Linking human harvesting behaviour to fisheries food webs: Human interactions in managed ecosystems

by

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Effective fisheries management requires an understanding of harvesting impacts and how they are influenced by human behaviour. Clearly not all harvesting impacts are the same, so it is important to classify fishing behaviour based on fisheries catches and human effort and decision-making. This thesis provides an important basis for classifying global fisheries based on human impacts and a framework for understanding the dynamics of holistic social-ecological harvesting systems. Chapter 1 presents a novel approach to characterizing harvesting behaviour based on the topology and distribution of human interactions throughout fisheries food webs, and shows that global fisheries exist along a continuum of human fishing generality. Further, I show that global patterns in fishing behaviour can be explained by geographic location and socio-economic conditions. With an understanding of societal motivations driving harvesting behaviour, holistic social-ecological resource management models that consider human decision-making and harvesting effort can be developed. Chapter 2 investigates the dynamical implications of harvesting in a simplified social-ecological model as a first step towards characterizing differences in human impacts based on harvesting behaviour. The results show that harvesting has the potential to drive stability in a resource at weak to intermediate levels of human impacts. However even a simple model has the potential to produce extremely complex dynamics, including human-driven cycles, chaos, long transients and alternate states. This thesis illustrates the importance of including human behaviour in resource management models by developing thorough social-ecological harvesting models.
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PROLOGUE

While fisheries science has a long history of population dynamics-based theory and statistics, and has more recently seen a push towards more holistic ecosystem-based fisheries management (EBFM), a common deficiency of both approaches is a thorough understanding of human impacts on whole ecosystems and the factors driving differences in these impacts. Human fishing behaviour is one of the main uncertainties in fisheries science, which makes it difficult to truly determine human impacts and fisheries' sustainability (Fulton et al. 2011). While economists have long been interested in human behaviour and decision-making, the link between fishing behaviour and ecosystem impacts is still unclear.

Harvesting behaviour is clearly not a static process, so understanding the dynamic human impacts throughout an ecosystem is crucial for proper fisheries management. Further, as noted by Travis et al. (2014) fisheries science is still lacking a dynamic approach to understanding the stability and sustainability of whole systems. A better understanding of the interactions within a system, including dynamic human interactions, is needed to get an idea of the structure and functioning of whole system fisheries.

There are many different types of fisheries around the globe, which all impact ecosystems differently, but little has been done to classify whole-system fishery types. Assessing fisheries at the ecosystem-scale, rather than individual fish population or gear used, gives us a better idea of the total human impact and we can get closer to understanding and characterizing the human interactions within a whole system. This would allow fisheries scientists to make effective management decisions based on the whole system fishery impacts of different fisheries and harvesting behaviours. Fisheries management cannot be seen as a one size fits all problem, however grouping fishery types based on a common indicator that classifies harvesting behaviour would provide the basis for a simple yet effective way to approach fisheries management.

An approach somewhere between population-based modelling and total EBFM is needed to
characterize human impacts on fisheries at a global scale, and understand the dynamics (in a whole system) and sustainability of these systems. This is where food web theory becomes relevant: an approach holistic enough to include many interactions while remaining dynamic, and general enough to be applicable across systems. Considering humans as part of the food web allows us to view fishing behaviour in a way that ecologists may think about a top predator’s foraging behaviour. That is, humans can be specialists or generalists and this fishing behaviour determines the human’s connectance through a food web. Chapter 1 of this thesis introduces a novel approach to characterizing ‘types’ of whole-system fisheries based on fishing behaviour and the distribution of human interactions throughout a food web. This approach can be scaled up or down based on the availability of data, but in any case allows us to compare different fishing behaviours – something that is needed to develop a more comprehensive fisheries management theory that considers different fishery types based on human impacts in a food web.

With an understanding of the different fishery types, I then ask what drives these differences in fishing behaviour and whether there are global patterns in the distribution of these fisheries. Economics is known to drive fishing pressure, but it is possible that the socio-economic circumstances of fishing people might determine the way fishing pressure is distributed throughout a food web. That is, there may be global patterns in how humans impact fisheries food webs (e.g., as specialists or generalists) based on those humans’ geographic location or economic situation. I investigate this relationship using preliminary topological data for whole-system fisheries food webs.

Researchers have recently begun to investigate the ecological implications of different fishing behaviours (e.g., Jacobsen, Gislason, and Andersen 2014), but there is still much more room to expand on these ideas for a thorough understanding of these systems. Further, fisheries science has until recently (e.g., Fryxell et al. 2010) typically considered humans as non-dynamic in resource management models. Chapter 2 provides a first step towards creating an understanding of the interaction between humans and harvested ecosystems by using a simplified social-ecological dynamical system to explore the effects of human behaviour on the stability of a harvested resource. I explore the dynamic nature
of harvesting effort as a base model for understanding human impacts on a fisheries food web.

Together, this thesis provides an important basis for classifying global fisheries based on human impacts, and a framework for understanding the dynamics of more holistic social-ecological harvesting systems. I show that even in a simple social-ecological model complex dynamics can be generated, highlighting the need for development of a comprehensive theory coupling humans and food webs.
References


CHAPTER 1: LINKING HUMANS TO FOOD WEBS – A FOUNDATION FOR THE CLASSIFICATION OF GLOBAL FISHERIES

Abstract

Effective fisheries management is paramount to conserving the production of fish biomass and biodiversity while simultaneously maintaining food security. Traditional approaches to fisheries management have focused on understanding and predicting the dynamics of harvested populations, often using static estimates of human impact. Much less emphasis has been given to the dynamics of human effort and harvesting behaviour and their influence on diversity, structure, and functioning of whole ecosystems. To address this gap, I link the well-studied human aspect of fisheries with the rapidly developing framework of food web theory to classify fisheries globally based on the nature of human impacts and harvesting behaviour. First, I explicitly link humans to fisheries networks by providing the first global perspective of human impacts on fisheries food webs that classifies fishing pressure based on topology and human interaction strength throughout a whole-system fishery. Based on this explicit integration of humans into the food web, I then establish a simple graphical multi-dimensional continuum that identifies and characterizes multi-species fishery types. I find that from a topological perspective there appears to be distinct classes of global fisheries along a continuum of human fishing generality and that socio-economic environments dictate fishing behaviour, allowing us to see global geographic patterns in fishery types. Specifically, people in less developed countries act more as generalists than specialists in their fishing behaviour. These results highlight the importance of managing whole system fisheries based human fishing behaviour to effectively preserve both biodiversity and food security.
Introduction

Fisheries science has developed a powerful set of statistical tools and population dynamic-based theory to manage harvested species (Beverton and Holt 1957; Fournier, Hampton, and Sibert 1998). Multi-species approaches to management have continued to build on this work, and extensive food web and ecosystem-based management approaches have been developed to consider whole system dynamics (e.g., Ecopath/Ecosim; Pauly, Christensen, and Walters 2000). These approaches, though, tend to still focus on understanding and predicting the dynamics of the harvested populations, and static estimates of human impact (e.g., total fishing mortality, F) with much less emphasis on how human impacts influence the diversity, structure and functioning of ecosystems (although see Garcia et al. 2012). Recognizing this, Travis et al. (2014) called for fisheries science to continue to develop a dynamic management approach that considers the structure and function of whole systems by accounting for the mosaic nature of species interactions. This approach has been more the research domain of ecologists, who have long recognized the need for building a comprehensive multi-species fisheries theory (May et al. 1979). Thus, to accomplish this newer dynamic fisheries management goal, a more ecological perspective is needed to investigate how a local fishery or a set of local fisheries impacts the diversity, structure and functioning of whole ecosystems.

One recently proposed approach to ecosystem-based management that does consider implications for biodiversity is the “balanced harvest” strategy (Jacobsen, Gislason, and Andersen 2014; Garcia et al. 2012; Zhou et al. 2010). The argument here, greatly simplified, is to harvest all species in proportion to their productivity and thus roughly maintain biodiversity in “balanced” proportions consistent with their natural unharvested state. While an interesting proposal, the notion of balanced fishing has proven contentious for a variety of reasons including the extreme difficulty of implementing such a strategy (Burgess et al. 2015; Froese et al. 2015; Charles, Garcia, and Rice 2015). Nonetheless, the balanced fishery argument has garnered interest simply because it highlights the important fact that the human impact of fisheries ultimately has large consequences on the sustainability, diversity and structure of the whole system, rather than a single population.
Further, it highlights that the system-wide impact of a distribution of fishing pressures, whether balanced or not, necessarily alters the structure and maintenance of biodiversity.

One way forward is to continue to link the well-studied human aspect of fisheries (e.g., direct measures of human impact on fish mortality) with the rapidly developing framework of food web theory, which seeks to understand how food web structure mediates the critical functioning of ecosystems (Rooney and McCann 2012; Dunne, Williams, and Martinez 2002; Wootton 1994; May 1972). Regarding fisheries from a food web perspective allows us to investigate human interactions and distributions of fishing pressure throughout the food web, to classify and characterize the human impacts on these systems. Such an approach broadens the scope of resource management to simultaneously include biodiversity research, while driving an axis of food web research that explicitly includes humans in the networks (Thompson et al. 2012; Cardinale et al. 2012).

Although tools designed for ecosystem-based management have been effective at characterizing fishing pressure and human impacts on the whole system (albeit not always dynamically), they generally rely on data and assumptions made on a case-by-case basis (Fulton et al. 2011; Christensen and Walters 2004). They are not appropriate for generalizing across ecosystems based on human impacts. A method that could classify fisheries globally based on the types of human impacts (i.e., human-induced fishing mortality throughout the food web) would help as a starting point to apply ecosystem-based management approaches to many fisheries globally based on the type of fishery.

