulnerable households have equitable and equal access to the resource, addressing ocean recovery and ensuring sustainable coastal communities.

1. Introduction

The tropical coastal seascape encompasses multiple habitats, including coral reefs, mangroves and seagrass meadows (Ogden 1988), and provides of ecosystem goods and services that are essential for society (Moberg and Ronnback 2003). Small-scale fisheries are arguably the most prominent example of human reliance on tropical coastal ecosystems (Ferrol-Schulte et al., 2013) and a foundation of food-security (Hicks et al., 2019). A plethora of marine species, many of which are easy to target using low-tech fishing gear or simply collection by hand, have allowed such fisheries to prevail across the tropics, more so in low income and emerging economies. In such economies, small-scale and artisanal fisheries are inherently difficult to manage as they are complex, multi-species and multi-gear (Berkes 2001), and are tied to the fate of coastal habitats like seagrass meadows (Nordlund et al., 2018), which are impacted by local and global stressors such as poor water quality and coastal development (Dunic et al., 2021).

Marine fauna – fish and invertebrates – play a central role within seagrass social-ecological ecosystems across the Indo-Pacific region, providing sources of subsistence and livelihoods to coastal communities (Cullen-Unsworth et al., 2014), and further contributing to these indirectly through support of coral reef populations (Verweij et al., 2008). Yet, there exists negative social-ecological reciprocity (e.g., Kittinger et al., 2012). For example, while seagrass meadows provide important

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* Corresponding author. Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden.
E-mail address: Benjamin.jones@su.se (B.L.H. Jones).

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ecosystem services for people, reciprocal anthropogenic impacts modify seagrass meadows (Unsworth et al., 2018; McKenzie et al., 2021a) and their associated fauna and fisheries across the Indo-Pacific Ocean (Nordlund et al., 2011; Exton et al., 2019). Such reciprocity places human communities that use seagrass at risk, but also places seagrass at risk from human actions. The links between seagrass, associated fauna and humans in the region, are well documented (e.g., Coles et al., 1993; Gell 1999; Bujang et al., 2006), yet only a handful of authors and studies have recognised this as a social-ecological system (e.g., de la Torre-Castro and Rönnbäck 2004; Nordlund et al., 2011; Cullen-Unsworth et al., 2014; Unsworth et al., 2014; Quiros et al., 2018; Furkon et al., 2020). Despite this, social dimensions within seagrass research are growing, for example, recent work has revealed how seagrass ecosystems and their fauna contribute to quality of life in the Pacific Islands (McKenzie et al., 2021b). Studies have shown how human development is negatively associated to faunal density in seagrass meadows (Alonso Aller et al., 2014) and can also predict seagrass health (Quiros et al., 2017). Level of economic development is likely a driver of seagrass resource use, where use is more prominent for subsistence in areas like the Tropical Indo-Pacific bioregion than others (Nordlund et al., 2018). Moreover, the use of certain fisheries management regimes, i.e., community and national management, can reduce seagrass fishing pressure and increase faunal size, biomass and value (Chirico et al., 2017).

While our understanding of the human dimensions of seagrass social-ecological systems is growing, especially in the context of faunal extraction, our knowledge of what drives human use of seagrass for fisheries is limited. Across the Indo-Pacific, we know that human well-being is strongly associated with provisioning services that the ocean provides (Kittinger 2013). However, such benefits can be highly variable within diverse communities; members of the same communities can derive different benefits from the same resources (Daw et al., 2016). Therefore, household characteristics are important for determining how ecosystems are used and valued by individuals. Such characteristics could include reliance on marine resources for subsistence and monetary income (de la Torre-Castro et al., 2017; Quiros et al., 2018), household livelihood diversity (Cinner et al., 2009; Cinner and Bodin 2010; Dacks et al., 2018), vessel and gear availability (Mamauag et al., 2013; Fröcklin et al., 2014) or even the number of household dependents (Muallil et al., 2013; Wallace et al., 2016; Nchimbi and Lyimo 2019).

In this study, we aim to better understand what characterises households that utilise seagrass meadows as a fishing habitat across the Indo-Pacific region, by exploring the socioeconomic factors that drive household dependence on seagrass meadows for food provisioning or livelihoods. We predict that household socioeconomic factors (household income, number of adults, number of children) and adaptive capacity (alternative livelihoods, ownership of fishing assets) will be directly and indirectly correlated with household dependence on seagrass meadows (Fig. 1, Table 1). We address this hypothesis using empirical household scale data collected in villages across four countries across the Tropical Indo-Pacific; the most diverse and productive

Table 1
Descriptions and justifications for links in hypothesized path diagram of household drivers of seagrass dependence.

Path	Hypothesis	References
a	Larger households will have greater livelihood diversity	Asravor (2018)
b	Greater livelihood diversification will increase household income	Torell et al. (2017)
c, d	Poorer households lack the capital to invest in gears and vessels	Crona and Bodin (2010); Ha and van Dijk (2013)
e	Households with greater access to gears will be less dependent on seagrass meadows, except for fishers utilising gears that are seagrass specific	Mamauag et al. (2013); Quiros et al. (2018); Exton et al. (2019)
f	Households with greater access to vessels will be less dependent on seagrass	Fröcklin et al. (2014); Quiros et al. (2018)
g	Households with lower income and expendable capital are more reliant on natural resources	Bell et al. (2009); Nchimbi and Lyimo (2019)
h	Greater livelihood diversification reduces reliance on natural resources	Cullen (2007); Cinner et al. (2009); Cullen-Unsworth et al. (2014); Dacks et al. (2018)
i	Households with greater number of children are more reliant on natural resources	Muallil et al. (2013); Wallace et al. (2016); Nchimbi and Lyimo (2019)

