University of California
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Uncertainty analysis in fisheries science–an interdisciplinary approach

A dissertation submitted in partial satisfaction
of the requirements for the degree

Doctor of Philosophy
in
Environmental Science & Management

by

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December 2018

The Dissertation of Laura C. Urbisci is approved.

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December 2018

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I dedicate my dissertation to the countless cups of coffee, wine, and whiskey I consumed in the past 5.25 years. I could be nowhere with out you.

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Curriculum Vitæ
Laura C. Urbisci

EDUCATION

2018	Ph.D. in Environmental Science & Managemnt (Expected), University of California, Santa Barbara.
2016	M.A. in Applied Statistics, University of California, Santa Barbara.
2012	BS in Environmental Science and Management *with honors* Emphasis in Ecology, Biodiversity and Conservation, Minor in Spanish University of California, Davis
2010	Education Abroad Program Universidad de Carlos III – Madrid, Spain

RELEVANT COURSEWORK

Regression Analysis	Probability and Statistics (3 part course)
Statistical Theory (2 part course)	Statistical Consulting
Advanced Statistical Methodology (3 part course)	Data Mining
Design and Analysis of Experiments	Time Series Analysis
Linear and Nonlinear Mixed Effects Modeling	Data Science
Bayesian Data Analysis	Machine Learning (audit)

RELEVANT STATISTICAL EXPERIENCE

Quantitative Consultant, Santa Barbara, CA
Bren School of Environmental Science & Management 9/16 – 3/17

- Assisted all graduate students, faculty, postdocs, and visiting researchers with their quantitative needs
- Advised the most appropriate statistical methods to use given the data set and research questions
- Explained how to code statistical models and interpret model results

Probability and Statistics Department, UCSB
Group Projects 4/16 – 6/18

- Worked on a multiple projects that utilized different data sets including: biological and political
- Select skills applied include: principal component analysis, categorical KNN, classification tree analysis (with pruning, bagging, and random forests), and Naïve Bayes
- Lead group by setting goals and determined course of action for a group of 4
- Presented ideas effectively and wrote a report which received positive feedback from instructor

Probability and Statistics Department, UCSB
Individual Projects 12/14 – 6/16

- Worked on a variety of projects to analyze results from various data sets including: medical, economic, and biological
- Overview of skills and select a few used: fitted a time series model (Seasonal ARIMA) to data and forecasted into the future to predict values, compared the efficacy of three weight-loss programs using linear mixed effects models, looked at the economic relationship between the 48 contiguous states using multivariate analysis methods and linear models
- Presented ideas effectively in project interview and wrote a report which received positive feedback

STATISTICAL LEADERSHIP EXPERIENCE

Teaching Assistant (TA), Santa Barbara, CA

University of California, Santa Barbara 3/17 – current

- Gave multiple guest lectures to 150 students on linear regression, binomial proportion test, and chi-squared tests
- Managed computer labs and showed students how to program in R, the R GUI R Commander, SAS, and Excel
- Taught material ranging from basic statistical concepts to advanced statistical theory to students who came from a wide range of backgrounds

Statistics Tutor, Santa Barbara, CA

Probability and Statistics Department 9/15 – current

- Aided undergraduate students with their quantitative coursework and taught R
- Helped students understand difficult concepts by explaining it to them in novel ways

Master's Group Project PhD Mentor, Santa Barbara, CA

Bren School of Environmental Science & Management 3/16 – 3/17

- Helped master student's set attainable goals, define research questions, and develop a feasible project timeline
- Reviewed and provided feedback on drafts of reports and presentations
- Recommended appropriate statistical analysis given data

Intern, La Jolla, CA

NOAA Southwest Fisheries Science Center 8/12 – 8/13

- Analyzed scientific data and presented findings at a professional meeting
- Trained lab assistants

PUBLICATIONS

Urbisci, L. C., Stohs, S. M., and Piner, K. P. 2017. From sunrise to sunset in the California drift gillnet fishery: An examination of the effects of time and area closures on the catch and catch rates of four key pelagic species: thresher shark (Alopias vulpinus), swordfish (Xiphias gladius), blue shark (Prionace glauca), and shortfin mako (Isurus oxyrinchus). Marine Fisheries Review. 78(3-4):1-12.

Ayres, A., Degolia, A., Fienup M., Kim J., Sainz, J., **Urbisci, L. C.**, Viana, D., Wesolowski, G., Plantinga, A. J., Tague, C. 2016. Social science/natural science perspectives on wildfire and climate change. Geography Compass. 10.2: 67-86.

Urbisci, L. C., Sippel, T., Teo, L. H., Piner, K. R., and Kohin, S. 2013 Size composition and spatial distribution of shortfin mako sharks by size and sex in U.S. West Coast fisheries. Submitted to ISC Shark Working Group Workshop July 6-11, 2013.

Urbisci, L. C., Runcie, R., Sippel, T., Piner, K., Dewar, H., and Kohin, S. 2012 Examining size-sex segregation among blue sharks (Prionace glauca) from the Eastern Pacific Ocean using drift gillnet fishery and satellite tagging data. Submitted to ISC Shark Working Group Workshop January 7-14, 2013.

