Title: Food Webs and the Sustainability of Indiscriminate Fisheries

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Abstract: Here, we introduce a novel theory for multispecies fisheries that exploit fish stocks evenly within and across trophic levels in an entire ecosystem (i.e., fishery comprises all fleets). These “indiscriminate” fisheries may be common in developing countries where fish provide the main source of dietary protein. We show that simple food web modules, motivated by empirical patterns in body size and energy flow, yield general and robust predictions about the fate of such a fishery. Specifically, high and uniform fishing mortality modifies the fish community in a manner that leads to increased productive capacity from a low diversity assemblage of small-bodied fish with rapid population growth and turnover (the productive monoculture effect). We then argue that catches are relatively indiscriminate in the Tonlé Sap, a highly productive inland fishery in Cambodia that feeds millions, and show consistent qualitative agreement between the theory of indiscriminate fishing and this existing empirical data. As the theory suggests, this indiscriminate fishery appears to be remarkably productive at the community level in the face of high fishing mortality; however, it tends to be unsustainable at the species-level as the Tonlé Sap has a much depleted species diversity under its current high fishing mortality. We end by arguing that the reduced diversity of these types of fisheries likely put them at severe risk of being heavily impacted by changing environmental conditions such as climate change and hydroelectric development.

Key words: Indiscriminate fishery, productive monoculture effect, food webs, Tonlé Sap
Main Text:

Fisheries research has a long tradition of focusing on the management of valuable species selected by a fishery (Pauly et al. 2002). Nonetheless, many fisheries are not so selective. Rather, many of the worlds' major fisheries (where for our purposes a fishery includes all fleets within a given ecosystem) are indiscriminate in that they harvest fish across most sizes and species (Welcomme 2008). This appears to be especially true for societies that rely on fish as their major source of protein, where small-scale fishing employing a variety of gears across a diverse range of species is a large component of the fishery (Baran et al. 2001). If we are to understand the impacts of human activity on the sustainability of these indiscriminate fisheries, it is necessary that we consider this as a multi-species ecological and social problem.

Recent research has begun to document the cascading influence of modern fisheries practices at the community and ecosystem-levels (Pauly et al. 1998; Essington et al. 2006). The phenomenon of “fishing down the food web” has been proposed for a broad array of aquatic ecosystems subject to human exploitation (Pauly and Palomares 2005). Other research has suggested that effects of fishing are more likely involve serial addition of trophic levels dubbed “fishing through the web” (Essington et al. 2006). Regardless, there is little doubt that intensive fishing can have substantial influence on fish and other communities within ecosystems (Pauly et al. 2005; Worm et al. 2006, 2009).

One approach to understanding the outcome of multispecies fisheries is to build models that attempt to mimic the vast complexity of natural ecosystems, based on extensive observations of key ecosystem components over time (e.g., Christensen & Pauly 1992; Christensen & Walters 2004). While there has been a surge of work on the multi-species approach (Christensen and Pauly 1992; Walters et al. 1997; Pauly 2000) further work remains to incorporate the role of food web structure into fisheries management (Travis et al. 2014). Here, we employ relatively simple, and analytically
tractable, food web models to elucidate the community-level outcomes of different types of fisheries.

In order to approximate whole system dynamics, we follow functional guilds based on size-structured trophic ecology (Peters 1983) and general life history attributes (e.g., growth rate), which simplify the food web and allow us to analytically generate empirically testable predictions of how functionally similar species respond to high and relatively uniform fishing mortality across an entire food web.

We develop a simple size-based modular food web model to simulate a class of fisheries where per capita fishing mortality ($F$) is identical on all species. This type of fishery, which we will define as an *indiscriminate* fishery, contrasts with a *balanced* fishery (Garcia et al. 2012) where fishing mortality is assumed to scale directly to species production. These two types of fisheries lie along a continuum of fishery types (depicted in one dimension in Fig. 1), from a purely indiscriminate fishery (i.e., all sizes and species have identical fishing mortality, $F$) through a *trophically-selective* fishery (where one trophic level is subject to higher fishing mortality than the others but fishing within any trophic level is indiscriminate – Pauly et al 1998, Essington et al 2005) to a *species selective* fishery (one species of fish is subjected to fishing mortality). Our study of indiscriminate fisheries will focus on three objectives: (i) developing a theory of the ecological impacts of indiscriminate fisheries; (ii) exploring the theory numerically to generate predictions; (iii) assessing existing empirical evidence for the relevance of the theory to an existing exploited ecosystem - the Tonlé Sap Lake in Cambodia.