To fill this void in fisheries research, a recent literature that employs size-based models has emerged to generically classify whole-system human impacts for different fisheries (Jacobsen, Gislason, and Andersen 2014; Law, Plank, and Kolding 2012). Here, researchers have approximated different ‘types’ of fisheries based on the distribution of fishing pressure on multi-species assemblages (cleverly approximated through size-based models). These fisheries types can be thought of as having different distributions of human impacts, or interaction strengths, throughout a food web. Consequently, the development of theory that relies on fisheries type allows researchers to empirically consider the nature
of whole-system fisheries globally. A classification of fishery types is needed to empirically identify patterns in the distribution of human interactions through an ecosystem, across the set of all global fisheries. The analysis of empirical patterns that may emerge when examining a range of fishery types may provide insight into the influence of whole-system fisheries on the structure and function of food webs.

Importantly, the classification and empirical identification of distinct whole-system fisheries will allow us to map fisheries types to global patterns in income and geographic location. It has long been recognized that economics drives fishing behaviour in terms of total effort as well as responses to changes in a resource (Mackinson, Sumaila, and Pitcher 1997; Gordon 1954). Interestingly, some researchers have conjectured that socio-economic aspects of a country or region can be expected to fundamentally alter not just effort, but how humans impact a system, through changes in harvesting behaviour (Béné et al. 2009; Dey et al. 2005; Dey 2000). It remains to be seen if and how socio-economic environments influence fishing behaviour, and more specifically the distribution of human interaction strengths through fisheries food webs. Once identified, a continuum of fishery “types” forms the basis for organizing a multi-species fisheries theory that looks at how different management strategies alter the stability, function and diversity of whole ecosystems. Integrating humans into fisheries ecology and classifying whole-system fishery types, therefore, forms a conceptual and empirical starting point for understanding fisheries and their sustainability in a global context.

In what follows, I first explicitly link humans to fisheries networks, both topologically (which species humans eat) and with estimates of human interaction strengths on different fish species (i.e., the pattern of fishing mortalities on each species $i$). With this explicit integration of humans into the food web, I then establish a simple graphical multi-dimensional continuum that identifies and characterizes multi-species fishery types. I end by empirically examining patterns in global fisheries in two ways: (i) I first look at the multi-species nature of global fishery types (i.e., topology), and; (ii) I assess the geographic and socio-economic patterns in these types of fisheries. I find that data on the multi-species
interaction strengths of humans on fish communities is poor at best, but from a topological perspective there appears to be distinct classes of global fisheries, and that these different types of whole-system fishing behaviours are strongly associated with geographic and socio-economic characteristics.

**Linking Humans to the Food Webs of Global Fisheries**

(i) **Topology and Human Interaction Strengths**

Let us start by simply building humans into the food web explicitly using the topological aspect of human interactions as a starting point to understanding the full set of interactions in whole system fisheries food webs. Conceptually, this would create binary topologies of whole food webs (0 for no interaction or harvesting, and 1 for an interaction) that include humans as a predator. Clearly fisheries models have explicitly included human interactions, but here I emphasize that I am concerned with the set of all fisheries (e.g., trawl, long line, gill net, traps, etc.) used within an ecosystem. Thus, I am interested in every species caught in large or small quantities, by all gear types and fleets, and as bycatch. This human fishing behaviour can be quantified as a simple metric I will refer to as the “degree of generality” of human impact in such a topological web. Specifically, if both the total species richness in an ecosystem \( S_T \) and the total number of species caught in a whole-system fishery \( S_F \) are known, then the percent of species harvested (i.e., Degree of Generality = \( S_F / S_T \)) can easily be calculated. From a simple topological perspective alone then, we can create a continuum of human fishery types ranging from highly selective or specialized fisheries (near 0) to extremely general, multi-species fisheries with every species being caught (Degree of Generality = 1; Figure 1a). Classifying fisheries in this simple way immediately allows us to determine where humans act as specialists and where they act as generalists and lets us assess the relative effects of specialist versus generalist behaviour on whole ecosystems.

After building topologies, the next logical way to incorporate human interactions is through strengths of the interactions. By far the more influential component of human impacts on an ecosystem lies in the nature of the direct and indirect interactions of humans (say, via
fishing pressure) on any given species (Paine 1980; van Altena, Hemerik, and de Ruiter 2016). Thus, the magnitude of fishing pressure on each species tells us how fishing impacts the food web as a whole. Strong human interactions, like strong C-R interactions, are known to generate cyclic dynamics (e.g., Fryxell et al. 2010) and can drastically amplify variations in population abundance (Hsieh et al. 2006), highlighting the importance of understanding the distributions of human interaction strengths through fisheries food webs.

Consistent with food web ecology, I will define fishing mortality from humans as the interaction strength between humans and each species. Following fisheries research, a simple first approximation of the negative impact on a given fish species $i$, where $N_i$ is abundance, is $-f_i N_i$ where $f_i$ is the fishing mortality. Given this, then I can define the negative component of the interaction strength as $f_i$ (or the entire term $f_i N_i$). For now, I will ignore the positive interaction strength of fish on humans, as dealing with this requires modelling the aspects of human response that are dynamic (see Fryxell et al. (2010) for a socio-economic approach that effectively employs effort dynamics as a means to understand this consumer-resource interaction). Given estimates of each $f_i$ and the full human-fisheries web topology, I am in a position to document how human interaction strengths are distributed through an ecosystem (Figure 1b).
Figure 1. a) Simplified representations of fisheries food webs along a continuum from specialist to generalist (i.e. *where* human interaction strengths, $f_i$'s, are distributed), with examples of different fishery types. b) Differences in human interaction strengths (i.e. *how* $f_i$'s are distributed) for various scenarios of generalist (multi-species fishing) fisheries food webs. Here, width of the arrows indicates strength of the human interaction or fishing pressure on each component. Each level on the continuum could have many different distributions of $f_i$'s.
On the Structure/Distribution of Interaction Strengths

Clearly, any level of human fishing generality can have an enormous number of different possibilities for the distribution of $f_i$'s throughout a food web. Figure 1b shows examples of a hypothetical generalist (multi-species) fishery under different interaction strength distributions. Ideally, multi-species estimations of $f_i$'s would allow us to quantify the distribution of interaction strengths and look at patterns in global fisheries – classifying fishery types based on the nature of fishing behaviour throughout the system.

Unfortunately, rigorous estimates for the set of all $f_i$'s in a system rarely exist (see Whipple et al. (2000) for classical methods of estimating $f_i$).

As a simple alternative, if I assume any given ecosystem is in equilibrium, that is the energy in equals the energy out of a system, then I can estimate the structure of the distribution of $f_i$'s, or at least the relative structure of the $f_i$'s in a system. For this, biomass data on the composition of catches ($B^*_{fi}$; star denoting assumption of equilibrium) and the actual community composition of species (thus, estimates of biomass or relative biomass of each species $i$, $B^*_i$, from fisheries-independent surveys) in the ecosystem are needed. Note, that any $f_i$ can be therefore estimated by:

$$f_i = \frac{B^*_{fi}}{B^*_i};$$

since $B^*_{fi} = f_i B^*_i$.  

Equation (1) implies that a preliminary way to understand the nature of the distribution of the interaction strengths, $f_i$'s, can be found by simply determining the correlation between the catch biomass data and the community composition data. If the correlations are strong and positive (e.g., near 1) then the fishery is reflecting a case where interaction strengths are passively following the biomass distribution of the whole fish community.
Using these insights on human interactions, I propose some simple graphical methods of interpreting the interaction strength structure of whole-system fisheries for a given ecosystem (Figure 2). Using two axes, Degree of Generality and correlation between catch and fish community composition, a range of fishery types can be investigated. Degree of Generality describes the topology of fisheries food webs ($S_F/S_T$, as defined above; Figure 1), and can be thought of as being similar to the connectance of humans through a food web based on the generality of their fishing behaviour. Correlation illustrates the relative distribution of human interaction strengths ($f_i$’s) throughout the food web. Comparing catch and community compositions ($B^*_f$ and $B^*_i$) by using the correlation between them immediately tells us how fishing mortality is distributed through a food web relative to biomass (Figure 2). Moreover, rank correlations can be used for systems where only relative species compositions in catch and ecosystem are known. This approach allows us to translate catch composition data to an easily quantifiable metric that allows us a glimpse of the distribution of human interaction strengths in a whole-system fishery.

Distinguishing fishery types in this way gives us more clarity on how human impacts in fisheries differ. Figure 2 demonstrates hypothetical fishery scenarios with various degrees of generality and distributions of $f_i$’s. Here, two multi-species fisheries with the same level of generality can be distinguished based on the composition of the total fishery catches ($B^*_f$; Figure 2a, b). Figure 2a demonstrates a so-called “indiscriminate” fishery (McCann et al. 2016), in which species are harvested in proportion to density, and Figure 2b shows a multi-species fishery where all species are caught but preference is given to the rare species. Alternatively, specialized fisheries that target one species (or a group of functionally similar species) can also be characterized graphically based on the location of $f_i$ in the food web (Figure 2c). Representing fisheries in this way allows us to easily distinguish between qualitatively distinct fishery types that can be expected to have drastically different ecological implications.
2. Understanding the structure of human interaction strength using catch and ecosystem composition: A two-dimensional fisheries continuum describes generality of fish harvest and how fish species are distributed through the food web. Correlation is the correlation between abundance of each species in fisheries catches and in the ecosystem. Hypothetical fisheries scenarios: a) density-dependent fishery (indiscriminate; McCann et al. 2016); b) generalist fishery with preference for rare species; c) specialist fishery catch, focusing on a rare species (e.g., large predators at low abundance); d) random or uniform catch with no correlation with community composition.
Similarly, one might be concerned with how fisheries harvest in accordance with body size (e.g., gillnet fisheries with little variation in mesh sizes; Wolff, Taylor, and Tesfaye (2015), trophic level (Gascuel et al. 2005; Pauly et al. 1998), or natural productivity (i.e., “balanced” fisheries; Garcia et al. 2012). Using the same catch composition data, correlation between $B^*_f$ and another variable of choice can be used to delineate fisheries’ dependence on these factors (i.e., substitute y-axes of continuum column in Figure 2). In this way, this graphical approach can be used to see global patterns in the distribution of $f’$s relative to these variables. While in some cases these features may be related (e.g., density and productivity), this will not always be the case. Fishery types that may otherwise appear similar from a topological perspective (e.g., indiscriminate and balanced, which would both catch all species in a system) can be distinguished from each other by adding rather than substituting a correlation axis and classifying fishing behaviour in three dimensions. This classification further allows us to differentiate between fishery types globally, and moves us towards a better understanding of human impacts on fisheries food webs.