Urbisci, L. C. 2011. Testing the unknown: the distribution, size and abundance of intertidal Haliotis rufescens (red abalone) and Haliotis cracherodii (black abalone) within Marine Protected Areas. (Unpublished student report. On file at the Cadet Hand Library, U.C. Davis Bodega Marine Laboratory).

PRESENTATIONS

Urbisci, L.C. 2018. Untangling uncertainty in food webs. Presented to Schmidt Family Foundation on March 9, 2018, Santa Barbara, CA.

Urbisci, L.C. 2017. Fishing through the food web leads to systematic overestimation of maximum sustainable yield. Presented at the NMFS-SG Annual Fellows Meeting on May 8-10, 2017, Beaufort, NC.

Urbisci, L.C., 2016. Developing an alternative estimate for virgin biomass using food web dynamics. Presented at the NMFS-SG Annual Fellows Meeting on June 28-30, 2016, Santa Cruz, CA.

Urbisci, L.C., 2016. Developing an alternative estimate for virgin biomass using food web dynamics. Presented at the Bren School PhD Symposium on February 19, 2016, Santa Barbara, CA.

Urbisci, L.C., 2015. Developing a new ecosystem-based management approach: using ecosystem model to calculate a better estimate of population scale for single-species models. Presented at the NMFS-SG Annual Fellows Meeting on June 9-11, 2015, Miami, FL.

Urbisci, L.C., Stohs, S. M., and Piner, K. P. 2014. From sunrise to sunset in the California drift gillnet fishery: An examination of the effects of time and area closures on the catch and catch rates of four key pelagic species: thresher shark (Alopias vulpinus), swordfish (Xiphias gladius), blue shark (Prionace glauca), and shortfin mako (Isurus oxyrinchus). Presented at the Highly Migratory Species Management Team Meeting on January 22, 2014, La Jolla, CA.

Urbisci, L.C Runcie, R., Sippel, T., Piner, K., Dewar, H., and Kohin, S. 2012 Examining size-sex segregation among blue sharks (Prionace glauca) from the Eastern Pacific Ocean using drift gillnet fishery and satellite tagging data. Presented at the ISC Shark Working Group Workshop January 10, 2013.

Urbisci, L.C. 2011. Testing the unknown: the distribution, size and abundance of intertidal Haliotis rufescens (red abalone) and Haliotis cracherodii (black abalone) within

Marine Protected Areas. Presented at the Sequence One and Two Student Symposium 2011, Bodega Bay, CA.

Abstract

Uncertainty analysis in fisheries science–an interdisciplinary approach

by

Laura C. Urbisci

Laura's dissertation is an interdisciplinary approach that combines fisheries science, ecological theory, and applied statistics. Her first chapter is a meta-analysis on transfer efficiency that describes and quantifies the variation in transfer efficiency. Her second chapter assesses uncertainty in food web models by creating multiple Monte Carlo simulations to test various ecological assumptions about net primary production and transfer efficiency. Her final chapter is a comparative analysis of two Bayesian models: a classic Bayesian surplus production model and a Bayesian surplus production model that incorporates ecological information. This chapter examines if the inclusion of ecological information informs and alters fisheries assessment models, with a focus on data-limited fisheries. Ultimately, Laura's work bridges the gap between applied statistics and ecological theory and encourages the use of uncertainty analysis to make more robust predictions in food web models.

Contents

Chapter 1

Introduction

Fisheries modeling take the complexity of a single heterogeneous stock with different sizes, ages, growth rates, movement patterns, reproductive abilities, behaviors in response to fishing gear, and risks of natural mortality and simplify these diverse dynamics into a cohesive model. These stock assessment models look at data such as the number of fish caught, total biomass over a certain range, catch per unit area, and mean size (weight or length) of fish harvested and attempt to predict how these attributes will respond to fishing over time. Depending on the available data and level of complexity desired, we can model open ocean ecosystems using several different approaches. Most models focus on an individual stock and fall under the category of a single-species model. The simplest single-species models look only at abundance and are referred to as biomass dynamic or production models. These models can be extended in three ways. They can include age-structure, the dynamics of fleets, spatial structure, and interactions with other species and the environment. The models that include species interactions and environmental fluctuations are a special class of models referred to as ecosystem-based models.

A multitude of ecosystem-based models have been developed within the past three decades to address the need to incorporate ecosystem-based science into fisheries management. These models help inform decision-makers about the effects of fishing mortality and the indirect trophic implications of fishing in changing ecological environments. There are various types of ecosystem-based models: whole ecosystem and dynamic system models, minimum realistic models (restrict a model to those species most likely to have important interactions with the species of interest), individual-based models (follow an individual through their life cycle), and bioenergetics models (use bioenergetics and allometric reasoning) (Plaganyi and Butterworth 2004, Collie et al. 2014). All of these classes of models aim to simulate the environment by including species interactions and environmental fluctuations.