We find that theory based on a set of common aggregated ecological modules predict a series of rules as to the fate of indiscriminate fisheries under high and sustained fishing mortality or, equally, a history of steadily increasing fishing mortality. These systems are predicted to become low diversity small-bodied communities dominated by a suite of fishes possessing fast-growth life histories that promote a high population growth rate at the lowest trophic level. This dominance by small fast-
growing fishes, in turn, enhances overall community-level productivity (i.e., fast population growth strategies (biomass/year) replace diverse growth strategies). While this increased biomass production potential makes these ecosystems more sustainable in terms of community biomass production, these same fisheries are unsustainable at the species level as many functional groups (e.g., trophic levels or trophospecies; Yodzis and Winemiller 1999) are either eliminated or fished to critically low density.

Finally, we end by discussing the implications of indiscriminate fisheries on sustainability and stability from different perspectives (Ives and Carpenter 2007). Specifically, while indiscriminate fisheries have operated in a manner that increased their community-level “productive” capacity through time, these fisheries have likely done this at the cost of a loss in species-level sustainability (i.e., species are eliminated or rare due to fishing) and system-level “adaptive” capacity (i.e., reduced functional diversity due to fishing).

**A Food Web Theory for Indiscriminate Fisheries**

(i) **Body Size and the Gross Architecture of Whole Food Webs**

In order to generate simple a theoretical framework, we first briefly review empirical patterns in the relationship between body size and the gross structure of food webs (i.e., topology and interaction strength). This gross structure will allow us to create an appropriate yet simple food web model. While the ability to produce numerous, well-resolved food webs has proven elusive (Cohen et al. 1993), the ability to grossly characterize food webs with their major energy flows has advanced rapidly with the increased use of ecological tracers (e.g., stable isotopes, fatty acids), complimented by stomach contents analysis (e.g., Peterson 1999). Additionally, and importantly, empirical patterns in body size (e.g., allometry) put forth decades ago by Rob Peters (1983),
simultaneously suggest outcomes that ought to reflect strongly on the gross patterning of food webs (McCann and Rooney 2009). Below, we argue that empirical body-size relationships align with food web patterns and so suggest a simple gross architecture for aquatic food webs.

In general, body size increases with trophic position in most aquatic ecosystems (Jennings et al. 2001). This simple relationship suggests that mobility ought to increase with trophic position (via body size), since the cost of movement per unit of weight decreases with increasing body size (Peters 1983). Organisms that are more mobile tend to be more generalist foragers because, all else equal, their mobility puts them in contact with a greater number of habitats and prey types (Peters 1983). We therefore expect the increasingly mobile organisms of each successive trophic level to increasingly couple different habitats. At low trophic levels, we expect consumers to couple strongly across smaller scales (microhabitats) and only weakly across different macrohabitats, while at higher trophic levels we expect the larger, more mobile, and increasingly generalized organisms to more strongly couple larger macrohabitat divisions (Pimm and Lawton 1980). Thus, this suggests that food webs should be compartmentalized at low trophic levels and coupled by highly mobile generalists at higher trophic levels (McCann and Rooney 2009) as represented by the coupled food chain module in Fig. 1. In lakes, for example, mobile piscivores can act to couple both benthic and pelagic macrohabitats via their consumption of littorally- and pelagically-derived prey (Vander Zanden & Vadeboncoeur 2002). This pattern by which higher trophic levels increasingly couple carbon across multiple habitats has been uncovered in both aquatic and terrestrial ecosystems (Vander Zanden and Vadeboncoeur 2002; Rooney et al. 2006).

In addition to this gross pattern of energy flow at the whole lake scale, body-size arguments suggest that different compartments (e.g., littoral and pelagic) tend to be constituted by different sized organisms (Rooney et al. 2008). In lakes, the littoral pathway tends to contain
smaller organisms than the pelagic pathway (Rooney et al. 2008). Clearly there are species that do not strictly obey this average property, but this gross patterning suggests that pathways composed of smaller body-sized organisms ought to contain faster growing species, with greater attack rates than the larger-sized pathways since allometric relationships find growth and attack rates, per unit of body size, scale with body size to the \(-1/4\) power (Peters 1983; see Yodzis & Innes 1992 for model parameterization example). This average trait relationship sets up fast (strong) and slow (weak) pathways in aquatic webs (Rooney et al. 2006), a gross architecture that we will employ in the models below to explore the whole food web response of an ecosystem to indiscriminate fishing. Table 1 summarizes these empirical patterns and their relationship to body-size.