(iv) Human Interaction Strengths: Fishery Types and Consequences

As discussed above, recent fisheries research has begun to consider the theoretical implications of different types of whole-system fisheries. Table 1 summarizes the results of modelling exercises adapted from Garcia et al. (2015), which includes specialist and generalist scenarios of fishing behaviour in a simple tri-trophic food web with four species, similar to the scenarios depicted in Figure 1. The examples include specialized fishing on top predators only (top TP), specialization on consumer species, as well as balanced and indiscriminate versions of multi-species fisheries. These scenarios are based on different assumptions of human interaction strength distributions ($f’$s), and the general effects of increasing fishing pressure on total biomass, fishery yield and diversity are shown.
Table 1. General ecological effect of increasing fishing pressure over time in different fishery types, based on the distribution of human interaction strengths through the food web. Trends are adapted from simulations by Garcia et al. (2015) using a tri-trophic model with four species. Each line is the general trend of biomass, fishery yield or diversity with increasing fishing pressure, where the dashed line sections show the inevitable crashes at very high levels of fishing pressure. Biomass is total biomass in the system and fishery yield is based on proportion of MSY.

<table>
<thead>
<tr>
<th>Fishery Type</th>
<th>Human IS Distribution</th>
<th>Biomass</th>
<th>Fishery Yield</th>
<th>Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selective (top TP)</td>
<td>specialized throughout top TP (top pred in model)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selective (consumer TP)</td>
<td>specialized throughout lower TP (TL2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Balanced</td>
<td>general; proportional to natural productivity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Indiscriminate</td>
<td>general; proportional to abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Clearly, different fishery types have different implications for food web stability, sustainability and biodiversity. As displayed in Table 1, trophically specialized fisheries harvest at just one trophic level in the model food web, and the positioning of fishing mortality ($f_i$) determines the response. For the scenario that selectively harvests the top predator, yield is based on a single stock or group of top predators and is similar to many single-species fisheries models (e.g., specialist example in Figure 1a; Pauly et al. 1998). Similarly, selectively fishing a lower trophic level means that $f_i$'s are distributed throughout the consumer trophic level in the model food web, with no pressure on the top predators. Smith et al. (2011) provide another example of how fisheries specialized on consumers affect fisheries yield and can negatively impact other trophic groups through indirect interactions. This situation can be related to typical anchovy and sardine fisheries around the world.
Finally, two recently proposed types of multi-species fisheries are represented here: balanced (e.g., Figure 1b. iii; also see Jacobsen, Gislason, and Andersen (2014); Garcia et al. (2012); and Law, Plank, and Kolding (2012) for details on balanced harvesting) and indiscriminate (e.g., Figure 1b. ii; see McCann et al. 2016 for more context). These two fishery types both catch all, or almost all, species in a system, but f's are distributed differently throughout the food web. As displayed in Table 1, the ecological implications of these distinct distributions of f's can be very different. For example, the loss of diversity ought to be considerably increased under indiscriminate fishing in comparison to balanced fishing (McCann et al. 2016; Jacobsen et al. 2014). Although ecosystem impacts depend on other factors, and authors may argue about specific details (e.g., biomass could actually increase under indiscriminate harvesting before decreasing because of shifts in species composition, with more productive species increasing; McCann et al. 2016), the main point here is that different fishing behaviours have the potential to produce very different ecological and management outcomes.

A First Look at Global Fisheries: Just Topology

There is literature to suggest that socio-economic environments alter fishing behaviour. Although the amount of animal protein (including fish) is positively related to income at both global and regional scales, it appears that the relative proportion of animal protein derived from fish is generally higher in less developed countries or regions (Allison 2011; Dey et al. 2005). It has been suggested that fishers in developing countries also tend to harvest more fish species (Kent 1997), and there is a disparity in the type of fish consumed based on income. Specifically, poorer people tend to consume lower-valued fish, while those with higher incomes spend more in high-quality, expensive fish (Dey et al. 2005). Although these patterns of fish consumption have been seen at both local and global scales, it remains to be seen if there are differences in how humans impact whole-system fisheries food webs globally. That is, if the generality of human fishing behaviour, or the proportion of fish removed from a system, is influenced by the socio-economic condition of the fishery. If this is the case, these global patterns in human generality can be used as a first step towards classifying fishery types at a global scale.
To explore global patterns in fisheries types, I first gathered purely topological data of human interactions with species from the whole-system webs. I gathered topological information for 30 freshwater fisheries (Table A1) from around the world (see Appendix A.1 for detailed methods on data acquisition and A.4 for data sources). Using these data, I quantified the Degree of Generality in each whole-system fishery (i.e., $S_r/S_T$). My first result is that there is clearly a wide range of fishery types along a continuum from specialist to generalist harvesting behaviour. Interestingly, the distribution of freshwater fisheries from a topological perspective does not appear to be uniform (Figure 3a), suggesting that different degrees of generality may be more common than others. This raises questions of whether or not there are global patterns in the occurrence different fishery types and what might be driving these patterns.

Using this data I then gathered socio-economic and geographic data for each fishery in order to investigate how different fishery types are distributed globally (see Appendix A.2 for details on analyses). For this, Human Development Index (HDI) was used as an indicator, along with (absolute value of) latitude for location. A country’s HDI value is determined by combined income, education and health metrics (UNDP, 2015), for a more comprehensive indicator of development than income alone. I found that the proportion of fish species removed (i.e., the Degree of Generality) shows a negative and significant trend with HDI such that developing countries are more likely to harvest throughout the fish community ($p = 8.42e-05$; Figure 3b). That is, humans in developing countries tend to behave more like generalists than specialists in whole-system fisheries. This socio-economic pattern also has an inherent, and correlated, geographic pattern suggestive that more tropical fisheries (low degree of latitude) harvest significantly more species relative to the total diversity ($p = 0.01$; Figure 3c). This suggests that the way humans are impacting aquatic ecosystems likely differs strongly across the globe. Latitude and HDI have a significant correlation (Figure A1), so multiple regression was not appropriate, but I used the residuals from the linear regression with latitude (named Generality$_{RESID}$; Appendix A.2, Figure A2) to determine the independent effect of HDI. HDI has a significant linear relationship with Generality$_{RESID}$ ($p=0.02657$; Figure 3d). Thus, although geographic
location seems to explain human generality, fishing behaviour is likely determined more by human development. Topologically speaking, the human portion of the food web is far more connected in tropical countries with lower HDI. This preliminary analysis has no real information on the strength of the human interactions (\( f_i \)'s) on all the species in the fisheries, but it is evident that there are clear global patterns in the structure of human-fisheries food webs based on differences in human fishing behaviour.
Figure 3. A continuum of global fisheries generality based on topology of fisheries food webs including human interactions. Degree of generality is measured as the proportion of species harvested from a system. a) frequencies of fishery types from specialist to generalist human harvesting behaviour where degree of generality is the proportion of fish removed by a fishery ($S_S/S_T$); b) showing the relationship between degree of generality (logit-transformed) and logit-transformed Human Development Index (HDI). Slope $=-1.0369$, $p=8.416e-05$, $R^2=0.4094$; c) showing the relationship between degree of generality (logit-transformed) and geographic location, measured as the absolute latitude of the fishery location. Slope $=-0.03188$, $p=0.01192$, $R^2=0.1769$; d) showing the relationship between the residual degree of generality (logit-transformed) after linear regression with latitude (absolute value) and logit-transformed Human Development Index (HDI). Slope $=-0.57$, $p=0.02657$, $R^2=0.1338$. 
Conclusion

Effective fisheries management is paramount to both conserving the production of fish biomass and biodiversity, while simultaneously maintaining food security. It is imperative to consider human behaviour and its governing social and economic factors as a dynamic part of the fishery if we wish to move towards a multi-objective approach to management. Here, I classify global fisheries types based on human impacts in fisheries food webs. I have provided a preliminary framework for classifying fisheries based on human behaviour and the distribution of fishing mortality (human interaction strengths, $f$/s) throughout these food webs. Such classification should allow fisheries scientists to compare different types of fisheries based on human impacts on the food web at a global scale, while remaining suitable for data-poor systems. The existence of a human generality continuum of fishing behaviour demonstrates the need for a range of fisheries management approaches, from the popular single-species assessments to thorough multi-species approaches.

These results provide the first global perspective of human impacts on fisheries food webs that classifies fishing pressure based on topology (generality) and human interaction strength throughout a whole-system fishery. Classifying fisheries in this manner immediately facilitates the development of theory that allows us to understand the implications of different whole-system fisheries types on the diversity, structure and functioning (i.e., secondary fish production) of fisheries food webs. I have shown that socio-economic environments dictate fishing behaviour, and this allows us to see patterns in fishery types globally. More detailed information on whole-system catches would allow us to better understand what the different distributions of human interaction strength are globally (e.g., where the different scenarios shown in Figure 1b might exist). My insights into HDI as an indicator for human generality highlight the importance of managing fisheries based on their type for both biodiversity and human food security.