Instead of attempting to explain all the ecological processes in one model, a new possible approach is to move away from focusing on small-scale details and look at the ecosystem in a broader context. We can combine ecosystem-knowledge to improve upon single-species models. For instance by applying ecological theory such as food web dynamics, we can develop a more feasible approach to estimate the unfished biomass and carrying capacity. By taking the amount of net primary production that enters into the system, we can use the principle behind energy transfer in food webs to approximate the amount of biomass at each trophic level. By taking a bottom-up approach, we can ensure that our estimates of unfished biomass are feasible, because we account for how much energy goes into the system. We can additionally include sensitivity analysis in our model to account for the natural variation in the environment.

Chapter 2

Tangled is the web we weave

2.1 Introduction

One of the crucial, and at times, most puzzling concepts in food web dynamics research is the transfer efficiency-?the movement of production between trophic levels. This paper addresses two aspects of transfer efficiency: first, we seek to provide clarity and untangle the web of confusion surrounding the conceptualization of transfer efficiency. Second, we address the often-cited claim that transfer efficiency is a constant 10%. We analyze extant research to show that transfer efficiency varies substantially across systems, trophic levels, and taxa.

2.1.1 Origin and conceptualization of transfer efficiency

The definition of transfer efficiency has been somewhat muddled since its inception. We refer to transfer efficiency as the fraction of production passing from one trophic level to the next (Slobodkin 1959). At times it has also been referred to as trophic (transfer) efficiency (Chapman and Reiss 1998). This term is often confused with other non-equivalent efficiencies such as ecological efficiency, assimilation efficiency, and consumption efficiency (Iverson 1990, Hairston 1993). However, each of these efficiencies addresses distinct ecological questions and thus require different data for their calculations. Slobodkin (1959) theorized a food chain efficiency metric and defined it as the ratio of the number of organisms removed from the targeted population to the food consumed by the targeted population (Slobodkin 1960, 1962). Removal includes both natural mortality and human harvesting. He subsequently renamed the concept "ecological efficiency" in his 1962 and 1972 papers (Slobodkin 1962, 1972). The energy budget requires a balance between inputs and outputs. When energy is ingested, some of that energy is lost to respiration and excretion. Then, the remaining energy that is assimilated is divided amongst basal maintenance, growth, and reproduction. Assimilation efficiency is defined as the percentage of energy ingested at trophic level n that is assimilated at trophic level n (Hairston 1993). The consumption efficiency measures the number of organisms from the prey population that is consumed by its predators and is defined as the percentage of net production at trophic level n that is consumed by trophic level $n+1$ (Hairston 1993). In an attempt to make the differences clearer, we provide a simple cartoon of a food web (Figure 2.1) that visualizes the definitions of four of the commonly used efficiencies.

Availability of data differs between ecosystems. It is difficult in aquatic systems, especially marine systems, to gather enough data on every species in order to calculate the assimilation and consumption efficiencies. Terrestrial studies, on the other hand, can collect detailed population data much easier. Thus, terrestrial studies do not need to rely as much on inferential techniques, like the transfer efficiency, and have the ability to calculate species-specific metrics, such as the assimilation and consumption efficiency. To clarify, the assimilation and consumption efficiencies can also be calculated at the trophic-level in addition to the species-level.