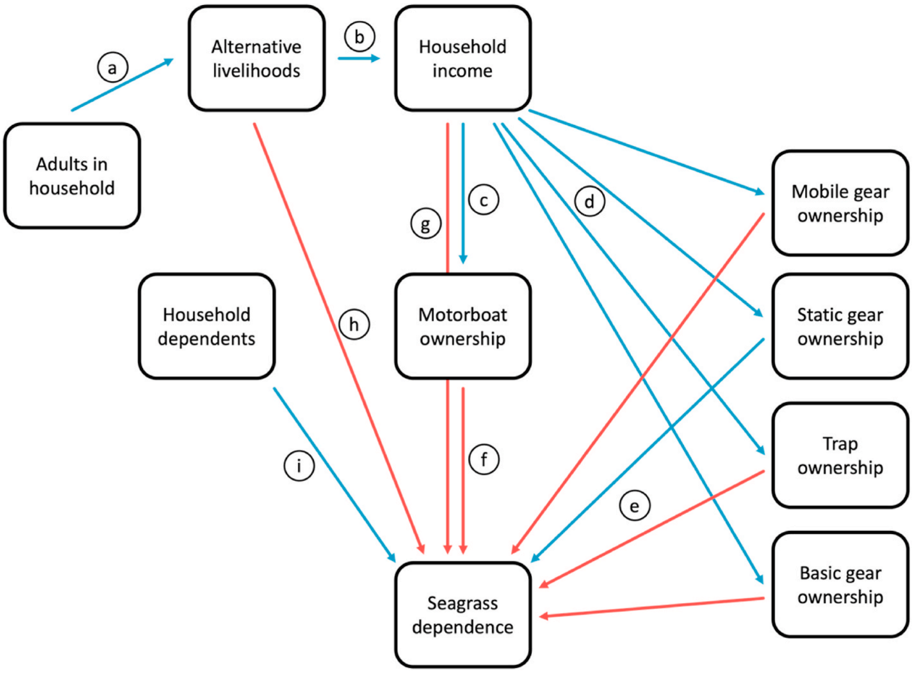

Fig. 1. Hypothesized path diagram of household drivers of seagrass dependence. Red links represent negative interactions and blue links represent positive interactions. Justifications and descriptions for hypothesized links are provided in Table 1.

seagrass bioregion on the planet (Short et al., 2007). We focus on coastal communities in Cambodia, Indonesia, Sri Lanka, and Tanzania where marine resources are highly important to local livelihoods and food-security.

2. Methods

2.1. Study locations

Between 2012 and 2017, we surveyed 147 villages spanning a range of environmental, social, and cultural settings across six regions covering Cambodia, Indonesia, Sri Lanka, and Tanzania (Table 2, Fig. 2). We considered a village to be a clustered human settlement or community that was recognised by either local custom or authority. We used a non-probability, convenience design to select villages (Etikan et al., 2016), specifically targeting villages in areas where coastal resource use is high. While this led to an uneven sample size across the Indo-Pacific, this is reflective of both the range in coastline length, percentage of rural population within the coastal zone and differences in regional populations between countries. Indonesia, for example, has the largest coastline length of all countries studied (54,716 km) and had the largest share of interviewed households.

Villages were located in a range of coastal environments consisting of brackish lagoon environments (e.g., Puttalam Lagoon, Sri Lanka), large coastal embayment's (e.g., Kampot, Cambodia) and archipelago chains (e.g., Wakatobi, Indonesia). In some villages, social infrastructure was poor with no plumbed drinking water, sewerage systems, or health centres and physical infrastructure was highly variable ranging from villages adjacent to boat and airports to areas with little to no transport or telecommunication links. Culturally, our survey spanned various ethnicities, languages, and religions; factors that may influence dietary practices and the consumption of meat and fish. For example, Buddhism is the primary religion with study areas of Cambodia and Sri Lanka, whereas for areas in Indonesia and Tanzania this was Islam.

2.2. Household surveys

To identify household drivers of seagrass use across the four countries, we conducted 1105 household surveys (Table 2) and utilised surveys previously developed by the authors to understand household coastal resource use patterns in the coral triangle (Cullen-Unsworth et al., 2011). Interviews were conducted in the local language and later translated to English; Khmer in Cambodia, Bahasa Indonesia for island communities and Bajaw for Bajo communities in Indonesia, Sinhala and Tamil in Sri Lanka and Swahili in Tanzania. Households were randomly selected, largely from fishing villages and semi-structured interviews were conducted with household heads. We considered a household to consist of one or several individuals who live in the same dwelling and share meals. Respondents were verbally introduced to the study, its aims, and objectives before being asked if they would like to participate. All respondents provided verbal informed consent; written consent was not obtained because a verbal questionnaire was used, and large proportions of society in the study regions cannot read or write. Ethical approval for working with human participants was obtained from Swansea University (SU-Ethics-Staff-250319/134). Semi-structured interviews lasted between 20 and 45 min where questions covered topics including household socioeconomics, fisheries assets, and marine and coastal resource use.

2.3. Socioeconomic factors

During household interviews, we asked respondents how many families, men, women, and children live in the household and could therefore ascertain household size. In addition, we asked respondents to report their total annual household income. We first converted local currency to US$, using the exchange rate relating to the period during which the data were collected. These values were then inflated using US inflation rates to the base year of the analysis (2021; Turner et al., 2019). Since, larger households face tighter budget constraints than smaller households with the same income, simply adjusting household income into per capita income ignores that there are economies of scale in household expenditure (Browning et al., 2013). Therefore, we adjusted for household size using an equivalence-scale method that recognises that the economic needs of additional individuals are not equal to the economic needs of the first adult and child (Buhmann et al., 1988). We used one of the most common equivalence scales, the square root scale, which is better suited when households are generally larger, such as in low income and developing economies like those in this study (Dudel et al., 2021).