As discussed above, varying the distribution of human interactions through fisheries food webs has important consequences for sustainability as strong interactions can drive
complex dynamics. Here I have provided a useful conceptual framework to account for these differences. Understanding the nature of human interaction strengths will allow us to better evaluate the stability and sustainability of diverse fisheries (Crowder et al. 2008; McCann, Hastings, and Huxel 1998). This allows us to move towards a multi-objective approach to fisheries management that connects fisheries production with biodiversity conservation and human livelihoods.
References


CHAPTER 2: THE DYNAMICAL IMPLICATIONS OF HUMAN BEHAVIOUR ON A SOCIAL-ECOLOGICAL HARVESTING MODEL

Abstract

The dynamic harvesting and decision-making aspects of human behaviour are often overlooked in resource management. Most resource management models consider harvesting without the complexities of dynamic human effort. Some researchers have recognized this, and a recent push has been made that aims to understand how human behaviour and ecological systems interact, through dynamic social-ecological systems. I use a recent example of a social-ecological dynamical systems model to investigate the relationship between harvesting behaviour and the dynamics and stability of a harvested resource. I employ dynamical systems and bifurcation theory to search for general rules in how relatively simple human behaviours can either stabilize or destabilize resource dynamics and yield. My results suggest that human effort can either be stabilizing or destabilizing and that weak to moderate behavioural and effort responses tend to stabilize dynamics by decreasing return times to equilibria or reducing the magnitude of cycles. Furthermore, relatively strong human impacts can readily lead to human-driven cycles, chaos, long transients, and alternate states. Given the potentially dramatic implications of harvesting effort on resource dynamics, it becomes critical to better understand how human behaviour determines harvesting effort through dynamic social-ecological systems. Much like consumer resource theory allowed for the development of food web ecology, I provide a framework for developing and understanding more holistic social-ecological models.
Introduction

Consumer-resource theory in ecology has recognized the importance of dynamic interactions within food webs for a long time, allowing for the development of a comprehensive dynamical systems theory that focuses on the structure of these interactions and their implications for stability and ecosystem function (Murdoch et al. 2003). Critically, the dynamics and behaviour of the consumer often play major roles in governing stability and function (Rosenzweig 1971; McCann et al. 1998; Estes et al. 2011). Alternatively, resource management has been slow to adopt this dynamical and behavioural view of consumers (i.e., humans) interacting with their resources. Instead, harvesting mortality is often simply estimated as a linear function of resource density (for example, the commonly used measure of total fishing mortality, $F$, used in fisheries science), while the dynamics of harvesting are ignored (i.e., $F$ is static). For example, Whipple et al. (2000) described many of the common approaches to modeling fishing mortality used for fisheries science, most of which employ this static view of human impact. In reality, though, harvesters are adaptive and likely dynamically respond to perceived changes in a resource based on environmental, social and economic conditions (Salas & Gaertner 2004).

Human harvesting behaviour is arguably a complex process and human-resource interactions are inherently dynamic in nature. Consistent with ecological theory and noted by Travis et al. (2014), it is important to consider the nature of these complex dynamical interactions for effective resource management. To address this need, a number of recent papers on the dynamical impacts of human interactions have argued that harvesting has tended to destabilize fisheries (Anderson et al. 2008; Shelton & Mangel 2011). Nonetheless, these studies have not fully considered the full role of human effort and behaviour dynamics in terms of resource stability. Similarly, it has recently been shown that variable harvesting can destabilize populations by driving high amplitude cycles, particularly if responses to changes in resource density are delayed or if societal motivations influence harvesting behaviour (Fryxell et al. 2010; Lade et al. 2013). Understanding the variation in harvesting caused by human behaviour is therefore crucial for effective fisheries
management. It remains interesting to fully investigate the implications of harvesting dynamics through human behaviour and interactions with a harvested resource.

In the past decade, a push has been made to understand how human behaviour and ecological systems interact, but there is still much to learn about the dynamics of these social-ecological systems (Schlüter et al. 2012). Combining social and ecological dynamics can be complicated if one wishes to be thorough in accounting for all influencing factors (Ostrom 2009). However, it has been found that even simple models can have complex dynamical phenomena that importantly reveal the potentially large influence of human behaviour on the stability and dynamics of social-ecological systems (Lade et al. 2013). Further research on the interacting components of dynamic social-ecological systems will allow managers to both better understand the factors influencing harvesting behaviour, as well as the dynamical implications of behaviour for resource sustainability.

A recent example of a social-ecological model is the discrete dynamical system employed by Fryxell et al. (2010) to investigate relationships between harvest effort, resource abundance and management quotas. Here, both the resource population and human effort are dynamic, so harvesting effort responds to changes in the resource and vice versa. This model was empirically motivated by examples of harvested ungulate populations, but is arguably applicable to any resource management scenario, including fisheries. Changes in harvesting effort are based on perceived resource abundance and shared information between harvesters. Due to the nature of stakeholders sharing information and the frequency of management surveys, these responses in effort are often necessarily lagged behind any changes in the resource. Fryxell et al. (2010) performed a preliminary stability analysis; however the model, as well as the dynamic social-ecological relationship in general, is relatively unexplored mathematically.

Interestingly, the effort-resource (E-R) model used by Fryxell et al. (2010) is a modified version of classical consumer-resource (C-R) models used in food web ecology. As such, this E-R model effectively forms a basic building block for including humans in food webs and understanding the dynamical implications of human behaviour. An understanding of
the base model for food webs – the C-R model – has proven a powerful tool for understanding whole web dynamics (Murdoch et al. 2003; McCann 2011). Similarly, the development of a full understanding of base E-R models may help our understanding in the development of the theory of multi-species resource management (and ecosystem management) scenarios. A thorough understanding of E-R interactions promises to allow researchers a means to develop holistic social-ecological webs, much like C-R theory has allowed food web research to grow.

In what follows, I examine the role of human behaviour on the dynamics and stability of harvested ecosystems using the E-R model introduced by Fryxell et al. (2010). I employ dynamical systems and bifurcation theory to search for general rules in how relatively simple human behaviours can either destabilize or stabilize resource dynamics and yield. Additionally, I will look for how human behaviour can drive complex dynamical phenomena like chaotic dynamics, long transients and alternate states. I end by comparing the dynamical outcomes of this E-R model with reference to the recent empirical evidence that suggested human effort dynamics have produced resource cycles (Fryxell et al. 2010). These recent empirical results suggest that it may be quite likely that human effort dynamics are capable of driving complex dynamical phenomena, which may seriously compromise the stability and sustainability of managed ecosystems.
Methods

Model Equations and Parameters

To facilitate analysis, I chose to use only the resource and effort equations defined by Fryxell et al. (2010), assuming an open-access harvesting policy with no quota. Thus, resource abundance (R) and harvesting effort (E) in year \( t+1 \) are determined as follows:

\[
\begin{align*}
R_{t+1} &= R_t e^{r \left(1 - \frac{R_t}{K}\right) - q E_t} \\
E_{t+1} &= E_t e^{c + w_R t - u E_t}
\end{align*}
\] (1)

where \( r = \) the maximum rate of increase of the resource (i.e., the population growth rate), \( K = \) resource carrying capacity, and \( q = \) proportion of the resource population removed by one unit of effort, which can be thought of as catchability or efficiency.

\( c = \) a constant for the exponential rate of change in effort, \( w = \) the effect of one unit increase in resource density on the exponential rate of change in effort, and \( u = \) the effect of one unit increase in effort on the exponential rate of change in effort.

Eigenvalues and Local Stability

It is straightforward to solve System (1) for the isoclines and equilibria by substituting \( R_{t+1} = R_t \) and \( E_{t+1} = E_t \). This yields the following simple linear isoclines:

\[
\begin{align*}
R &= K \left(1 - \frac{q E_t}{a}\right) \\
E &= \frac{(c + w R_t)}{u}
\end{align*}
\] (2) (3)

where Equation (2) is the R-isocline and Equation (3) is the E-isocline. After substitution, the interior equilibrium is calculated as follows:

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\[ R_{eq} = \frac{K(au-qc)}{au+Kqw} \]  
\[ E_{eq} = \frac{a(c+wK)}{au+Kqw} \]

Additional boundary equilibria are at \( R_B = K \) when \( E = 0 \) and \( E_B = c/u \) at \( R = 0 \). Finally, there is the trivial equilibrium at \( R^* = 0, E^* = 0 \). Collectively, these are the set of all equilibria for the model, System (1).

The Jacobian matrix from System (1) evaluated at the interior equilibrium \( R_{eq}, E_{eq} \) gives rise to the community matrix:

\[
A = \begin{bmatrix}
1 + \frac{a(cq-au)}{au+Kqw} & \frac{Kq(cq-au)}{au+Kqw} \\
\frac{aw(c+wK)}{au+Kqw} & 1 - \frac{au(c+wK)}{au+Kqw}
\end{bmatrix}
\]

The characteristic equation for determining eigenvalues of (6) follows the form:

\[
\lambda = \left(\frac{1}{2}\right)(\alpha_{11} + \alpha_{22} \pm \sqrt{(\alpha_{11} - \alpha_{22})^2 + 4\alpha_{12}\alpha_{21}})
\]

where \( \alpha_{11}, \alpha_{12}, \alpha_{21}, \alpha_{22} \) correspond to components of the community matrix (6).