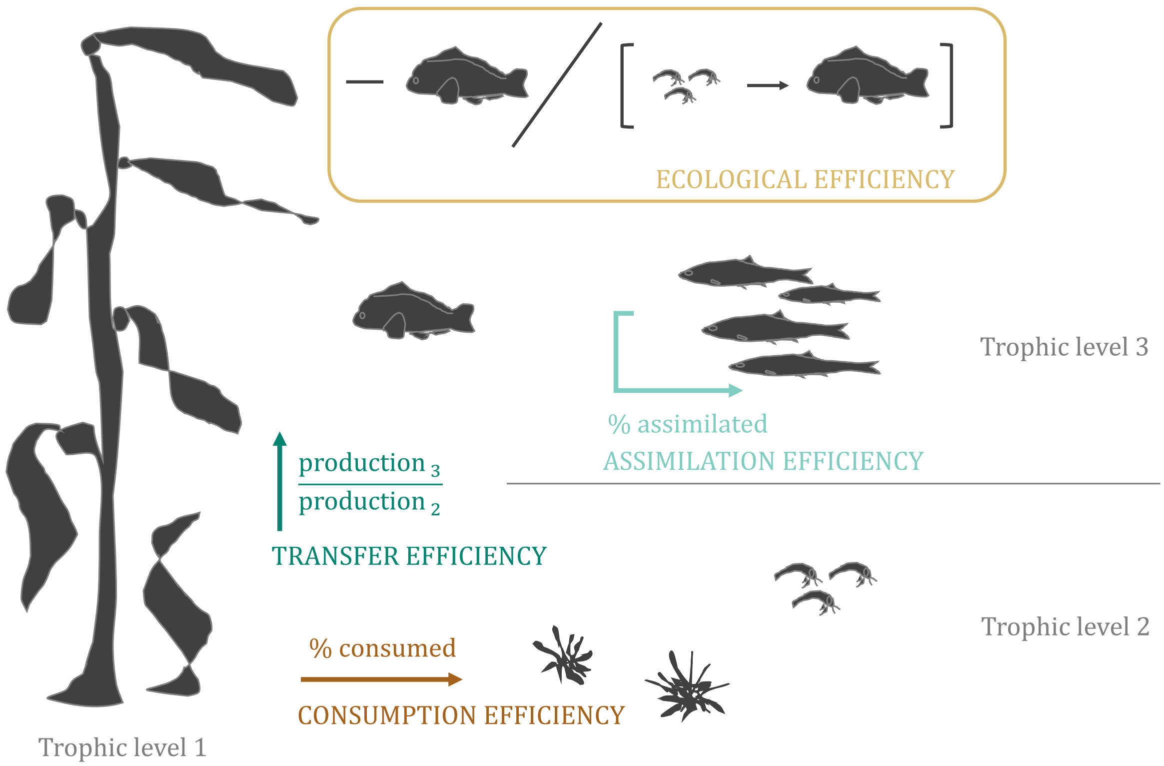

Figure 2.1: Cartoon of a food web that visualizes different efficiencies. The consumption efficiency is in brown, the transfer efficiency is in teal, the assimilation efficiency is in light blue, and the ecological efficiency (food chain efficiency) is in tan. In the consumption and ecological efficiency, the head of the arrow indicates the direction of consumption, where the species at the arrow head represent the species consuming the species at the arrow's origin. The diagram of the ecological efficiency includes a negative sign, division sign, and parentheses. Plot created using Microsoft office 2013.

The confusion around the definition is not the only complication with transfer efficiency–the values themselves have been disputed over the years and remain a point of contention. It is surprising that some scholars treat transfer efficiency as a fixed constant (i.e., 10%) for all trophic levels in light of the fact that other scholars have found that physiological, and potentially behavioral, characteristics influence transfer efficiency (May 1983, Pauly and Christensen 1995, Ware 2000, Cury et al. 2005, Libralato et al. 2008, Chassot et al. 2010, Trebilco et al. 2013, Watson et al. 2014).

Physiological and behavioral characteristics of transfer efficiency in freshwater and marine ecosystems

Multiple factors have been shown to affect transfer efficiency in both freshwater and marine ecosystems. In freshwater systems, the sources of variability in transfer efficiencies include the body of water, season, trophic level, and species composition (Lindeman 1942, Gaedke and Straile 1994, Rybarczyk and Elkaım 2003, Karlsson et al. 2007). In marine systems, transfer efficiency varies by ecological system, geographic location, trophic level, metabolic strategy, and species composition (May 1983, Persson et al. 2007, Libralato et al. 2008, Barnes et al. 2010).

Ecological system within freshwater and marine ecosystems

Transfer efficiency has been found to be specific to the geographical region. Multiple marine studies found distinct transfer efficiencies between upwelling, temperate and tropical ecosystems (i.e., 5% upwelling, 10% temperate, and 14% tropical) (Libralato et al. 2008, Coll et al. 2008, Chassot et al. 2010). Even within a single ecosystem, Baird et al. (2004) found that each community within an intertidal ecosystem had unique transfer efficiency values. Distinct transfer efficiency values have also been found to occur not only between lakes and within trophic levels in freshwater ecosystems (Lindeman 1942), but also in bays and estuaries as well (Rybarczyk and Elkaım 2003).

Additionally, research has found that the amount of sunlight a region receives affects transfer efficiency. San Martin et al. (2006) suggest that transfer efficiency from phytoplankton to zooplankton in marine ecosystems decreases as latitude increases due to the decrease in sunlight. Gaedke and Straile (1994) found seasonal variation in transfer efficiency between the first and second trophic level in lakes, with transfer efficiency rising in the summer and fall and decreasing in the winter and spring. The seasonal variation in transfer efficiency can be attributed to the decrease in phytoplankton abundance in winter due to limited sunlight. As daylight increases in early spring, there is a gradual increase in phytoplankton blooms–culminating in the maximum phytoplankton production in summer (i.e., peak hours of sunlight). As the days become shorter in fall and the hours of sunlight decreases, there is a decrease in the amount of phytoplankton. There is a time lag corresponding to the change in sunlight in the spring and fall seasons. Therefore, the amount of sunlight indirectly influences transfer efficiency between the first and second trophic level by directly impacting the phytoplankton abundance.

Trophic level

Size spectrum studies report that transfer efficiency decreases with body size, and by association, trophic level (Barnes et al. 2010). Therefore, the size ratio of prey to predators (e.g., phytoplankton to zooplankton) impacts transfer efficiency and trophic structure (Havens 1998, García-Comas et al. 2016).

Metabolic strategy

Furthermore, May (1983) found ectotherms are more efficient than endotherms in transferring energy from trophic level n to trophic level $n + 1$, with energy transfer efficiencies around 20-50% for invertebrate ectotherms, around 10% for vertebrate ectotherms and less than 2% for endotherms. This discrepancy in transfer efficiency is due to the metabolic efficiency: ectotherms rely on environmental heat sources and therefore have a lower metabolic cost in comparison to endotherms. Much of the metabolic energy in endotherms goes to the production of heat. Therefore, transfer of energy in the higher trophic levels where endotherms are prominent is less than the lower trophic levels were ectotherms make up more of the composition in marine ecosystems (McGarvey et al.

2018).