(ii) A Simple Body-Size Food Web Theory For Indiscriminate Fisheries

To understand the implications of food web architecture on community responses to fishing, we employ the following general Lotka-Volterra model formulations of the modules depicted in Fig. 2.A-C (indiscriminate) and Fig. 2.A'-C' (i.e., analogous, more selective modules), with the addition of linear loss rates due to fishing mortality, \(F\). In what follows, we consider the following predation-driven model (food chain), competition-driven model (within trophic level interactions) and a combined predation-competition model (coupled food chain module) that mimics the gross food web architecture discussed above (summarized in Table 1):

Food Chain (Predation):

\[
\begin{align*}
\frac{dR}{dt} &= rR(1 - R/K) - a_c CR \\
\frac{dC}{dt} &= ea_c CR - m_c C - a_p PC - F_c C \\
\frac{dP}{dt} &= ea_p PC - m_p P - F_p P
\end{align*}
\]  
(Eqs. 1)

Competition:
\[
\begin{align*}
\frac{dC_F}{dt} &= r_F C_F (1 - (C_F - \alpha_{FS} C_S)/K_F) - F_{CF} C_F \\
\frac{dC_S}{dt} &= r_S C_S (1 - (C_S - \alpha_{SF} C_F)/K_S) - F_{CS} C_S \\
\frac{dP}{dt} &= e_a P C_F + e_a P C_S - m_P - F_P P
\end{align*}
\]
(Eqs. 2)

Coupled Food Chains:

\[
\begin{align*}
\frac{dC_F}{dt} &= r_F C_F (1 - (C_F - \alpha_{FS} C_S)/K_F) - a_F P C_F - F_{CF} C_F \\
\frac{dC_S}{dt} &= r_S C_S (1 - (C_S - \alpha_{SF} C_F)/K_S) - a_S P C_S - F_{CS} C_S \\
\frac{dP}{dt} &= e_a P C_F + e_a P C_S - m_P - F_P P
\end{align*}
\]
(Eqs. 3)

where \(C_F\) represents the smaller-bodied intermediate fast-growing consumer guild/pathway, \(C_S\) represents the slower growing intermediate consumer guild/pathway and \(r_i\) is the per capita growth rate of guild \(i\), \(K_i\) is the carrying capacity of group \(i\), \(a_i\) is the attack rate on group \(i\), \(e\) is conversion efficiency, \(m_i\) is the mortality rate on group \(i\), \(F_i\) is the harvesting rate on group \(i\), \(\alpha_{ij}\) is the competition coefficient of group \(j\) on species/group \(i\), \(R\) is the biomass density of primary producer group \(R\) and is unharvested, \(C_i\) is the consumer biomass density of group \(i\), and \(P\) is the biomass density of top predators (see Supplement S.1 for parameter values used in the paper). Here, the first two models are employed as a means to allow us to develop rules that inform our final empirically-motivated model. The food chain model allows us a look at the simplest model that informs us about within food chain effects of indiscriminate fishing while the competition model is the simplest model that allows us a look at across chain effects. Together, they inform the analysis of the more complex empirically-motivated coupled food chain model (see Supplement S.1).

Our goal is to reproduce the gross architecture of the previous section (Fig. 1, 2.C) and the final model is indeed a simplified version of this gross architecture (see Supplement S.1 rule 3 for...
further discussion). The simple modules we employ unfold trophic structure (e.g., large-bodied fish tend to eat small-bodied fish; Fig. 2.A,A’), different growth rates, as well as embody the ability for different pathways to respond differently to changing competitive or predatory conditions (Fig. 2.B,C; 2.B’,C’). Differential response of community structure is critical to understanding how system-level stability and productivity are altered by fishing mortality and even the gross compartments (e.g., benthic and pelagic) of aquatic webs are known to display compensatory responses (Vadeboncoeur et al. 2002). So, while the approach is simple, it embodies a large amount of biology and still allows us mathematical analysis that yields general predictions. For more detailed body size driven community approaches see the recently developing fisheries work of Andersen and colleagues (Andersen & Brander 2009; Hartvig et al. 2011; Jacobsen et al. 2014) and Law and colleagues (Law et al. 2009; 2012).

To remain consistent with gross food web architectures discussed above, we aggregate the food web into groups based on fish population body size and growth rates. We assume that, on average, general attributes of fish life history corresponds to food web characteristics such that top trophic levels tend to contain relatively slow growing populations of fish, while intermediate trophic levels have a range of life histories from small, fast growing populations that often continuously reproduce to slower growing species (Winemiller and Rose 1992). So, one food web pathway has smaller faster growing species with higher attack rates than the other (Rooney et al. 2006). While there has been numerous aquatic and terrestrial ecosystems (lake, ocean and soil ecosystems) showing this compartmentation and strong-weak pathways, these results have been less studied in tropical floodplain ecosystems. Winemiller (1990), though, has provided detailed stomach contents data across seasons that show evidence of detrital and classic grazing channels coupled by higher order predators.
The definition of an indiscriminate fishery type effectively creates a continuum of fishing scenarios (where a fishery includes all fleets within a given ecosystem), from a purely indiscriminate fishery (Fig. 2.A-C) to the more traditional selective fisheries, of varying degrees (Fig. 2.A’-C’). In the purely indiscriminate fishery models we assume that the fishing induced mortality rate, $F$, is equal on all fish species at all trophic levels (Fig. 2.A-C; hereafter the purely indiscriminate assumption: i.e., $F_i = F_j$ where $i$ and $j$ are different trophic levels and $F_i$ is the fishing mortality within a given trophic level, $i$). For the selective fishery, we assume some fish are simply not targeted at all (i.e., $F=0$) while others species, or groups, are selected (Fig. 2. A’-C’). This range of assumptions moves us from a purely indiscriminate fishery model to a related selective fishery models (Fig. 1).