2.4. Household adaptive capacity

Adaptive capacity may be defined as the ability of fisheries-dependent households to anticipate, respond to, cope with, or recover from changes to fish catches (Cinner et al., 2012), which may be a result of intensifying human impacts on the world's oceans (Halpern et al., 2015). Based on this definition, as well as previous studies on the topic (e.g., Daw et al., 2012; Cinner et al., 2015; Maina et al., 2016; Quiros

Table 2
Locations of household surveys conducted in four countries within the Indo-Pacific Ocean. The number of villages sampled within each Sub-Area are reported as well as the number of household interviews.

Country (n = 4)	Length of coastline (km)	Known seagrass area (km^2)	Rural population in coastal zones (%)	Region (n = 6)	Sub-region (n = 12)	Villages (n = 147)	Household interviews (n = 1105)	Regional Population Size
Cambodia	443[a]	338.14[a]	18[b]	Kampot	Teouk Chhou District	5	30	13,083
				Preah Sihanouk	Kaoh Rung Archipelago	1	15	1396
Indonesia	54,716[a]	2934.64[a]	60[b]	Selayar Regency	Selayar Island	5	150	12,005
				Wakatobi Regency	Binongko Island	14	70	13,086
					Kaledupa Island	29	269	16,643
					Tomia Island	19	95	15,367
					Wangiwangi Island	34	170	47,899
Sri Lanka	1,340[a]	1404.06[a]	68[b]	Puttalam District	Kalpitiya	25	129	86,405
					Puttalam	7	38	82,443
					Wanathawilluwa	5	33	17,460
Tanzania	1,424[a]	46.07[a]	10[b]	Zanzibar Island	Unguja North	2	71	105,780
					Unguja South	1	35	76,346

[a] (McKenzie et al., 2020).

[b] Center for International Earth Science Information Network - CIESIN - Columbia University (2012).

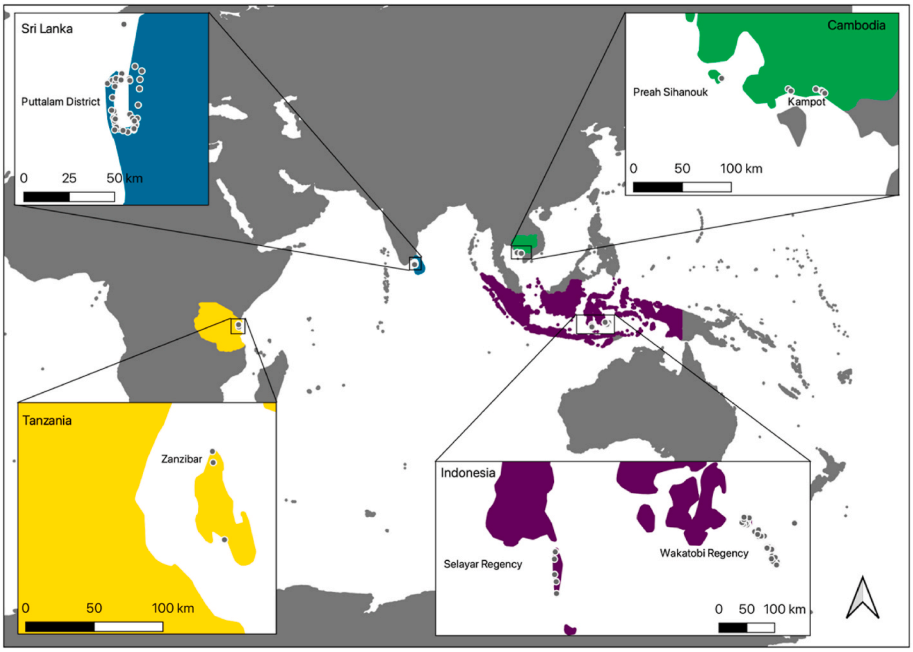

Fig. 2. Map indicating the four countries in which household surveys were conducted within the Indo-Pacific region. Points (grey circles) represent unique villages.

et al., 2018; Silas et al., 2020; Quiros et al., 2021) we considered alternative livelihoods and ownership of fishing assets as indicators of household adaptive capacity. Given that fishing households with a broad set of alternative livelihoods are considered to have reduced vulnerability (Cinner et al., 2009; Islam et al., 2014), we asked household heads to specify their number of income sources based on 17 livelihood categories; agriculture, aquaculture, building, carpentry and wood trade, civil service, fish trading, fishing, hotel and tourist trade, housing rental, manufacturing, mining, religious service, retail and trading, services and administration, teaching and transport.

Many fishing households utilise a ‘portfolio’ approach (Allison and Ellis 2001; Berkes 2001), shifting their focus in response to social and ecological challenges and opportunities (Finkbeiner 2015). Technologically, fishers may use different techniques and gears to account for changing conditions (e.g. currents, depths and tides), for use in different fishing habitats (e.g. coral, seagrass, mangroves, open water), or to respond to species behaviour or movements (Ruddle 1996). By switching and using multiple gears, fishers can respond to changes in abundance, conditions, or markets by utilising gears with lower or greater effort (Ruddle 1996; Anderson et al., 2011; Selgrath et al., 2018). This capacity provides higher catch efficiency and fisheries yields (Silas et al., 2020), allowing fishers to escape poverty traps, but greater catch efficiency may also come with greater environmental costs (Lokrantz et al., 2009). To account for this, we asked household heads whether anyone in the household owned a fishing vessel and what type. We grouped responses into motorised and non-motorised vessels, and did the same for fishing gear, grouping responses into mobile gear (e.g., trawl net), static gear (e.g., fyke nets, fixed lift nets), traps and pots or basic gear (e.g., handline, fishing rod). We decided against grouping passive gears together (e.g., fyke nets and traps) due to the nature of fyke nets used within countries in this study; these consist of stationary structures built using wooden poles and netting that are used to funnel fish or shrimp into a trap and require a considerable time investment to dismantle and move (Exton et al., 2019). Questions surrounding ownership of gears did not take into consideration gleaning (e.g., the absence of gear), which is therefore not considered within this analysis.