Species composition

Consuming nutritionally imbalanced food has been shown to lead to large respiratory losses, which negatively affect transfer efficiency (Persson et al. 2007). Karlsson et al. (2007) and von Elert et al. (2003) found that the species composition of prey, in particular different species of zooplankton crustaceans and the absence of long-chain polyunsaturated fatty acid in cyanobacteria, influence transfer efficiency. In addition, the presence of jellyfish blooms has been found to reduce the transfer of energy to higher trophic levels (Condon et al. 2011).

Trussell et al. (2006) and Schmitz et al. (2008) found that the risk of predation modifies prey conversion efficiencies and biomass production, which could therefore influence trophic structure and energy transfer. While these results refer specifically to assimilation and consumption efficiencies, it is plausible that this behavior influences transfer efficiencies as well. While the specific factors previously discussed influence transfer efficiency individually, these components interact in the natural environment. Because of this interaction, researchers must consider the impacts of the synergistic effects of these factors on the variability of the transfer efficiency and in turn how to account for them in the modeling process.

The 10% transfer efficiency

Although the studies above highlight that a number of factors can greatly affect trophic efficiencies, we still see broad use of the assumption of a constant value of 10%. To explore how (un)reasonable this assumption might be in different contexts, we synthesize the pattern of variation that has been observed in empirical studies that measured transfer efficiencies. Our goal is to provide guidance for what is reasonable to assume and what is necessary to measure.

It is unclear where the 10% transfer efficiency assumption came from. Looking back at the historical records, we find a "tangled web" of misattributions and a general lack of empirical evidence. Semper (1881) might have come up with the theory that there is a 10% transfer between trophic levels, but he lacked empirical evidence to back this claim (McIntosh 1986). Lindeman (1942) developed more general theory by looking at energy flow diagrams and mentioned a progressive efficiency which is currently known as transfer efficiency. However, no explicit mention of a 10% value shows up in this work even though he is often credited for it (i.e., Lindeman?s law of trophic transfer efficiency– Chapman and Reiss 1998). Slobodkin (1959, 1972) stated that ?the values mentioned by Lindeman, as well as other values presented by other field workers, for ecological efficiency tended to cluster around 10%.? Yet, Lindeman never explicitly discusses the ecological efficiency. He talked about the progressive efficiency, which as mentioned previously is a different concept. Regardless, Slobodkin and his students used laboratory experiments to formalize the hypothesis that there was an approximately 10% transfer between trophic levels (Slobodkin 1959). He referred to this as the food chain efficiency, which was later renamed to the ecological efficiency. However in a later study, Slobodkin (1972) found empirical and theoretical objections to the 10% ecological efficiency and rejected the theory. According to McIntosh (1986), ?Nevertheless, May (1967b) in pursuit of the ?perfect crystals? of ecology, included Slobodkin?s 1961 hypothesis in a series of community properties he described as ?constant and predictable?.? In a more recent edition of May?s Theoretical Ecology textbook , however, the authors reach a very different conclusion:

> One such [generalization] in the early 1960s suggested that the food-chain

> efficiency for transfer of energy from one trophic level to the next was generally around 10%. Subsequent studies showed that such food-chain efficiencies can vary over two or more orders of magnitude, from less than 0.1% to significantly more than 10%. Some evidence suggests such efficiencies may, other things being equal, be higher for carnivores and detritus feeders than for herbivores, possibly because biochemical conversion efficiencies are higher for animals eating plants. (May and McLean 2007)

In Figure 2.2, we present a flowchart showing the muddled origin of this concept. Given the unclear origin and application of the 10% transfer efficiency assumption, this assumption warrants further analysis, which is the focus of this current study. In the following section, we synthesize studies that provide empirical estimates of transfer efficiencies.