Other intermediate cases exist and likely are better representations of real fisheries. As an example, one can imagine indiscriminate fishing mortality within a given trophic level, $i$, whereas fishing mortality occurs differently across different trophic levels (i.e., the fishery is trophically selective such that $F_i \neq F_j$; Fig. 1). This latter case may happen readily, for example, when a fishery first selects for bigger fish before moving to smaller fish after the higher trophic level fish are depleted (Jacobsen et al. 2014). In what follows, we outline 3 general theoretical rules that robustly hold for both the purely indiscriminate fishery as well its’ weaker, perhaps more realistic form, the trophically selective fishery. Where appropriate, we discuss the rules with respect to the classical selective fishery.

**Rule 1: Fishing Down Food Webs (Food Chain or Predation: Fig. 2A, A’)**

All else equal, under increasing fishing mortality, $F$, the top predator trophic level is necessarily lost before the lower trophic levels. This result is broadly true for fisheries on the indiscriminate side of the fishery continuum since it occurs readily for a purely indiscriminate, or a trophically selective
fishery. This means that a fishery solely focused on the intermediate trophic level would still deplete the top predators first via the indirect repercussions of fishing the lower trophic levels. Omnivory weakens this result, but since empirical estimates of omnivory have tended to suggest that omnivorous interactions are weak (Polis 1991; Link 2002, Thompson et al. 2007; Gellner and McCann 2012), the result presented here suggests that indiscriminate fishing generally tends to hit the higher trophic levels hardest (See Supplement S.1 for proof).

True selective fisheries, on the other hand, should not directly result in truncated food chains, since untargeted fish from all trophic levels will not necessarily be depleted. Fishing down the food web, therefore, ought to be a more common empirical finding within indiscriminate fisheries, or selective fisheries that collectively harvest all species that form a focal food chain. This prediction is in line with recent findings that show declines in mean trophic level of catches are not always mirrored by declines in the mean trophic level of the whole ecosystem, assayed from independent scientific surveys (Branch et al. 2010). The theory above predicts that the mean trophic level of catch should be closer to the mean trophic level of the whole ecosystem for indiscriminate fisheries.

**Rule 2: Fishing Across Food Webs (Competition; Fig. 2.B,B’)**

Under increasing fishing mortality, $F_i$, within a trophic level $i$ (Fig. 2.B), the fastest growing life history strategy becomes dominant under a purely indiscriminate fishery (See Supplement S.1 for proof). The purely indiscriminate fishery often responds initially by increasing total system production (due to the fast growing stocks being released from competition from the competing slow-growth strategists); however, with sufficiently high fishing mortality total production must eventually decline when all fish become severely depleted.

While not explicitly modelled here, the outcome of the traditional selective fishery clearly
depends on whether the fishery targets fast-growth, slow-growth or some combination of fishes. If
growth rate of fish stocks correlates positively to price/protein, for example, then selective fisheries
may select for fast growing fish yielding the exact opposite community outcome (mean community
fish growth is depleted). Nonetheless, it is also possible that fisheries select for slow or moderate
growth fish (e.g., many fisheries target large bodied fish that are slow-growing). If selective fisheries
target different growth strategies (i.e., fast, intermediate or slow), then these more selective fisheries
should collectively show no clear patterning in changes in the average growth life history in the fish
community, while one fishery may increase the presence of slow growth strategies (by selecting fast
growth species) another may also increase the presence of fast growth species (by selecting slow
growth species). The collection of many such selective fisheries, therefore, would tend to produce an
idiosyncratic response as opposed to the singular fast-growth domination of the indiscriminate fishery.

Rule 3: Fishing Down and Across Food Webs (Coupled Energy Pathways; Fig. 2C, C’)

One of nature’s ubiquitous food web structures is the coupled food chain module (Fig. 2.C,C’) as it
combines the interactions of competition and predation together, and empirically describes the
pathway of major carbon flows coupled by higher order generalist predators in food webs (see above
discussion). As discussed, empirical results suggest the existence of slow (weak) and fast (strong)
pathways in many aquatic and terrestrial ecosystems that often arise due to different body-size
patterns in separate compartments (e.g., littoral versus pelagic; or fungal versus bacterial), and further,
it has been theoretically shown to promote system-level stability (Rooney et al. 2006). In this case,
under increasing fishing mortality, \( F \), in the indiscriminate fishery, the food web is fished down
relative to the lower trophic levels, while as above, the fast growing life history strategy in the
intermediate trophic level becomes dominant (see Supplement S.1). As in rule 2 above, the dominance
of the more productive strategist often initially drives an increasing overall system production before extremely high fishing mortality begins to reduce overall production. This increased production is amplified as in this case, with increased fishing effort, slower growing top predator biomass is replaced by fast growing smaller-bodied intermediate consumer biomass.