In discrete dynamical systems, the norm of the maximum eigenvalue (7) is used for local stability analysis and is calculated as follows:

\[
Norm(\lambda) = \sqrt{\text{Max}(|\text{Real}(\lambda)|)^2 + \text{Max}(|\text{Imaginary}(\lambda)|)^2}
\]

System (1) is stable when the norm(\( \lambda \)) < 1, and it has oscillatory dynamics (either stable or unstable) when \( \lambda \) has a complex component.
Bifurcation Analysis: Unfolding parameters and human interaction strength

Since I wish to understand the specific role of human harvesting dynamics, I chose to use behavioural parameters that alter harvesting dynamics. In System (1) above these are the parameters $w$, $c$ and $u$ (see System 1 for definitions). Below, for simplicity, I concentrate on $w$ and $c$; however, I will discuss $u$, which yields similar qualitative dynamics, presenting the results for $u$ in Appendix B. By unfolding these bifurcation parameters, I investigate the dynamical implications of these human behavioural responses.

Note that the effort equation in (1) is functionally similar to the Ricker logistic equation (Ricker 1954), where the parameter $c$ is comparable to growth rate of effort. The parameter $c$ can be considered to be representative of the spread of information between harvesters or responsiveness to changes in a resource. Not surprisingly, as with the Ricker model, increases in $c$ drive period-doubling dynamics in effort ($E$ of System (1)).

The parameter, $w$, on the other hand reflects the capture rate of resource $R$ per unit of effort, $E$. As a result, $w$ is similar in spirit to the attack rate of a type I functional response. There are many approaches to measuring interaction strength in food webs (see Berlow et al. 2004). As such, following Gilbert et al. (2014) and Nilsson and McCann (2016), $w$ can be used as a measure of human interaction strength (hereafter, $IS_H$) where $w$ effectively keeps track of the harvest rate per unit of $ER$. In consumer-resource models the attack rate per unit of $CR$ is a measure of the intensity of colliding $C$’s and $R$’s so to speak, and recent work has suggested that this measure of interaction strength maps consistently, in terms of stability, with a number of general consumer-resource models (Nilsson & McCann 2016). Here, I will equate $w$ with human interaction strength ($IS_H$) in order to relate social-ecological dynamics with food web theory.

Finally, the parameter, $u$, governs the effect of one unit of increase in effort on the exponential rate of change in effort. In a sense, it is density dependent response to increases in effort. Equating this ER model (1) to typical CR models, this parameter is
comparable to mortality of C, however in this model it effectively maintains harvesting effort at realistic levels.

Given the above behavioural bifurcation parameters, I can then ask how altering these parameters influence the dynamics of System (1) by following how these parameters alter the local stability (and some non-local through numerical analysis) of the interior equilibrium. In dynamical systems, a local bifurcation occurs when the stability of an equilibrium changes qualitatively (Guckenheimer & Holmes 2013). In discrete dynamical systems, local bifurcation points occur when an eigenvalue of a discrete dynamical system, at a given equilibrium, have a norm($\lambda$) = 1. The sign of the real part of $\lambda$ (+/-) and existence of an imaginary component at the bifurcation point determine the type of bifurcation as well as other crossing conditions influencing how generic or degenerate the bifurcation is (see Guckenheimer & Holmes 2013 for more details). In what follows, I concentrate less on the specific analysis of any particular bifurcation and instead classify bifurcations using generality arguments (e.g., I initially overlook the possibility of degenerate bifurcations). Where needed, and to add clarification to some of my bifurcation diagrams, I use numerical simulations to suggest the possibility of other bifurcations, although the scope of these more complex dynamical phenomena are beyond this paper.

Note, that the non-equilibrium dynamics on the axis form invariant sets (i.e., if $R = 0$ and $E > 0$ then the dynamics necessarily remain on the E-axis since an initial value of $R_0 = 0$ in System (1) necessarily yields $R_{t+1} = 0$). These invariant sets, after long enough transients, end up on non-equilibrium steady states that, although they attract on the dimension of the axis, potentially attract or repel in the second dimension. For example, if $c > 3$ and we start off with an initial value in System (1) with $R = 0$, and $E > 0$ then the dynamics will move to a complex set of invariant points (i.e., the non-equilibrium steady state such that once on it the system remains on it). In System (1), the boundary equilibria are always unstable for biologically possible values of my behavioural parameters. Stability conditions of these equilibria are discussed in Appendix B.1.
Generically, flip bifurcations occur when $\text{Real}(\lambda) > 0$ (norm($\lambda$) = 1) and $\lambda$ is real. Flip bifurcations can change a stable equilibrium to an unstable equilibrium with the unstable equilibrium giving way to a two-point cycle (or vice versa). Such cycles can also give way to further flip bifurcations (i.e., 2 point to 4 point to 8 point cycles and so on; Strogatz 2014). Flip bifurcations are known to occur with increasing growth rate in the well-known Ricker equation leading to a period-doubling route to complex or chaotic dynamics (May & Oster 1976). Thus, $R$ is able to undergo a series of flip bifurcations as $r$ is increased, causing the underlying $R$ dynamics to go from stable equilibrium solutions ($r < 2$), to cyclic ($2 < r < 3$), to complex ($r > 3$). Since $E$ is functionally similar to the Ricker equation, as discussed, it will also independently undergo flip bifurcations with increasing ‘growth’ (parameter $c$), regardless of $R$ density. Given this, when $R = 0$, the dynamics of $E$ undergo a flip bifurcation at $c = 2$ and will also under period-doubling route to chaos with increases in $c$.

Finally, discrete dynamical systems with dimension two or greater can also undergo dynamical changes from equilibrium to an oscillating solution that in a manner similar to the Hopf Bifurcation of continuous systems (Hone et al. 2010). If the system is complex and norm($\lambda$) = 1, this generically reflects a Neimark-Sacker bifurcation in which the system transitions from stable to oscillatory, typically characterized by longer-period oscillations than the period that two-point cycles tend to produce. This final bifurcation (the Neimark-Sacker) and the flip bifurcations driven by $c$, in effect, signal non-equilibrium dynamics of the resource that are driven largely by harvesting. Using this logic, and where appropriate, I comment on when the dynamics of System (1) are largely human-driven ($E$ is unstable or $E-R$ interact to drives Hopf-like cycles) or largely biologically driven (i.e., the system oscillates even in the absence of effort dynamics).
Results

Effects of Human Behaviour on Stability, Dynamics and Yield

As discussed above, harvesting has been shown to destabilize a resource. However, recent food web literature has shown that weak interactions have the potential to stabilize systems. To consider socio-ecological systems in light of food web theory, I thus first investigate the stability implications of human harvesting behaviour by altering $w$ (i.e., $IS_H$). I explore the effects of $IS_H$ through three measurements that quantify the stability and dynamics of the system. As discussed above, the norm($\lambda$) (Equation 8) gives us a measure of equilibrium stability. While eigenvalues tell us a lot about local stability of equilibria, the coefficient of variation, CV (SD/mean), is commonly used as a measure of stability in empirical studies and also allows us a simple metric to understand non-equilibrium outcomes. As I will show here, they are functionally similar; as a system becomes less stable locally (norm($\lambda$)), CV also tends to increase. Finally, I also comment on the dominant periodicity of the attractor in order to see how behaviour and biotic dynamics interact to produce different types of dynamical outcomes. Periodicities have often been employed to empirically identify drivers of non-equilibrium dynamics (see Turchin 2003 for examples).

To fully understand the effect of $IS_H$ on resource dynamics I employ three different starting conditions, whereby each condition yields different underlying resource dynamics. These scenarios are where $R$, given $E = 0$, is stable ($r = 1.5$), cyclic ($r = 2.5$) and chaotic ($r = 3.5$). This allows us to robustly look at how human effort dynamics influence different underlying biotic dynamics, from equilibrium to non-equilibrium (i.e., cyclic or chaotic). For each case, I then examine the results at low $c$ (here, $c = 0.1$) and high $c$ (here $c = 1.6$) in order to begin to investigate the interaction of the behavioural parameter $c$ with the interaction strength parameter, $w$. All other parameters were kept the same in order to isolate the effect of $IS_H$.

Figure 1a-c shows the effects of increasing $w$ ($IS_H$) on the stability and dynamics of the resource in these three cases for low $c$, while Figure 2a-c shows the same results at high $c$. 
Below, I highlight the results for each case.

**Case 1 (r = 1.5; Figures 1a, 2a)**
The starting conditions for the resource in Figure 1a are stable so CV remains at 0 as $w$ is increased slightly, however $\text{norm}(\lambda)$ decreases meaning the system becomes relatively more stable with moderate harvesting intensity. With increasing stability, the system will return to equilibrium more quickly after a perturbation. Increasing $IS_H$ past this point of maximum stability destabilizes the system and eventually drives cycles and complexity in the resource. The equilibrium becomes unstable at the bifurcation point ($\text{norm}(\lambda)=1$) and CV increases as $IS_H$ is increased further. With high $c$ in Figure 2a, increasing $w$ seems to only destabilize the resource. This is because the increase in $c$ causes the point of maximum stability to shift past the axis into negative $w$ values. Here CV increases past the bifurcation point, similar to the low $c$ case.

**Case 2 (r = 2.5; Figures 1b, 2b)**
Similar to case 1, weak $IS_H$ increases the stability of the system as seen by a decrease in $\text{norm}(\lambda)$. Even though the underlying dynamics in the resource are cyclic, increasing $IS_H$ actually drives stability in the resource. Past this weak level of $IS_H$, however, harvesting then leads to destabilization of the resource. It can be seen here that the biologically-driven variation (low $IS_H$) and effort-driven variation (high $IS_H$) have characteristically different oscillations based on the differences in CV and periodicity of the resource. Although the bifurcation points are different and the region of stability is smaller, it can be seen in Figure 2b that the effect of increasing $w$ is functionally similar to Figure 1b in terms of equilibrium stability and CV. Human interactions have the potential to drive stability in a harvested resource.