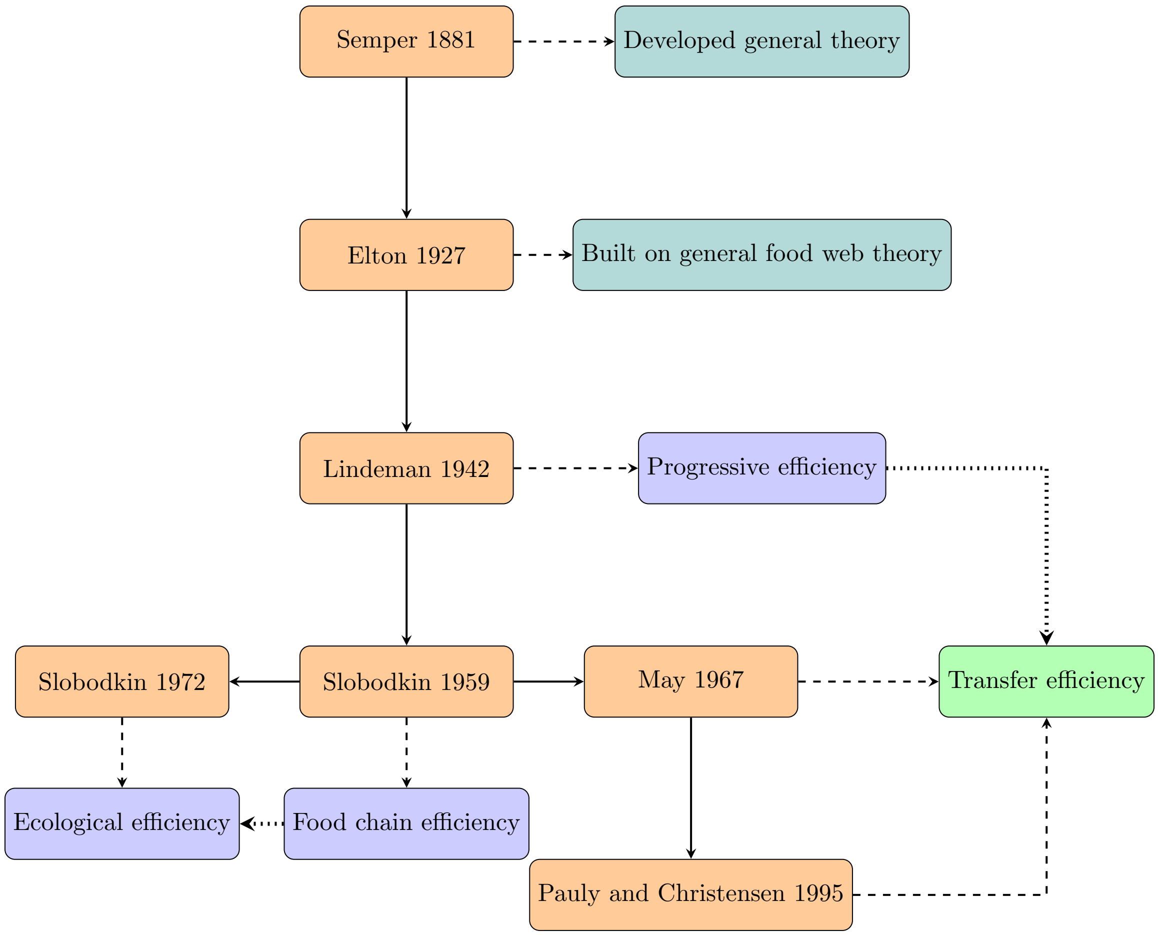

Figure 2.2: Flow chart of the origin of the 10% transfer efficiency theory (green icon). A subset of key journal articles are highlighted in the orange icons. The dashed lines point to the efficiency mention in a particular article. The dotted lines represent a change in the name of an efficiency. Teal icons denote that the article discussed general theory, while periwinkle blue icons represent the discussion of a type of efficiency. The arrowhead attached to the solid line denotes the downstream flow direction of citations. Plot created using LaTeX v.2.9.6211 (Lamport 1994) package tikz v.3.0.1a (Tantau 2015).

Methods

To explore the empirical distributions of transfer efficiencies, we collected articles that mentioned both food web and transfer efficiency. We then selected from these studies those that included relevant data, whether model-based or empirical. While we initially hoped to include terrestrial as well as freshwater and marine studies, we found nearly all of the terrestrial studies were on the consumption and assimilation efficiency, not the transfer efficiency. Therefore, we broke our analysis into two sections: freshwater and marine and ignored terrestrial. We primarily applied exploratory data analysis techniques such as summary statistics to distinguish patterns between the systems.

If the sample size was sufficient large, we also used decision tree analysis (i.e., regression trees with pruning, bagging, and random forests) and Monte Carlo simulations (See Table 2.1 and 2.2). Decision tree analysis was employed to determine which factors had the largest impact on transfer efficiency. Using an approach similar to (Libralato et al. 2008), we clustered the marine ecosystems into the following regions: temperate shelves and seas, tropical shelves and seas, lagoons, upwelling ecosystems, and open oceans. Although we also clustered the freshwater ecosystems into lakes, springs, and ponds, the sample size of the freshwater transfer efficiency data was too small to run regression tree analysis. We used regression trees with pruning, bagging, and random forests on the marine transfer efficiency data set and used relative importance plots to determine which factors accounted for the largest sources of variation and were most useful in predicting transfer efficiency. In the discussion, we used Monte Carlo simulations to aid in the conversation.

Freshwater

Many of the preliminary studies on transfer efficiency occurred in freshwater systems. All of the early studies were empirical (i.e., data used to calculate the transfer efficiency were collected either through laboratory experiments or from the field), but over time studies shifted to being increasingly model-based (i.e., data used to calculate the transfer efficiency were generated as the product of computer models). We found a total of 11 systems with transfer efficiency data (Table 2.1). Only the empirical studies reported transfer efficiency values for multiple trophic levels. The model-based studies reported the system-wide average. Most of the transfer efficiency data is empirically based.

The distributions of the freshwater transfer efficiencies are given in Figure 2.3. The empirical observations are skewed-right, while the model-based observations appear bimodal (albeit with a small sample size–$n = 4$). Combining the empirical and model-based estimates, the collective freshwater transfer efficiencies ($n = 19$) range from 0.1% to 22.3% with a median of 8.4%. When we calculate the average transfer (progressive) efficiency values provided in Lindeman (1942), we found that the average actually is 9%. If we consider just transfer efficiencies between phytoplankton (trophic level 1) and zooplankton (trophic level 2), we found the median transfer efficiency to be 12.2%. Unfortunately, the sample size in each group (i.e., trophic level and geographical region) is insufficiently large to draw any strong conclusions with relative certainty about which factors are the biggest sources of variation.