Even in the absence of the strong-weak pathway assumption, the top predator is generally first depleted under indiscriminate fishing and the system tends to reduce to dominance by fast growth intermediate consumers (see Supplement S.1). The result is not dependent on the strong-weak pathway assumption but its generality is dependent on the topology (Table 1), and the assumption of weak competition between different habitat compartments (see Supplement S.1). This latter assumption of weakly competing compartments results from the fact that empirically-derived macrohabitat compartments (e.g., littoral versus pelagic) are spatially separated and so likely to only compete weakly. Nonetheless, the dominance of fast growing strategies in the ecosystem (i.e., productive monoculture effect), though, arises more rapidly with increasing $F$, relative to the competition case above (i.e., rule 2), given the empirical observation of strong-weak pathways in whole ecosystems. Here, as top predators are reduced from fishing, the fast growing intermediate consumers ($C_F$) gain both a competitive advantage (the fast growth consumer outgrows the slow growth species in the absence of predation) and benefits simultaneously from a greater release in predation than the less consumed slow growth consumer. This synergistic response drives an even greater probability of increased total system production before high culling eventually overwhelms the fast growth species. Again, given that the selective fisheries may target any organism, regardless of growth rate, then the selective fisheries can be expected to produce a suite of possible outcomes (see Supplement S.1).
**Numerical Results**

Fig. 3A shows an example of the response of the equilibria for the fully integrated food web module under a trophically indiscriminate fishery assumption, as well as the assumption that the fast growth intermediate consumers ($C_F$) are attacked by predators at higher rates (i.e., the fast-slow pathway assumption).

In many fisheries, $F$ has actually increased through time so this figure can be envisioned as a simple prediction, consistent with the rules outlined above, of the historical fate of these fisheries. Fig. 3A shows that indiscriminate fisheries should be both fished down and across thus freeing a dominant group of high production stocks at lower trophic levels. Similarly, selective fisheries should experience both fishing down, and across the web, within focal webs of targeted species but non-targeted species should not necessarily decline.

In a sense, the indiscriminate fishery unintentionally reduces diversity (extremely unsustainable at the species level) and yet increases the community-level sustainability and production of the remaining stocks. Fig. 3B and 3C compares the whole community production (3B) and population-specific production (3C) from all three possible selective fisheries (on $P$, on $C_F$, and on $C_S$) to the indiscriminate case where the community ultimately dominated by the high-growth life history endpoint (i.e., all $C_F$). The selective fisheries are generally far less productive, for the same amount of fishing effort, than the low diversity community of fast-growth fish. In some cases, the total fishery production of the selective fishery on the high growth species can match, or exceed, the indiscriminate fishery but, regardless, the indiscriminate fishery undoubtedly generates a strong community level production response. This occurs, effectively, because the relative biomass of high growth species continually increases across $F$ (see Fig. 3A) suggesting that such a fishery tends to replace low growth biomass with high growth biomass.
There is an additional outcome of a heavily fished indiscriminate fishery. Except for extremely weak biotic interactions that produce monotonic dynamics (i.e., population dynamics without overshoot), trophic interactions readily produce dynamics with periodic signatures under stochasticity (Pineda-Krch et al. 2007). In the presence of abiotic forcing, the strength of these oscillations, or quasi-cycles, reduces correlations of population dynamics with the environment. As such, we expect the correlation between the environmental forcing signals and the population dynamics to be weakened in the presence of biotic interactions (transient quasi-cycles are the signature of top-down control). However, with high and indiscriminate harvest by humans these biotic oscillations are ultimately muted (Martin and Ruan 2001; McCann 2011). Thus, with high indiscriminate fishing mortality, the internal dynamics of the system become less variable and the dynamics are expected to become more temporally-driven by bottom-up forces (i.e., by physical drivers like flooding, temperature, nutrients, etc.).

To investigate this dynamic, we ran the above model for an indiscriminate fishery across a range of $F$ and kept track of the population-level variability and the correlations between the sum of the populations (i.e., $P$, $C_F$, and $C_S$) and our stochastic driver (See Supplement S.2; red noise process on the carrying capacities, $K$). Fig. 4 shows that, indeed, the correlations of the population dynamics and the environmental noise increase as fishing mortality increases in strength. We refer to this as the productive monoculture effect as the dominance of the single fast growth strategy makes the system behave like a single species agro-ecosystem selected for high production. This synchronization of a dominant fast-growth guild also means that the community stability is compromised as the ability to respond differentially to variable conditions is lost (i.e., Portfolio Effect; Doak et al. 1998; Tilman et al. 1998; Schindler et al. 2010). We suggest that this increased positive correlation, therefore, may be seen as an indicator of the loss of a systems “adaptive capacity” (i.e., there is no capacity for
differential response to changing conditions).