**Case 3 (r = 3.5; Figures 1c, 2c)**
The resource dynamics in Figure 1c and 2c are both too complex for effort to make the system stable ($\text{norm}(\lambda) < 1$), but the decrease in $\lambda$ with weak $IS_H$ is consistent across all scenarios.
Figure 1. Stability analysis of a harvested resource, measured by the norm of the maximum eigenvalue ($\lambda$) and coefficient of variation (CV), as human interaction strength ($w$) is increased. Resource growth rate is manipulated to influence biologically-driven dynamics as follows: a) $r = 1.5$, b) $r = 2.5$, c) $r = 3.5$. Here, $c = 0.1$. 
Figure 2. Stability analysis of a harvested resource, measured by the norm of the maximum eigenvalue (\( \lambda \)) and coefficient of variation (CV), as human interaction strength (\( w \)) is increased. Resource growth rate is manipulated to influence biologically-driven dynamics as follows: a) \( r = 1.5 \), b) \( r = 2.5 \), c) \( r = 3.5 \). Here, \( c = 1.6 \).
**General Results**

My first major result is that effort dynamics can both drive stability and destabilize a harvested resource. It can be seen that harvesting (through weak $I_{SH}$) has the potential to drive stability in a resource. Perhaps unsurprisingly, this result is consistent with the weak interaction effect found in theoretical food webs (Gellner & McCann 2016; Gellner et al. 2016; Bascompte et al. 2005; McCann et al. 1998; De Ruiter et al. 1995). That is, for webs comprised of C-R interactions, researchers have found that systems can be increasingly stabilized by the addition of a weak interaction that shunts energy away from a strong C-R interaction (that potentially contains an oscillator) embedded in the web (see McCann (2011) for details). Here, weak human harvesting appears to similarly shunt energy away from a potentially cyclic resource dynamic. However, as $I_{SH}$ is increased further, effort dynamics drive instability in the E-R interaction. At high $I_{SH}$, E drives its own cycles that influence the resource regardless of underlying R dynamics. Here, E and R cycles couple to create complex dynamics.

Interestingly, this pattern of stabilization followed by destabilization (i.e., $\lambda$ ‘checkmark’ pattern) holds regardless of other parameters in the model that determine resource-driven dynamics (Figures 1 and 2 a, b and c, $\lambda$ column). In Figure 2a, increasing $w$ only destabilizes the dynamics, however the bottom of the ‘checkmark’ is in negative $w$ space (biologically impossible) and thus the pattern holds. All model parameters will either shift the ‘checkmark’ (eg. changing $c$) or push the resource to another starting condition (eg. changing $r$; case 1, 2 or 3).

Since the effort equation in (1) follows flip bifurcations similar to the Ricker equation governing the resource, values of $c > 2$ also cause period-two cycles in the system. At values of $c < 2$, changes in the dynamics can explain effort-driven effects that drive a cycle between E and R. These effort-driven dynamics can be seen to cause increases in the periodicity of the effort-resource fluctuations, in comparison to the period-two cycles typical of the underlying logistic growth equation when R is cyclic. By increasing $w$ through the values displayed in Figure 1a ($c = 0.1$, $r = 1.5$), the dominant period goes from 0 (stable equilibrium) up to periods of 6 as it becomes unstable, until the dynamics become chaotic.
Other numerical parameter combinations not explored in this paper can result in periods on the order of decades. Following the increase in $w$ displayed in Figure 2a ($c = 1.6, r = 1.5$), the periodicity transitions from 0 to 2 as $\lambda$ becomes unstable, and increases by $2^n$ until chaos. This latter scenario is characteristic of a flip bifurcation, likely effort-driven and triggered by a coupled E-R cycle (since $c, r < 2$).

In general, different mechanisms often yield different periodicities thus potentially allowing us to differentiate drivers of complex dynamics (Murdoch et al. 2003; Turchin 2003). Human-driven cycles, that are much like classical predator-prey cycles, and biologically-driven cycles (i.e. purely R), may have different characteristics that can be determined by the periodicities. Here, I see that these behavioural parameters influence characteristically different dynamics, and I can thus differentiate between biologically- and effort-driven dynamics, and regions where E and R cycles couple. Empirical evidence presented in Fryxell et al. (2010) showed long effort-resource cycle lengths, which is consistent with Neimark-Sacker type cycles. I am able to generate long cycles of this type in this E-R model, which do not display the common two-cycle sub-harmonics influenced by flip bifurcations in E and R alone.

**Human interaction strength and resource yield**

Resource managers wish to maximize yield while maintaining sustainability (i.e., the commonly used maximum sustainable yield (MSY) assessment). Aligned with this popular MSY approach, I next explore the effects of human interactions in this E-R model in terms of resource yield. Figure 3 shows the implications of increasing human effort ($IS\mu$) on average yield, where yield at time $t$ is calculated as follows:

\[
Yield_t = R_t e^{r(1-R_t/K)}(1 - e^{-qE_t})
\]

and then averaged over 100 time steps, after a 1900 time step transient, for each value of $w$. 

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My second major result is that increasing harvesting effort, through $IS_H$, can have negative effects on resource yield in addition to driving instability. While $IS_H$ directly influences effort and therefore yield (9), it might seem obvious that yield will increase as $IS_H$ increases. However once $IS_H$ increases past a certain threshold and the system becomes unstable, yield dramatically drops off and becomes increasingly more variable while following a consistent decline. As shown in Figure 1, the system becomes unstable at high $IS_H$ and develops complex dynamics. These complex dynamics attain near zero densities (Fig. 1,2), with non-equilibrium dynamics spending more time near zero the average yield becomes skewed towards the low yield associated with low R densities. This result shows that high levels of human interactions can lead to unpredictable management outcomes for both biological production and economic reliability.

Figure 3. Average harvest yields over 100 time steps, after a 1900 time step transient, with increasing human interaction strength, $w$.

Unfolding the bifurcation structure of human behaviour parameters

Expanding on this understanding of how behaviour ($w$ or $IS_H$) influences the dynamics of a harvested resource under low and high $c$ values, it is useful to look at the bifurcation structure of these behavioural parameters simultaneously to fully unfold the dynamical implications of human harvesting behaviour on an exploited resource. Such information
allows for a more holistic perspective on the implications of harvesting behaviour on resource population dynamics and sustainability. I will not focus on the parameter $u$, however further analysis on the influence of $u$ on stability and dynamics and the bifurcation unfolding with other behavioural parameters is provided in Appendix B.2.

Figure 4 shows an example of a $w$-$c$ parameter space with bifurcation curves (transitions between stable and unstable regions) that delineate different dynamical regions. Generic bifurcation type is identified in Figure 4 by line type, and was determined by $\lambda$ characteristics and numerically confirmed by transitions in the time series dynamics. I investigate this $w$-$c$ unfolding with different underlying conditions of resource dynamics. As in Figure 1, I examine when $R$ is i. stable ($r = 1.5$) and ii. cyclic ($r = 2.5$) without the influence of effort. This allows us to further investigate how $E$ impacts different stating conditions, as well as encompass the general dynamical implications of harvesting behaviour.

Here I show that harvesting effort, which is increased by both $c$ and $w$, drives instability of the system. In Figure 4a i., the system is biologically stable without the influence of harvest (i.e., $r = 1.5$, as in Figure 1a). Similar to Figure 1b when $R$ is cyclic ($r = 2.5$), there is a region where harvesting can drive stability (Figure 4a ii.). Consistent between the two scenarios it can be seen that harvesting, through interactions with a resource and response to changes in that resource, has the potential to promote stability in a resource and also drive complex dynamical outcomes.
Figure 4. $c$-$w$ parameter space and regions of stability based on eigenvalue characteristics (the system is stable when the Norm($\lambda$) < 1 grey fill). Transitions between stable and unstable regions indicate bifurcations, with the bifurcation type illustrated by line type (flip (F) = solid line; Neimark-Sacker (N-S) = dashed line). i. underlying resource dynamics are stable ($r = 1.5$), and ii. resource dynamics are cyclic ($r = 2.5$). Other parameters remain consistent between i. and ii. ($K = 7$, $u = 0.4$, $q = 0.07$).

The behavioural parameter $u$ is discussed in Appendix B2, but the main results remain consistent. That is, $u$ has the ability to alter the points where $w$ or $c$ drive stability and bifurcations, but $w$ still drives Neimark-Sacker type bifurcations and $c$ can drive both flip and Neimark-Sacker bifurcations as seen in Figure 4. One difference that can be seen in Figure B3 is that $u$ drives a transcritical bifurcation. The parameter $u$ is essentially density-dependent mortality of effort, so low values of $u$ cause effort to grow exponentially and the resource is unable to persist. Moderate levels of $u$ allow effort to drive human-driven cycles rather than drive the resource to extinction. Here, $u$ effectively dampens the effect of effort, but does not functionally change the dynamical effects of behavioural parameters $c$ and $IS_H$. 

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My final major result is that harvesting effort dynamics can couple with resource dynamics and drive extremely complex cycles, long transients and alternate states. I numerically explored the potential for multiple basins by recording local maxima for randomly selected starting conditions. Generally, the maxima would fall to different values depending in initial conditions, and I took this as evidence for alternate states if the basins held after a transient of $5 \times 10^6$ time steps. In cases where dynamics were chaotic, I found evidence for alternate states when maxima were contained in distinct groups of similar values separated by at least 10%. I found that certain parameter conditions and different initial R and E values can lead to different attractors (Figure 5). Interestingly, the alternate states occur in a region with potentially multiple cycles (combined biologically- and human-driven dynamics). In other words, the R and E cycles couple to create very complicated dynamics, more so than the individual sub-systems. There are no obvious local bifurcations that may be causing these dynamics and the boundary equilibria are always unstable (see Appendix B1). It is likely these are caused by some sort of global bifurcation (e.g., homoclinic bifurcation), however a thorough analysis of these bifurcations are beyond the scope of this paper.