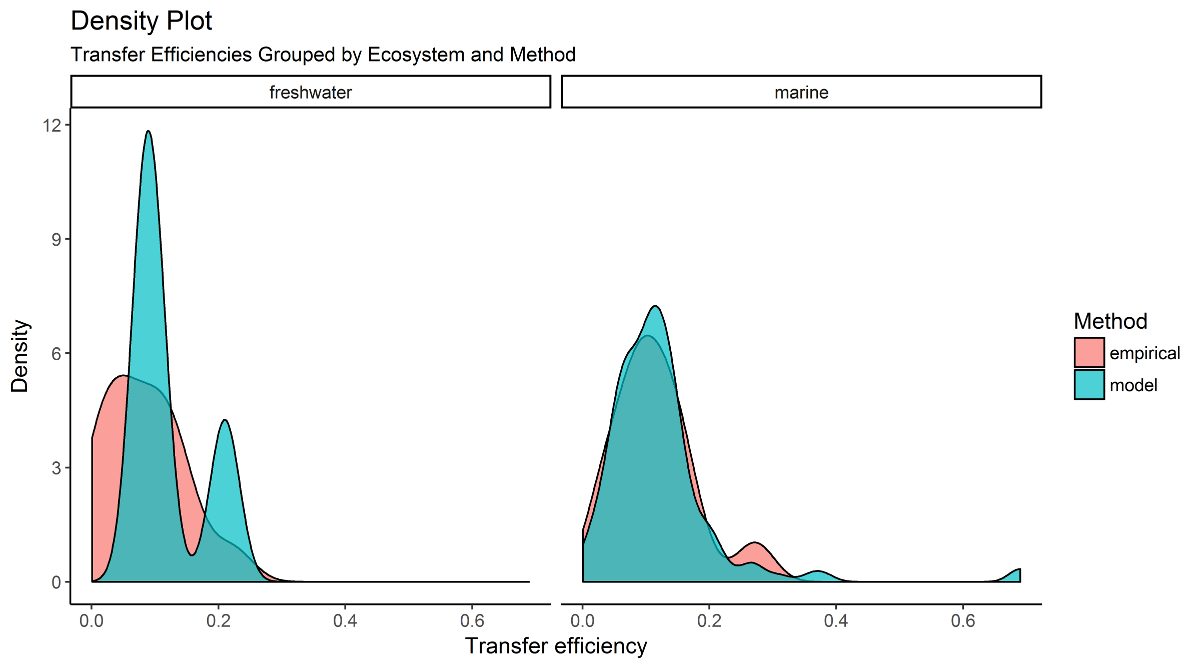

Figure 2.3: Density plot of transfer efficiencies where transfer efficiencies are grouped by ecosystem (i.e., freshwater vs. marine) and method (i.e., empirical and model-based). There are a total of 15 transfer efficiency observations gathered from freshwater empirical studies, 4 observations from freshwater model-based studies, 13 from marine empirical studies, and 134 from marine model-based studies. Plot created using R v.3.4.3 (R Core Team 2017) ggplot2 package v.2.2.1 (Wickham 2009).

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Chea et al. 2016	Tonle Sap Great Lake	lakes	model	average	8.3
Gaedke 1993	Lake Constance	lakes	model	average	21
Lindeman 1942	Cedar Bog Lake	lakes	empirical	producers	0.1
Lindeman 1942	Cedar Bog Lake	lakes	empirical	primary consumers	13.3

Lindeman 1942	Cedar Bog Lake	lakes	empirical	secondary consumers	22.3
Lindeman 1942	Lake Mendota	lakes	empirical	producers	0.4
Lindeman 1942	Lake Mendota	lakes	empirical	primary consumers	8.7
Lindeman 1942	Lake Mendota	lakes	empirical	secondary consumers	5.5
Lindeman 1942	Lake Mendota	lakes	empirical	tertiary consumers	13
Odum 1959	Silver Springs	springs	empirical	producers	1.2
Odum 1959	Silver Springs	springs	empirical	primary consumers	16
Odum 1959	Silver Springs	springs	empirical	secondary consumers	11
Odum 1959	Silver Springs	springs	empirical	tertiary consumers	5
Rand and Stewart 1998	Lake Michigan	lakes	empirical	tertiary consumers	3.2
Rand and Stewart 1998	Lake Ontario	lakes	empirical	primary consumers	11.1
Rand and Stewart 1998	Lake Ontario	lakes	empirical	secondary consumers	8.3
Rand and Stewart 1998	Lake Ontario	lakes	empirical	tertiary consumers	4.6
Villaneuva et al. 2008	Lake Kivu	lakes	model	average	8.4

Villaneuva et al. 2006	Lake Nokoue	lakes	model	average	10.3

Table 2.1: Freshwater transfer efficiency data

Marine

Marine studies on transfer efficiency did not commence until decades after the start of freshwater studies. The popularity of marine transfer efficiency research has increased rapidly in the past 20 years and has overall now exceeded the number of freshwater studies. A total of 115 sites have transfer efficiency data (Table 2.2). In contrast to the freshwater studies, most marine transfer efficiency data ($n = 134$) come from model-based studies rather than empirical experiments ($n = 13$). Most marine studies report the average value for an entire system ($n = 94$). In studies that focused on individual transfer efficiencies between specific trophic levels, most focused on the transfer efficiency between phytoplankton (trophic level 1) and zooplankton (trophic level 2).