2.5. *Marine and coastal resource use*

To ascertain importance of marine and coastal resources to households, respondents were asked whether they received income benefits, food benefits or both from the marine environment. We also asked households what type of resources they collected from the marine environment which included the categories fish, octopus and squid, shark, sea cucumber and other invertebrates. To ascertain habitat use we asked households whether they presently used seagrass, reef, mangrove, or other habitats (e.g., mud, rock, open ocean) and if multiple, which habitat they preferred. If households preferred to use seagrass over other habitats, we also asked them why this was in the form of an open question and responses were transcribed at the time of interview. We used a four-step process to systematically condense these responses to understand the factors influencing seagrass use. Following Malterud (2012), we first read responses in order to recognise the general themes associated to seagrass preference (e.g., fish, abundance, gear, closeness). We then sorted these themes into unifying codes (e.g., close proximity, catch availability) and condensed these codes into a unifying meaning (e.g., reliability) for which we provided a defined concept (Table S1).

2.6. *Statistical analysis*

We first analysed interviews to identify households that utilised and collected marine and coastal resources. Households that did not collect any marine resources (e.g., fish, sea cucumber, other invertebrates) were removed from any further analysis. We explored data to ascertain which habitats households utilised; firstly, across the full dataset (n = 869) and secondly across a subset of the data (n = 737) accounting for distance to other tropical coastal habitats used for fishing (i.e., reefs). To do this, we calculated the distance to seagrass and reef from the centre point of each village, utilising our knowledge of the study system, the global distribution of seagrass meadows (McKenzie et al., 2020) and coral reefs (UNEP-WCMC et al., 2021). We then subset villages where seagrass and coral reefs were within 10 km. We chose 10 km as this reflects the distance fishers may be willing to travel to fish (Sesabo and Tol 2007; De Silva et al., 2017; Silas et al., 2020). This subset of data was highly skewed towards Indonesia (n = 619) and to a lesser extent Tanzania (n = 90) since abundance of live reefs in the study areas in Cambodia (n =

13) and Sri Lanka (n = 15) were low (UNEP-WCMC et al., 2021).

Structural equation modelling (SEM) is a useful tool to analyse social-ecological systems, in that it allows us to assess both direct and indirect relationships between variables (Grace 2006). Within our analysis, we wanted to explore which households were dependent on seagrass, and those that were not (i.e., using multiple habitats). To do this, we created a new binary variable where 1 = households where seagrass is the only habitat used and 0 = households that use seagrass as well as other habitats, or do not use seagrass at all. This new variable, termed *seagrass dependence* was used for further analysis. We first produced a conceptual model (Fig. 1), where individual paths reflect causal relations known from previous studies (Table 1) and our existing knowledge of the study systems. Given that villages were nested within unique sub-regions of each country, we sought to use a model structure that included a random effect of sub-region, nested within region, nested within country, to account for environmental, social and cultural conditions (see study locations). In addition, since our dependent variables also included binary, count and proportional data, we used a piecewise estimation approach to model drivers of household seagrass dependence, as implemented in the *piecewiseSEM* package (Lefcheck 2016) for R (R Core Team 2021).

Prior to fitting our full SEM, we omitted samples that contained NA's and tested for multicollinearity using the *vif* (Variance Inflation Factor) function in the *car* package (Fox and Weisberg 2018). For all predictors, VIF values were <3 (Zuur et al., 2010). Drivers of seagrass dependence and ownership of fishing assets (e.g., motorboat ownership, static gear) were modelled using binomial generalised linear mixed-effects models (GLMM), fitted with the *glmer()* function in the *lme4* package (Bates et al., 2015). We used a poisson GLMM to model the effects of household size on alternative livelihoods, and a linear mixed-effects model to test for the effects of alternative livelihoods on household income using the *lmer()* function in *lme4* (Bates et al., 2015). We used *tests of directed separation* (d-sep) to evaluate whether there were missing paths in our hypothesis model; this identified several missing paths, the majority of which were not grounded in theory or knowledge. However, one path emerged that we felt was important to include. This was a link between household income and number of dependents (Castañeda et al., 2018). After modifying our model, we removed non-significant drivers (using p-values) to produce a best-fit model which was then compared with our hypothesis model using Akaike's Information Criterion (AIC; Grace 2006).

3. Results

3.1. Household marine and coastal resource use

Out of the 1105 households we interviewed, 78.6% (869) reported that they collect marine species from the environment (e.g., fish and/or invertebrates). Marine and coastal resource use was most common in Kampot, Cambodia, where 93.3% (n = 30) of households engaged in activities, followed by Selayar, Indonesia (85.3%; n = 150). Coastal resource use was also high in Zanzibar, Tanzania (84.9%; n = 106) and across the Wakatobi, Indonesia (80.5%; n = 604), but generally lower in Puttalam Lagoon, Sri Lanka (60.0%; n = 200) and Preah Sihanouk, Cambodia (53.3%; n = 15).

Across full the dataset (n = 869), seagrass meadows were the most used habitat, with nearly two thirds (63.3%) of households stating that they used them either exclusively (22.4%) or within a multi-habitat strategy (40.9%). Moreover, most households preferred to fish in seagrass (49.8%) followed by coral reefs (27.2%), substrates like mud and sand (11.3%) and deep-water areas (10.8%; Fig. 3). Those households that utilised seagrass did so primarily within a multi-habitat strategy (44.5%), where 30.4% used both seagrass meadows and coral reefs. Less than one fifth used seagrass exclusively (16.1%).