The basins of attraction for these alternate states are dependent on the initial values of the time series simulation. Figure 5a shows the model’s sensitivity to initial R and E values, indicating that a small change in harvesting effort or perturbation to a resource can rapidly cause a population to unexpectedly change states. I found evidence for alternate states in both scenarios displayed in Figure 5, which depict very different underlying R dynamics. It can be seen here that small changes in parameters (in this case $r$) can change the sensitivity to initial conditions (Figure 5a i. vs. ii.).
Figure 5. a) Basins of attraction based on initial resource density and effort level. i. parameters: $r = 1.5, K = 7, u = 0.4, q = 0.07, c = 0.1, w = 0.42$. ii. parameters: $r = 2.5, K = 7, u = 0.4, q = 0.07, c = 0.1, w = 0.27$. b) Time series of resource yield, after a transient, following different trajectories. i. and ii. with colour (grey vs. black line) corresponding to initial value basins in (a).

Figure 5b shows the time series dynamics of each attractor for resource yield, after a transient. The alternate basins (grey vs. black, corresponding to Figure 5a) clearly lead to different yield outcomes, and the specific patterns or trajectories change with different parameter combinations. The $IS_{th}$ used for simulating Figure 5b i. ($w = 0.42$) is extremely close to the model’s transition between stable and unstable conditions (see Figure 1a and 4 where $w$ goes through a Neimark-Sacker bifurcation), and in this region initial conditions can lead to drastically different yield outcomes (stable vs. oscillating attractors).
Alternatively, parameter conditions with two oscillatory attractors also exist. Figure 5b ii. shows two yield scenarios corresponding to the basins seen in Figure 5a ii., and although functionally similar in that they are both oscillatory, the grey trajectory approaches values dangerously close to zero that could easily collapse with any stochasticity included in the model. These results are evidence that slight changes in effort or perturbations to the resource could lead to unexpected and unwanted shifts to alternate states in such a socio-ecological system with behaviourally driven effort dynamics.

Near the regions where alternate states exist, I find trajectories with extremely long transients. Here, the time series seem to fall onto what appear to be alternate attractors, but converge after unusually long transients. Figure 6 shows examples of these long transients where the trajectories converge. I was able to find evidence of both long transients and alternate states in all regions of the $w$-$c$ parameter space shown in Figure 4 (i.e., stable and unstable). Figure 6a shows a long oscillatory transient converging to a stable equilibrium ($c = 0.1$, $w = 0.3360185$), and Figure 6b displays a chaotic transient that converges to an oscillator ($c = 1.5$, $w = 0.52$). These changes, like other examples of long transients in ecology (Schreiber 2003; McCann & Yodzis 1994) can occur precipitously and without warning. In the chaotic transient case, for example, the trajectory effectively finds a hole and rapidly transitions to the real attractor (McCann & Yodzis 1994).
Figure 6. Examples of extremely long transients found in stable (a) and unstable (b) regions of parameter space displayed in Figure 4i. a) $c = 0.1, w = 0.3360185, r = 1.5, K = 7, u = 0.4, q = 0.07$. b) $c = 1.5, w = 0.52, r = 1.5, K = 7, u = 0.4, q = 0.07$. 
Discussion

Here, I have investigated the dynamics of a recently introduced harvesting effort (E)-resource (R) model developed by Fryxell et al. (2010). This E-R model is in a sense akin to the C-R model that underpins consumptive food theory. Similar to patterns known from food web theory, my results suggest that human effort can either be stabilizing or destabilizing and that weak to moderate behavioural and effort response (via w and c) tend to stabilize dynamics by decreasing return times to equilibria or reducing the magnitude of cycles (Figures 1 and 2).

Further, relatively strong responses in human effort (c), and technology capable of catching resources efficiently (w), readily lead to human-driven cycles, chaos, long transients and alternate states. Given that Fryxell et al. (2010) found empirical evidence for human-driven cycles, and that these more complex dynamical phenomena are generally nearby the Neimark-Sacker bifurcation, it seems extremely plausible that effort dynamics are capable of driving chaos and alternate states (and long transients that functionally yield alternate states). These complex dynamical situations are an obvious concern for sustainably managing resources. Additionally, rapid growth in effort, as true in most ecological models (e.g., Ricker 1954; more generally discussed in Gellner and McCann 2016), has the ability to produce entirely human-driven fluctuations if human effort growth capacity (see parameter c) is high.

Clearly, some of the dynamical complexity of this model is driven by the discrete dynamical system approach taken by Fryxell et al. (2010). Continuous versions of E-R dynamics would be far less complex dynamically. Nonetheless, the biology behind this likely does involve human behaviour, and organismal biology, that ought to display these lags. As explained by Fryxell et al., resource breeding seasons often impose discrete-like dynamics to the system, and harvesting is often contained to a short season each year. Additionally, human effort and catch information is likely passed between stakeholders which produces lagged responses to changes in a resource population.
Given the potentially dramatic implications of effort dynamics on resource dynamics, it becomes critical to garner a better understanding of how human behaviour determines harvesting effort through dynamic social-ecological systems. Further, it is important to better understand harvesting behaviour in general and how human-driven dynamics affect the stability and sustainability of social-ecological systems. Here, I have explored a reasonable base model, already shown to match with existing empirical data (Fryxell et al. 2010), for more holistic E-R webs to develop an understanding of complex social-ecological systems.

It is important to understand human harvesting behaviour and decision-making in these social-ecological systems, given its large contribution to uncertainty in fisheries management (Fulton et al. 2011; Milner-Gulland 2011). Lade et al. (2013) provided a recent example of how human harvesting behaviour coupled with resource dynamics can cause regime shifts that result in unexpected but catastrophic collapse of the resource. These regime shifts could happen even with no sign of decline in the population or early warning signals (EWS) to indicate an impending transition between states, particularly if they occur in complex dynamical regions such as what is seen in this model (Boettiger & Hastings 2012). Since harvesting effort may lead to alternate states, it is entirely reasonable that some of the signatures of EWS may be found in human effort or behaviour dynamics. As an example, an increase in variance in effort might be expected just prior to a loss of equilibrium-like dynamics. However, the model used here produces many examples of complex alternate state transitions that can yield more complicated EWS signatures than the traditional saddle node type of transition (Boettiger & Hastings 2012).

Increasing dependence on a resource (i.e., increasing $\lambda_H$) has the potential to drive complex dynamics in resource populations, with the possibility of unexpected shifts to alternate states and/or collapse. I have shown that human-driven dynamics can couple with biologically-driven fluctuations to cause complex dynamical outcomes, even in such a simple E-R system. Changes in the period of resource oscillations could be an indication of human-driven destabilization. As seen in Fryxell et al. (2010), these long-period cycles are characteristic of some harvested populations and managers should be wary of the complex
nature of these human-impacted systems.

Weak management in the form of small and/or lagged responses to changes in a resource (as discussed in Fryxell et al. (2010)) or insufficiently accounting for feedback between human and ecological systems (as discussed in Horan et al. (2011)) seems to be the most detrimental to resource populations when impacts are relatively large (i.e., strong harvesting). However, I show here that human interactions are not always detrimental, and harvesting does not necessarily cause populations to become unstable. With effective management, including extensive monitoring and consideration of both human and ecological dynamics, harvesting has the potential to preserve or strengthen stable states, allowing resource populations to maintain stability (Horan et al. 2011). My model reaffirms this argument; weak human interactions have the potential drive stability in a resource, even when influenced by underlying biological complexity.
References


Effective fisheries management requires an understanding of harvesting impacts and how they are influenced by human behaviour. Clearly not all harvesting impacts are the same, so it is important to classify fishing behaviour based on fisheries catches and human effort and decision-making. The two chapters in this thesis provide an important basis for classifying global fisheries based on human impacts and a framework for understanding the dynamics of holistic social-ecological harvesting systems. Chapter 1 presents a novel approach to characterizing harvesting behaviour based on the topology and distribution of human interactions throughout fisheries food webs, and explores the socio-economic factors contributing to global patterns in these fishery types. Chapter 2 investigates the dynamical implications of harvesting in a simplified social-ecological model as a first step towards characterizing differences in human impacts based on harvesting behaviour.

Inland fisheries in developing countries, particularly those in Asia and Africa, have vastly different approaches to fishing than the heavily managed regimes from developed nations. Fishers typically do not have the luxury to selectively catch only the large valuable fish. Instead, fisheries in these developing nations characteristically catch a wide variety of species using many different fishing gears to effectively harvest all species from all habitats. In Chapter 1 I show that socio-economic conditions may influence human harvesting behaviour by altering the distribution of human interactions throughout fisheries food webs, resulting in global patterns in fisheries impacts.

With an understanding of societal motivations driving harvesting behaviour, researchers can begin to develop holistic social-ecological resource management models that consider human decision-making and harvesting effort. Chapter 2 explores a simplified social-ecological harvesting model as a first step to understanding the dynamical interactions between harvesting behaviour and a resource population. I see that harvesting, through weak human interaction strength, has the potential to drive stability. However, altering harvesting behaviour can also readily drive complex dynamics, including alternate states, long transients and chaos, with negative implications for fisheries sustainability and yield.
These results illustrate the importance of including human behaviour in resource management models by developing thorough social-ecological harvesting models. Harvesting effort is not a static process, so understanding the socio-economic factors influencing human behaviour will allow for a better understanding of human impacts on managed ecosystems.