Empirical Results: The Tonlé Sap Floodplain Ecosystem

A globally important example of large-scale indiscriminate fishing is the Tonlé Sap Lake ecosystem that is connected to the lower Mekong River. This large, shallow lake is fished in a variety of ways including: (i) the commercial bagnet (Dai) fishery that traps fish moving along the Tonlé Sap river between the lake and the Mekong River; (ii) commercial trap and net fisheries (e.g. gillnets, seine nets, barrage traps); (iii) artisanal fisheries (hook and line, throw nets, small gill nets); and (iv) small-scale rice field fisheries (Baran et al. 2001). The breadth of methods and places where fish are sought after makes the Tonlé Sap a prime example of a top-to-bottom indiscriminate fishery (see Fig. 5A-C).

Data for gear type and usage suggest that fish are caught relatively indiscriminately from all taxa, habitats and across a range of gear sizes (Fig. 5A-C). Further, fishing mortality has likely increased due to increases in population, increases in gear efficiency and increased percentages of the population actively participating in the fishery (Baran et al. 2001). As such, we expect that this fishery has experienced a slow and steady increase in $F$ over time. The Tonlé Sap has effectively lost the stocks of many of its large predators and large herbivores/detritivores, both slow growth life history strategies relative to the smaller high growth fishes (Zalinge et al. 2000). The indiscriminate nature of these fisheries is such that fish alone are not targeted; rather turtles, snakes, mammals and other aquatic or semi-aquatic organisms are also sought after (Campbell et al. 2006). Notable examples of large organisms being depleted abound in the Tonlé Sap floodplain, with the Mekong giant catfish, Irrawaddy dolphin, Siamese crocodile, and the Giant barb as representatives for this serial historic depletion of mega-fauna (Hogan and Moyle 2004; Campbell et al. 2006).

To get at this reduction in size more quantitatively we examined the mean size of all fish
species found to be listed as “at risk” within the Tonlé Sap versus the mean size of all fish species found to be listed “of least concern” within the Tonlé Sap (Supplement S.3). The mean size of at risk species (59.7 cm) was nearly double that than those of species of least concern (35.2 cm) suggesting that larger, slower-growing species have tended to be impacted most through history ($p=0.03$). Additionally, other research (Baird and Flaherty 2000; Zalinge et al. 2000; Sverdrup-Jensen 2002; Baran and Myschowoda 2008) has shown that some of the smaller, more opportunistic fast growth strategies dominate the catches. The group of fish commonly referred to as Trey Riel (dominated by a few *Henicorhynchus* sp.) are consistently 30-50% of the Dai fishery catch (Campbell et al. 2006), an amazing dominance given that this system is believed to have over 500 fish species and many are migratory. The bagnet method used in the Dai fishery is not selective for size or species and therefore represents a reasonable approximation of the migrating fish stock. Unfortunately, as with many of these important fisheries, it is difficult to assess how different this is from historical levels. While some research has found evidence of a significant reduction in diversity (Lim et al. 1999), others (Baran et al. 2001) have found little evidence for temporally changing community structure in the major species of the Tonlé Sap. However, very little data exists before Cambodian independence in 1993 and there remains the distinct possibility that the real signature of diversity change occurred before this time and the system has long-since settled into a new high-production fishery. Nonetheless, like many of the important, yet understudied, world fisheries, this system now resides at the brink of massive environmental change (Stone 2011). With climate change and dams both likely reducing the amplitude of the flood-pulse nature of this system (Kummu and Sarkkula 2008; Lauri and Moel 2012), this ecosystem will be forced to adaptively respond to novel environmental conditions.
Discussion

Here, we have described a continuum of fisheries types and then developed a food web model for indiscriminate community fisheries. Our theory proposes that a diverse fish community subjected to high and indiscriminate fishing mortality ought to experience the following:

(i) a depletion in top trophic levels (*Fishing down the food web*);  
(ii) a depletion in slower-growing stocks (*Fishing down and across the web*), and;  
(iii) a dominance in fast-growing fish that consequently tend to increase the overall system production (*Productive monoculture effect*) and decrease community level stability (i.e., lost *Portfolio Effect*).