When we accounted for distance to alternative habitats, there were 737 households where both seagrass meadows and coral reefs were present within 10 km. This greatly reduced the number of samples from Sri Lanka, due to the low abundance of reefs in the area studied. In these 737 households, seagrass use remained high and were again the most used habitat (Table 3); seagrass meadows were used by nearly two thirds of households (60.6%), whereas coral reefs were used by slightly less than half (47.7%).

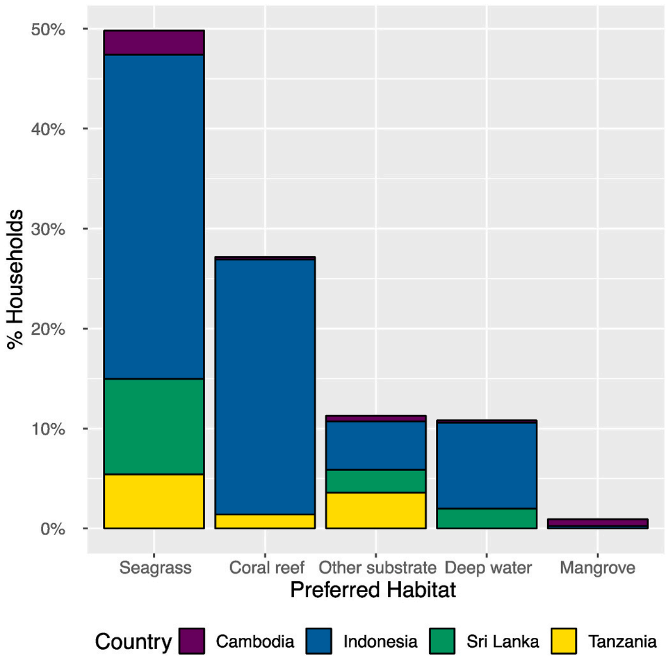

Fig. 3. Preferred habitat choice for collecting fish and invertebrates across 869 households in four countries across the Indo-Pacific Ocean. Villages were located in the following areas, Preah Sihanouk and Kampot, Cambodia; Wakatobi Regency and Selayar Regency, Indonesia; Puttalam District, Sri Lanka and Zanzibar, Tanzania.

Table 3

Coastal habitat uses by fishing households in four countries across the Indo-Pacific Ocean. Values represent percentage of households where seagrass and coral are within 10 km from the community centre. Villages were located in the following areas, Preah Sihanouk and Kampot, Cambodia; Wakatobi Regency and Selayar Regency, Indonesia; Puttalam District, Sri Lanka and Zanzibar, Tanzania.

Habitats	Cambodia (n = 13)	Indonesia (n = 619)	Sri Lanka (n = 15)	Tanzania (n = 90)	Total (n = 737)
Seagrass only	23.1%	11.1%	60.0%	41.1%	16.1%
Seagrass + other	15.4%	15.9%	–	4.4%	14.1%
Seagrass + coral	15.4%	29.5%	–	11.1%	26.4%
Seagrass + other + coral	–	4.4%	–	2.2%	4.0%
Coral reef only	15.4%	17.9%	–	11.1%	16.6%
Coral + other	15.4%	4.9%	–	2.2%	4.7%
Other only	15.4%	16.2%	40.0%	27.8%	18.1%
Total seagrass use	**53.8%**	**61.0%**	**60.0%**	**58.95%**	**60.6%**
Total coral use	**46.2%**	**52.3%**	**-**	**24.4%**	**47.7%**

3.2. Factors influencing seagrass use

Of the 49.8% of households that preferred to fish in seagrass, just under 90% provided responses for their preference. Using systematic text condensation to group these responses (Table 4) we found that "reliability" was the most frequently cited reason for using seagrass, mentioned by 70.7% of households. Seagrass meadows are dependable, and households reported that they could expect a *"big catch"*, that *"more fish were available"* or that they could always expect their target species to be there (e.g., rabbitfish, sea cucumbers, shellfish). This "reliability" was followed by "suitability" (21.4%), where households utilised seagrass because it was the only habitat that allowed for a certain type of gear (e.g., fish fence or shrimp fyke nets), or that it was less likely to damage nets. Common responses were *"because the net does not get stuck on the coral"*, *"the location of fish fence can only be in seagrass"* and *"you can keep the net for long hours on seagrass meadows"*. Just over 6% of households reported that "accessibility" was the primary reason for seagrass use with households stating that the *"coral reef is too far"*, that their *"boat can't handle waves"*, that *"the seagrass area is close to the village"* or that *"by using this craft, [they] can't go deeper"*. One household suggested that environmental change was a factor, stating that they used seagrass because *"the sea water temperature is increasing"*, but the details underlying this were not fully clear (i.e., whether this is due to effects of coral bleaching or warmer seagrass areas being more productive).

Table 4
Reasons influencing seagrass preference at the household level (n = 379). The proportion of households stating each reason is grouped by country. Villages were located in the following areas, Preah Sihanouk and Kampot, Cambodia; Wakatobi Regency and Selayar Regency, Indonesia; Puttalam District, Sri Lanka and Zanzibar, Tanzania.