By bridging the gaps between socio-economics, fisheries management, and ecological theory I provide a basis for understanding harvesting behaviour and human impacts on different fishery types globally. This continuum of fishery types and implications for fisheries sustainability highlights the importance of approaching fisheries management from a multi-objective approach to successfully protect fisheries production and biodiversity. Connecting fisheries with people’s reliance on fish for protein and their economic conditions will highlight the need to change management strategies in many developing nations that inordinately rely on inland fisheries for food. The importance of preserving fish biodiversity goes beyond having biological significance; it is crucial to protecting people’s livelihoods.
APPENDIX A: SUPPLEMENTARY INFORMATION FOR CHAPTER 1

A.1 Data Collection

A.1.1 Fisheries ecosystem and catch data
Fisheries data were collected by performing a literature search for spatially defined bodies of freshwater, with exact species richness (\(S_T\)) measures of fish in the body of water and all fish caught throughout the area (all people, gears, locations, etc.; \(S_F\)). Searches were done by country, and the first reliable source found was used as a representative of each country. One example from each country was used for standardization across differing levels of scientific data collection among countries. Keywords such as “fish catch composition”, “fishery catch”, “species richness”, in various combinations, along with the country of interest were used, in combination with “inland” or “freshwater” if necessary (e.g., for coastal countries). Sources include both primary literature and fisheries/governmental/NGO reports.

A.1.2 Fisheries location data
Human Development Index (HDI) was downloaded from the UNDP site on 26 Feb, 2015 from [http://hdr.undp.org/en/content/human-development-index-hdi-table](http://hdr.undp.org/en/content/human-development-index-hdi-table) and 2011 data was used.


Coastline length (CL) was obtained from the CIA World Factbook on 28 Oct, 2015 from [https://www.cia.gov/library/publications/the-world-factbook/fields/2060.html#download](https://www.cia.gov/library/publications/the-world-factbook/fields/2060.html#download)

Latitude for each location was taken from Wikipedia for the water body, or nearest city when not available. The absolute value of each location’s latitude was used for analysis.
A.2 Statistical Analyses

Since only freshwater fisheries were included in this analysis, countries outside the sample 95th percentile for the coastline length:land area (CL:LA) ratio were excluded. This was done to account for countries with a possible high dependence on marine fisheries and thus excluded small island countries. Two samples were removed, an inland fishery from the Soloman Islands and Estonia, whose CL:LA ratio were well above the rest. After reduction, the dataset contained 30 countries with sufficient ecosystem and fisheries data that met all requirements. With the remaining data, Degree of Generality for each fishery was calculated as $S_f/S_T$ to generate a continuum from 0 to 1, where a measure of 1 means all species are harvested to some extent. Table S1 shows the fisheries catch information and sources.

HDI and Degree of Generality were both logit-transformed, as they are both ratios and these transformations were used for all analyses. Simple linear regressions were used to test the relationships between Degree of Generality and both HDI and latitude. HDI and latitude are significantly positively related (p = 9.864e-05; Figure S1) so multiple regression was not appropriate. After linear regression between Degree of Generality and latitude was performed, the residuals (Generality$_{RESID}$; Figure S2) were used in a second linear regression with HDI. This normalized the Degree of Generality against the effect of latitude to see the independent effect of HDI.
A.3 Figures and Tables

Figure A1. Linear regression between Human Development Index (HDI) and absolute value of latitude for 30 freshwater fisheries. Slope = 0.028975, p = 9.864e-05, R² = 0.4029.

Figure A2. Residuals vs. fitted values from a simple linear regression of Degree of Generality on absolute value of latitude for each fishery location.
Table A1. Location of 30 freshwater whole-system fisheries and the species richness in each water body \((S_T)\), along with the total species richness found in fisheries catches \((S_F)\). 2011 Degree of Generality is the proportion of species caught in each system \((S_F/S_T)\). Human Development Index (HDI) for each country was used for analysis.

<table>
<thead>
<tr>
<th>Location</th>
<th>Country</th>
<th>HDI</th>
<th>Catch ((S_F))</th>
<th>Ecosystem ((S_T))</th>
<th>Degree of Generality</th>
<th>Source(s)</th>
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<td>0.75</td>
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<td>0.19</td>
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<td>195</td>
<td>0.22</td>
<td>Fremling et al. (1989)</td>
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<td>46</td>
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<td>296</td>
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<td>Age (years)</td>
<td>Larg. (m³/s)</td>
<td>Date</td>
</tr>
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<td>Brazil</td>
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A.4 Data References


B.1 Boundary equilibria and stability

There are boundary equilibria at \( R = K, E = 0 \) and \( E = c/u, R = 0 \), as well as the trivial equilibrium at the origin \( R = 0, E = 0 \). To determine the stability properties and possibility of bifurcations at these equilibria, I substitute these values into the Jacobian and calculate \( \lambda \) as described in the Methods. To determine if these boundary equilibria undergo bifurcations in the parameter space used in these analyses, I can numerically solve for stability conditions based on \( c \) and \( w \), after substituting other parameter values \( r = 1.5, K = 7, u = 0.4 \) and \( q = 0.07 \) consistent throughout analyses.

- Equilibrium at \( R = K, E = 0 \)

After substituting the equilibrium into the Jacobian, the community matrix is determined as follows:

\[
A = \begin{bmatrix}
1 - r & -qK \\
0 & e^{c+wK}
\end{bmatrix}
\]

where the two eigenvalues are equal to \( \lambda_1 = 1 - r \) and \( \lambda_2 = e^{c+wK} \). Solving for \( c \) determines that \( \lambda_1 = -0.5 \) (since \( r = 1.5 \)), and \( \lambda_2 \) is only stable when one of \( c \) or \( w \) is negative. This is not biologically possible so \( \lambda_2 \) is never attracting within the parameter range used for analysis. Thus, this equilibrium is never stable.

- Equilibrium at \( R = 0, E = c/u \)

After substituting the equilibrium into the Jacobian, the community matrix is determined as follows:

\[
A = \begin{bmatrix}
e^{r-qc/u} & 0 \\
wc/u & 1 - c
\end{bmatrix}
\]

where the two eigenvalues are equal to \( \lambda_1 = e^{a-qc/u} \) and \( \lambda_2 = 1 - c \). Solving for \( c \)
determines that $\lambda_1$ is stable when $c \geq 8.57143$, but $\lambda_2$ is stable for $0 \leq c \leq 2$. Thus, $\lambda_1$ and $\lambda_2$ are never both attracting and this equilibrium is never stable.

- **Equilibrium at $E = R = 0$**

After substituting the equilibrium into the Jacobian, the community matrix is determined as follows:

$$A = \begin{bmatrix} e^r & 0 \\ 0 & e^c \end{bmatrix}$$

where the two eigenvalues are equal to $\lambda_1 = e^r$ and $\lambda_2 = e^c$. $\lambda_1$ and $\lambda_2$ are only stable when $r, c, < 0$ so the origin is never stable.

**B.2 Influence of behavioural parameter $u$ on stability and dynamics**

The parameter $u$, described in Methods, accounts for the effect of one unit increase in effort on the exponential rate of change in effort. This is effectively a density-dependent ‘mortality’ term in the effort equation. Here, I explore the dynamical implications of varying $u$ on stability of a resource with different underlying resource dynamics (i.e., R stable, cyclic and complex). I also determine differences in the effect of $u$ at different levels of the parameter $c$ (analogous to ‘growth’ in effort). Figure B1 displays the low $c$ ($c = 0.3$) case, and Figure B2 displays the high $c$ ($c = 1.65$) case.
Figure B1. Stability analysis of a harvested resource, measured by the norm of the maximum eigenvalue (λ), as \( u \) is increased and \( c \) is low. Resource growth rate is manipulated to influence biologically-driven dynamics as follows: a) \( r = 1.5 \), b) \( r = 2.5 \), c) \( r = 3.5 \). In all cases, \( c = 0.3 \), \( w = 0.4 \), \( K = 7 \) and \( q = 0.07 \).
Figure B2. Stability analysis of a harvested resource, measured by the norm of the maximum eigenvalue ($\lambda$), as $u$ is increased and $c$ is high. Resource growth rate is manipulated to influence biologically-driven dynamics as follows: a) $r = 1.5$, b) $r = 2.5$, c) $r = 3.5$. In all cases, $c = 1.65$, $w = 0.4$, $K = 7$ and $q = 0.07$. 
The parameter $u$ is a behavioural component of harvesting effort, and it remains to be seen how $u$ interacts with other behavioural components in parameter space. I unfold these parameters and examine the bifurcation structure of $c-u$ (Figure B3) and $w-u$ (Figure B4) parameter space. Here, I show stable and unstable regions, and evidence for flip and Neimark-Sacker bifurcations.

**Figure B3.** $c-u$ parameter space and regions of stability based on eigenvalue characteristics (the system is stable when the Norm($\lambda$) < 1 (grey fill). Transitions between stable and unstable regions indicate bifurcations, with the bifurcation type illustrated by line type (flip (F) and transcritical (T) = solid line; Neimark-Sacker (N-S) = dashed line). Neimark-Sacker bifurcations occur when the eigenvalue has a complex component. Other parameters: $r = 1.5$, $w = 0.4$, $K = 7$ and $q = 0.07$. 
Figure B4. $w$-$u$ parameter space and regions of stability based on eigenvalue characteristics (the system is stable when the Norm($\lambda$) < 1 (grey fill). Transitions between stable and unstable regions indicate bifurcations, with the bifurcation type illustrated by line type (flip (F) = solid line; Neimark-Sacker (N-S) = dashed line). Other parameters: $r = 1.5$, $c = 0.3$, $K = 7$ and $q = 0.07$. 