These results suggest that indiscriminate fishing at moderate to high $F$ values is incompatible with maintaining a high-diversity fishery. However, indiscriminate fishing moves the community and fishery to a low-diversity, high-productivity state that is capable of sustaining resilient community biomass even at high fishery mortality. Intense indiscriminate exploitation of a community of fishes can therefore be effective at maximizing fisheries yield. This comes at the extreme cost of creating a strongly bottom-up driven ecosystem that is synchronized with, and dominated by, major physical forcing events. While such ecosystems can be robust to high fishing pressure on average, they are also expected to be extremely unstable (i.e., high coefficient of variation, CV) in “noisy” environmental conditions.

While we have focused on a food web theory for indiscriminate fisheries, it is also interesting to compare these fishery types to alternative management models. As discussed, one alternative that emerges from the more temperate literature is the notion that many fisheries target a select group of high value species. Based on our theory, these fisheries are expected to produce dominance of organisms that humans, for whatever reason, have not targeted. Examples have emerged where such
non-preferred fish have begun to dominate (Mills 2001; Purcell et al. 2007). Also consistent with our
theory for selective fisheries, recent research has found that unselected top predators in whole
ecosystems do not decline and may in fact increase in density (Branch et al. 2010). Intriguingly, our
type suggests that indiscriminate fisheries ought to be the fishery type that truly displays
consistently strong signatures of “fishing down the food web” (i.e., fished mean trophic levels show
same decline trends as ecosystem level mean trophic levels).

There are several caveats to our theoretical results. First, we have concentrated on a simple
aggregated food web model that characterizes the major flows of carbon in many real webs (i.e.,
multiple competing energy channels coupled by mobile predators); however, it is unclear whether
more reticulate speciose models operate the same way. Existing recent approaches in the balanced
fishery literature (where whole communities are fished proportional to their productivity) have
examined similar questions using size and trait-based models and found results, in terms of
productivity, consistent with those presented here (Jacobsen et al. 2014; Law et al. 2012). Specifically,
Jacobsen et al. 2014 compared several system-wide fisheries cases and found that unselective
balanced fishery (effectively our indiscriminant fishery) tended to be the most productive. Although
not examined here, it is important to point out that truly balanced fisheries (i.e., species selection by
productivity) are both relatively productive and much more sustainable/stable at the species-level than
the indiscriminate approach of countries that rely on fish protein (Jacobsen et al. 2014; Law et al.
2012). Here, we have introduced an alternative to the balanced fishery perspective that is an
indiscriminate multispecies fishery. We note that the true test of whether a multi-species fishery is
balanced or indiscriminate depends on whether fish are fished in proportion to their productivity
(balanced) or simply fished in proportion to their density (indiscriminate). To our knowledge the few
ecosystems that have been argued to examples of balanced fisheries have not explicitly demonstrated
the correlation between productivity and fishing selectivity (Garcia et al. 2012).

Further, fish communities are clearly replete with stage-structure and, for simplicity, we have ignored this complexity. We argue that the indiscriminate results ought to remain as long as juveniles of higher order predators that compete with smaller, lower trophic level fish are outcompeted by their intraguild prey. This common assumption of IGP theory is required for coexistence (Holt and Polis 1997) and facilitates the sequence of depletion outlined in our rules. Nonetheless, the addition of stage structure will add some interesting further predictions (e.g., fishing down the web will be preceded by the strong truncation of each species size classes and trophic level), that are beyond the scope of this paper. Recent work by Hartvig et al. (2011) have begun to create a framework that makes this approach very feasible, and future work in this area is important. Similarly, Zhang et al. (2013) have developed a spatial model analogous to the habitat simplification embodied in our simple approach here.

Our results suggest that sustainability, in terms of community-level biomass productivity, is inversely related to diversity in the case of indiscriminate fishing. Here, as emphasized elsewhere (Ives and Carpenter 2007), it is important to consider multiple axes on which issues like sustainability and stability operate. While production sustainability at the whole community scale may temporarily increase, it is becoming clear that diversity operates to buffer against changing conditions (Tilman et al. 1998; McCann 2000). Ecosystem theory on stability has also recently argued that the loss of diversity (be it species, population, or functional group diversity) likely reduces the “adaptive capacity” of ecosystems, and so reduces the ability for these systems to respond to novel human impacts on the horizon (Levin and Clark 2010; Schindler et al. 2010; McCann 2011). In the case of highly productive floodplain ecosystems that are the basis for many of the World’s inland fisheries, fisheries productivity is strongly linked to the seasonal hydrological pulse that has been coined the
“life blood” of these ecosystems (Junk et al. 1989). While the indiscriminate fishery may be stable to fishing mortality alone and often can increase current fisheries yields, it remains to be seen if the history of pushing these systems towards acting like “productive fast-growth monocultures” places them at heightened risk to the changing environmental conditions that loom over these same ecosystems that furnish protein for millions of people.