Reason	Cambodia (n = 12)	Indonesia (n = 250)	Sri Lanka (n = 81)	Tanzania (n = 36)	Total (n = 379)
Accessibility – *Close to village or community. Easy to access and travel to.*	16.7%	6.8%	3.7%	8.3%	6.6%
Environmental change – *Other areas are degraded. Climate change.*	–	0.4%	–	–	0.3%
Familiarity – *Good knowledge of seagrass areas. Where to place nets etc.*	8.3%	0.8%	–	–	0.8%
Reliability – *Many fish and invertebrates are present. Good and large catches and/or presence of specific target species. Fisher preference.*	66.7%	60.4%	93.8%	91.7%	70.7%
Routine – *Usual place to fish. Household/family always uses this habitat.*	–	–	1.2%	–	0.3%
Suitability – *Habitat has characteristics that suit the fisher's gear type or vessel. Favourable environmental characteristics for fishing; calm, sheltered or protected, location can be used all year.*	8.3%	31.6%	1.2%	–	21.4%

3.3. Drivers of seagrass dependence

From 1105 interviews, we identified 161 households that exclusively used seagrass (i.e., seagrass was the only habitat used), and were dependent on the habitat to collect marine resources either for sustenance (8.1%), income (1.8%), or both (90.1%). Just over half of these households (53.4%) utilised seagrass as part of a portfolio approach to collect both fish and invertebrates, whereas other households exclusively targeted fish (32.3%) or invertebrates (14.3%).

Our best fit structural equation model (Fisher's C = 16.017, χ^2 = 0.19, df = 12, n = 654; Fig. 4) explained 54% of the variation in the likelihood of being dependent on seagrass; that is, seagrass being the only habitat utilised by the household to obtain food or livelihood benefits from the marine environment. The most striking finding of the model was a dual influence of household income, which ranged from 31 USD to 4877 USD (1108 ± 980). There was positive influence of household income on ownership of fishery assets (e.g., motorboat and static gears); the wealthier a household the more likely they were to own either of the two assets. Therefore, household income had both a negative influence on seagrass dependence, partially mediated by motorboat ownership (indirect path coefficient = −0.62), as well as a positive influence on seagrass dependence, mediated by static gear ownership (indirect path coefficient = 1.08). Households with income at the lower end of the scale were less likely to own motorboats (direct path coefficient = 0.55; $p < 0.001$) and households that did not own motorboats were more dependent on seagrass (direct path coefficient = −1.17; $p < 0.001$). However, data also revealed that households with income at the higher end of the scale were more likely to own static gears (direct path coefficient = 0.70; $p < 0.05$). Such households were also more likely to be dependent on seagrass than other habitats (direct path coefficient = 1.54; $p < 0.05$); static gear ownership had a strong negative effect on coral use (Fig. S2). The effects of motorboat ownership that we report were unique to households dependent on seagrass; we ran the same model for households that utilised seagrass and other habitats or coral reefs and found no significant path (Fig. S1, Fig. S2).

We found marginal effects of alternative livelihoods on household income (direct path coefficient = 0.07; $p < 0.001$), but no effects of household size on alternative livelihood diversity. However, an increasing number of alternative livelihoods had broadly positive effects on seagrass dependence (direct path coefficient = 0.35, $p < 0.05$); for every additional non-fishing livelihood, likelihood of depending on seagrass increased by ~35% when accounting for other factors. This effect was not unique to household's dependent on seagrass, and the likelihood of households utilising seagrass as part of a multi-habitat strategy was also positively linked to additional livelihoods (Fig. S1). However, for coral reef use, there was no effect (Fig. S2). We found no effects of basic gear ownership on seagrass dependence (or seagrass use, Fig. S1), likely revealing that households with access to hand lines or spears choose to fish elsewhere (e.g., coral reefs, Fig. S2).

In summary, we found that household seagrass dependence was positively influenced by ownership of static fishing gears (e.g., fyke nets, fish fences, fixed lift nets) and alternative livelihoods within the household. Ownership of motorboats and the number of household dependents negatively influenced seagrass dependence. Number of household dependents negatively impacted household income, and household income positively influenced ownership of motorboats and static fishing gear.

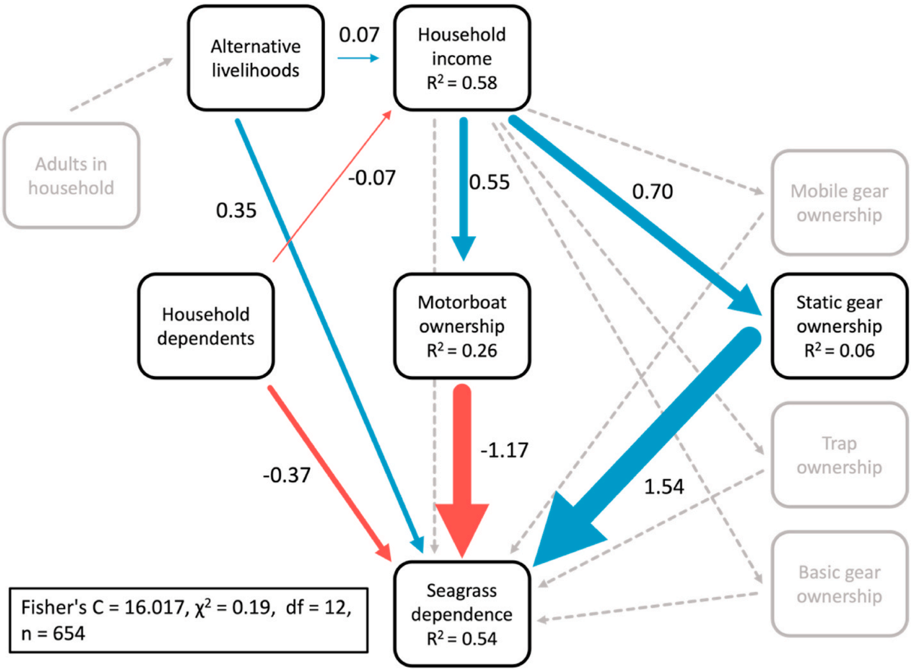

Fig. 4. Path diagram for best fit structural equation model of household drivers of seagrass dependence across the Indo-Pacific region. All solid paths are significant ($p < 0.05$) and weighted to reflect path coefficients (red arrows are negative and blue arrows are positive). Grey boxes and dashed paths represent non-significant drivers and links from our hypothesis model that were removed to construct the best fit model. For each path, the coefficients can be interpreted as follows: If, for example, household income goes up by 1 unit, the likelihood of owning a motorboat goes up by 0.55 units. Response R^2 values indicate the explained variance.

4. Discussion

In this study, we reveal that seagrass meadows are the most used habitat for collecting fauna in 147 distinct coastal villages across four countries within the Indo-Pacific region. These findings add greater context to large-scale (e.g., Nordlund et al., 2018; Ambo-Rappe 2020) and small-scale analyses (de la Torre-Castro and Rönnbäck 2004) on the topic, showing that seagrass meadows may be the preferred coastal habitat choice for fishing across a variety of different environmental, social, and cultural settings. Additionally, even in locations where small-scale fisheries reportedly depend on "coral-reef fish" (e.g., Zanzibar, Tanzania; Thyresson et al., 2013), seagrass use was more common than coral reef use at the household level and was preferred for its reliability. We present evidence that seagrass meadows act as a safety net for the poor, but poor adaptive capacity places these same individuals at risk if seagrass loss continues. Below we outline why and how this information is vital for improved spatial planning and scenario analysis to inform management to meet sustainability goals.

First, our findings highlight the central role that seagrass-associated fauna play in shaping the human dimensions of seagrass-social-ecological systems. We found that seagrass meadows are favoured for fishing over other habitats primarily because their faunal communities are reliable; respondents were motivated by the fact that they can always expect a large and quality catch in seagrass meadows suggesting that if all else fails, seagrass is where they turn. In previous studies, we found that seagrass catches can be so large and reliable that multiple species are discarded as bycatch (Jones et al., 2018; Ambo-Rappe et al., 2021), and others have shown that seagrass catches can be economically rewarding (de la Torre-Castro et al., 2014). Other pull factors such as gear maintenance and suitability were reported by household heads when asked about habitat preference, where seagrass was used because it did not damage their gear or the gear that they used could only be placed in seagrass. While other habitats likely yield larger fish that would be more lucrative to fishers (Thyresson et al., 2013; Thoya and Daw 2019), households utilised seagrass for safety; to eliminate the risk (and potential cost) of damaging gear on hard structures like reef or rock. These findings support previous studies suggesting that decisions on fishing effort or fishing site are mediated by economic trade-offs (Daw 2008).

Our best fit structural equation model exposed the duality of certain household variables (e.g., household income) and their effect on seagrass dependence. We revealed a potential dichotomy between rich and poor; the reliability of seagrass meadows provides a safety-net for households with lower income, yet this same reliability provides extrinsic incentives for households with higher income. On the one hand, households with lower income were more likely to be dependent on seagrass due to a lack of capital to purchase motorboats, which would enable them to fish further away from the shore (e.g., Silas et al., 2020); seagrass is close to shore and easy to access on foot or by wading. While this could also be down to household choice (e.g., households choosing not to purchase a motorboat since seagrass is reliable and they do not need an engine), our analysis revealed this link to be unique to seagrass dependent households. It is therefore more likely an artefact of household access to capital, as with other areas in the Indo-Pacific region (Thoya and Daw 2019). Seagrass meadows, and the fauna they support, therefore provide resilience, and prevent households from falling into deprivation (Quiros et al., 2018). On the other hand, we found that households with relatively higher income were more likely to own expensive static gears that cost up to USD 400 (De Silva et al., 2017; Exton et al., 2019). These households were potentially forced to be dependent on seagrass by a need to recover capital investments but could also be motivated to utilise seagrass by extrinsic incentives like low fishing effort requirements (limited labour needed), low operating costs (engine and fuel not needed) and reliability (high catch).

We also found broadly positive effects of alternative livelihoods on seagrass dependence. Across the four countries, households with a greater number of alternative livelihoods were more likely to be dependent on seagrass meadows, but we found no relationship for coral reef use. We thought that this could be a statistical artefact of the number of adults in the household, but tests of directed separation found no missing path here. Seagrass therefore supports households with a wider range of livelihood strategies than coral reefs. Seaweed farming is frequently practiced as an alternative livelihood across the tropics and is generally conducted in seagrass meadows, revealing that dependence on seagrass may not only be driven by their fish and invertebrate communities. However, seaweed farming can negatively influence seagrass meadows, compete with fishing activities, or supplement fishing activity (Jones et al., 2022). Alternative livelihood programmes, a common sustainable development intervention used across the Indo-Pacific to reduce fishing pressure (Hill et al., 2012), focus on promoting substitute livelihoods to reduce reliance on natural resources. However, our findings suggest that it may not be a lack of alternative income generating activities that determines dependence on seagrass, but instead close cultural or social connections to fishing (de la Torre-Castro and Rönnbäck 2004; McKenzie et al., 2021a). This supports existing literature showing that fishing households may already have high occupational multiplicity to compensate for seasonality or catch variability as well as notions that attachment to fishing is more than just economical (Cinner et al., 2015).