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Figure Legends

Fig. 1. A continuum of world fisheries from the purely indiscriminate fishery, where all trophic levels and organisms, are equally sought after to a purely selective, or target, fishery where one or a few species are selected. Note, the strengths of $F_j$'s effectively vary across this continuum so the continuum is more appropriately multi-dimensional. In practice, fisheries lie somewhere on this continuum and different forms of selectivity, or indiscriminateness, can occur. As an intermediate example, we show the case where the entire middle trophic level is caught while the lower and top trophic levels are not fished (i.e., indiscriminate within the middle trophic level or middle trophic level is targeted). Symbols P, C, and R stand for predator, consumer and basal resource respectively. The module shown represents a graphical example of coupled food chains whereby compartmentalized lower trophic levels (R and C) are coupled by larger, higher trophic position and more mobile generalist predators (P).

Fig. 2. Fisheries food web modules for indiscriminate fisheries and selective fisheries. A) indiscriminate food chain; A') selective food chain; B) indiscriminate competition within trophic level; B') selective competition within trophic level; C) indiscriminate fishery in food chain and competition case; C') selective fishery in food chain and competition case.

Fig. 3. The general model equilibrium solutions for: A) an indiscriminately fished food chain with competition at the intermediate trophic level (model from Fig. 2C'), and; Panel B) displays the maximum sustainable yield (MSY) curve for an indiscriminant fishery (indisc), compared to the estimated total system MSY (of all fish; P, C_F and C_S) of the given selective fishery (here MSY is estimated from community biomass patterns, not just the selective fishery patterns) or C) the
indiscriminant fishery MSY is compared to the species-level MSY of the given selective fishery. The MSY of the indiscriminate tends to show the larger MSY curves due to the release of the fast growth species productive capacity. Parameters given in Supplemental Information.

**Fig. 4.** Simulations of the complete model food web under indiscriminate fishing (Fig. 2C) showing the correlation between the community biomass density and the stochastic environmental forcing variable, \( \rho \), (following a red noise process, see Supplement S.3). At low \( F \), the internal biotic signatures of the dynamics dominate (system is more top-down driven) the time series and so correlation is low, while at high \( F \), the system becomes dominated by r-strategists (opportunistic n terms of Winemiller & Rose (1992) and entrains with the environmental forcing dynamics (system more bottom-up driven). Parameters given in Supplemental Information.

**Fig. 5.** The Tonlé Sap fishery is fished consistently across A) taxa, B) habitats, and C) sizes. While there is modest seasonal signal (annual water level shown as thick, grey line), the Tonlé Sap fishery is a multi-species fishery that shows a signature of being fished in all habitats by many gear sizes in all months. Data for gear type and usage in the Tonlé Sap were taken from Deap et al. (2003) and are reported here as: A) the number of species targeted by all combined gear types (reported as a % of total species), B) the number of gears used in each habitat (shown as a % of total gear types), and C) the number of small, medium and large scale gear types (shown as a % of total gear types).
Table 1. Body-size assumptions and the implications for food web topology and model parameters. See text for full discussion.

<table>
<thead>
<tr>
<th>Body Size Relation</th>
<th>Model Topology</th>
<th>Model Parameterization</th>
</tr>
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<tbody>
<tr>
<td>Per capatia growth of resource ((r)), attack rates ((a)), and mortality rates ((m)) decrease with increasing body size because the per unit biomass allometric relationship decreases (Peters 1983, Yodzis and Innes 1992).</td>
<td>Small fast channel consumers ((C_F)) have higher growth rates ((i.e., r_F)) than smaller slower consumers, (C_S) (McCann and Rooney 2009, McCann 2011).</td>
<td>Top predator consumes faster grower consumers with greater attack rates. This common assumption mediates the coexistence of the food web and completes the fast pathway empirical pattern found by Rooney et al. (2006, 2008).</td>
</tr>
<tr>
<td>Body size tends to increase with trophic level within different macrohabitats (Jennings et al. 2001).</td>
<td>Predator body size &gt; Consumer body size &gt; Resource body size.</td>
<td></td>
</tr>
<tr>
<td>Movement costs decrease with size (Peters 1983). Consequently movement increases with size and trophic position.</td>
<td>Increased mobility tends to increase generalist foraging and the ability to consumer from different macrohabitats.</td>
<td>This drives a more compartmented lower trophic level food web that is coupled by more mobile, generalist predators (Rooney et al. 2006).</td>
</tr>
</tbody>
</table>
Fig. 1. World Fisheries Continuum
Fig. 2

Indiscriminate

A.

B.

C.

Analogous, More Selective

A'.

B'.

C'.

189x261mm (300 x 300 DPI)
Fig. 3

A. Indiscriminate Fishery

B. Total Community Production

C. Species Specific Production

171x266mm (300 x 300 DPI)
Fig. 5

A. Taxa

B. Habitat

C. Gear size