Viewing our findings through the lens of the capabilities approach (CA) reveals that seagrass dependent, low-income households are potentially the most vulnerable to reciprocal social-ecological interactions, such as habitat loss and overfishing. Central to the CA is whether individuals have the capability (i.e., ability and freedom) to convert resources into ‘functioning’s’ that contribute to human well-being, where functioning’s are things people value having, being or doing (i.e., having food on the table, having good health; Sen 2001). Presently, seagrass meadows inherently provide individuals with the ability and freedom to convert faunal resources into livelihoods and food, providing a safety net function. However, the critical question here is whether these individuals would have the same freedom and ability to continue collecting coastal resources if their access to seagrass fauna is removed. While such a question requires a much deeper investigation, our findings suggest that some seagrass dependent households do not have the capacity to choose which habitat to target. For example, Silas et al. (2020) reported that the freedom to shift fishing from nearshore coastal fisheries (e.g., seagrass meadows) to offshore waters was critical to escape effects of overexploitation of finfish, yet such a shift requires the economic capacity to upgrade fishing vessels or gear (Wallner-Hahn et al., 2016). This lack of freedom is also present for gleaning fishers; following seagrass decline in the Western Indian Ocean, invertebrate catches used for subsistence also declined with communities unable to make up the difference elsewhere (Nordlund et al., 2011). Therefore, ongoing, and future seagrass loss will greatly accentuate the differences between the rich and the poor.

Our study adds further evidence to the paradigm shift from the traditional “reef fisheries” architype of coastal small-scale fisheries within the Indo-Pacific, to one which recognises that these are broad coastal fisheries (e.g., de la Torre-Castro et al., 2014; Unsworth et al., 2014; Nordlund et al., 2018; Ambo-Rappe 2020). We revealed that some households employed multi-habitat strategies, targeting seagrass, coral, mangrove, rock, mud, or sandy areas, whereas others were primarily dependent on single habitats. While management measures, such as implementation of no-take areas, would be positive for seagrass faunal communities (Chirico et al., 2017), only those households with the capacity and capital to move elsewhere would benefit (Tilley et al., 2021); with increasing dependence on seagrass comes an increased risk of entering social–ecological traps if we ignore these dependencies in management (e.g., Cinner 2011). Therefore, a key requirement to support effective management of coastal areas is to address the barriers to resource security that exist at the household level. This is vital for eradicating poverty and ensuring sustainable development success more broadly (Wackernagel et al., 2021), as well as to help individuals deal with natural and anthropogenic shocks. For example, in Fiji, Cyclone Harold and the COVID-19 pandemic revealed that social inequities characterised fishers resource insecurity, and that to escape such shocks, individuals sought help to purchase boats, engines and gears (Mangubhai et al., 2021). While seagrass meadows potentially help to alleviate poverty at the household level, they likely do not reduce poverty *per se*, but instead prevent further poverty. Therefore, targeting socio-economic inequities and inequalities could continue to help alleviate poverty by increasing resilience to shocks.

As highlighted by UN Decade of Ocean Science for Sustainable Development (Ryabinin et al., 2019), evidence at the macro-scale is critical to policy and the achievement of ocean-related Sustainable Development Goals (von Schuckmann et al., 2020). However, top-down initiatives operating at macro-scales that ignore finer-scale information from individuals, can be unsuccessful in terms of sustainability (e.g., Eriksson et al., 2015), and potentially result in unintended consequences that influence the entire seagrass social-ecological system (Jones et al., 2022). In Kenya for example, gear subsidies were used as a management tool (McClanahan and Kosgei 2019), despite growing evidence that reducing fishing costs (e.g. by providing subsidies) is a poor solution (Schuhbauer et al., 2017). As a result, the gear subsidies led to reductions in catch-per-unit effort, and personal incomes, and had no effect on local fish prices (McClanahan and Kosgei 2019). Instead, fishers transitioned away from using nets, for fear of competition due to greater number of fishers. The findings of our study reveal how variable households can be and how household-level and fine-scale data is crucial to understand this variability. Such fine-scale data can be used to support grassroots community efforts towards seagrass conservation (e.g., Unsworth et al., 2019). Importantly, networks and programmes now exist to fill gaps in our knowledge of Indo-Pacific social-ecological seagrass systems at such a fine-scale (e.g., Indo-Pacific Seagrass Network, IKI Seagrass Ecosystem Services Project), but this information must be acknowledged and used in policy and management decisions.

Our study employed an non-probability, convivence design to sample villages (Etikan et al., 2016), where we specifically targeted villages where coastal resource use is high in areas known to the authors. This led to a relatively unbalanced sampling strategy, with the number of household surveys conducted being skewed towards countries with longer coastlines (e.g., Indonesia). While our findings may not be generalizable to the whole of the Indo-Pacific, they can be used to inform understanding across the region and serve as a foundation for future studies. Due to availability of data, we did not include gleaning or the effects of seagrass meadow type and condition in our study. Use of seagrass as a gleaning habitat is high (Nordlund et al., 2018; Furkon et al., 2020) and may contribute greatly to seagrass dependence, especially for households with limited access to gear (Fröcklin et al., 2014). Moreover, in the Philippines, Quiros et al. (2018) showed that seagrass abundance and diversity influenced seagrass catch diversity, and in Tanzania, Jones et al. (2021) showed that certain seagrass traits drive fish abundance suggesting that household dependence on the habitat, especially for fishing, may be influenced by the diversity and abundance of seagrass that exist within an households location.

Safeguarding seagrass meadows across the Indo-Pacific is vital to alleviate poverty. We show that low-income and low adaptive capacity households are dependent on seagrass meadows for safe and nutritious food and that high income households are potentially incentivised to use seagrass due to high rewards. Our study reveals that seagrass meadows are preferred over other habitats for their reliability and note that this likely lies at the heart of their potential safety-net function; the freedom and ability to access seagrass resources either briefly or continuingly. However, if seagrass meadows are lost, the most vulnerable in society will have the most to lose and a need to be considered in management. Moreover, we provide context specific evidence of the prevalence of seagrass fisheries across the region, while highlighting the importance of household-level empirical data to expand our understanding of interactions between the socio-economic and ecological elements of seagrass use in fisheries. The support that seagrass meadows provide to communities can no longer be ignored, doing so would create further poverty for the most vulnerable in society.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2022.106247.

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