The empirical and model-based transfer efficiency data both form skewed-right distributions with large amounts of dispersion around the 10% value (Figure 2.3). For model-based observations, there are a few outlying points from a study on bays and estuaries that skew the distribution (Figure 2.3). The combined transfer efficiency data ranges from 0.2% to 69% with a median of 10.6%, while the range constricts with a minimum of 3.12% to a maximum of 27.2% for just the marine empirical studies (Figure 2.3).

To explore the potential drivers of variation in transfer efficiencies, we calculated importance plots from the decision tree analysis. When interpreting importance plots, the larger the score, the more influential the variable. A number close to zero indicates the variables is not important and could be dropped. When determining the importance of a variable, the mean decrease in accuracy (i.e., mean square error, MSE) or the mean decrease in node impurity are used to measure how well the trees split the data. Thus, the relative importance plots from the decision tree analysis indicate that trophic level had the greatest influence on transfer efficiency, followed by the clustered region (i.e., temperate shelves and seas, tropical shelves and seas, lagoons, upwelling ecosystems, and open oceans) (Figure 2.4). The method employed (i.e., empirical or model-based) did not appear to be a useful predictor.

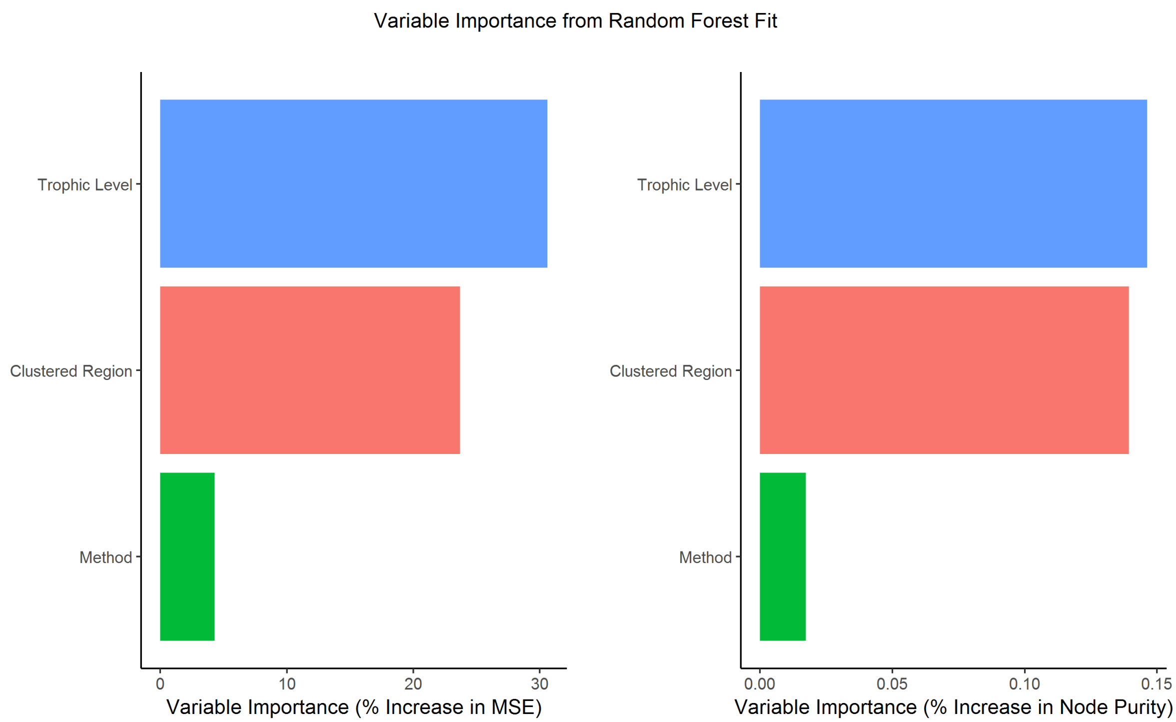

Figure 2.4: Relative importance plots for random forest fit on marine transfer efficiency observations. In panel a), the predictors are ordered by percent increase in Mean Square Error (MSE). In panel b), the predictors are ordered by increase in node purity. Plot created using R v.3.4.3 (R Core Team 2017) ggplot2 package v.2.2.1 (Wickham 2009).

We combined results across both marine and freshwater systems to examine differences among trophic levels (Figure 5). We combined data for all the systems to increase the sample size. Whether the different densities are due to the sensitivity to small samples sizes or systematic differences is unclear. Nonetheless, our results support the hypothesis that transfer efficiency decreases as trophic level increases (see Garcia et al. 2012). This in turn supports the results from May (1983) that in the marine environment ectotherms (invertebrates then vertebrates), which dominate the lower trophic levels, are more efficient than endotherms, which are more prominent at higher trophic levels (Figure 2.5).

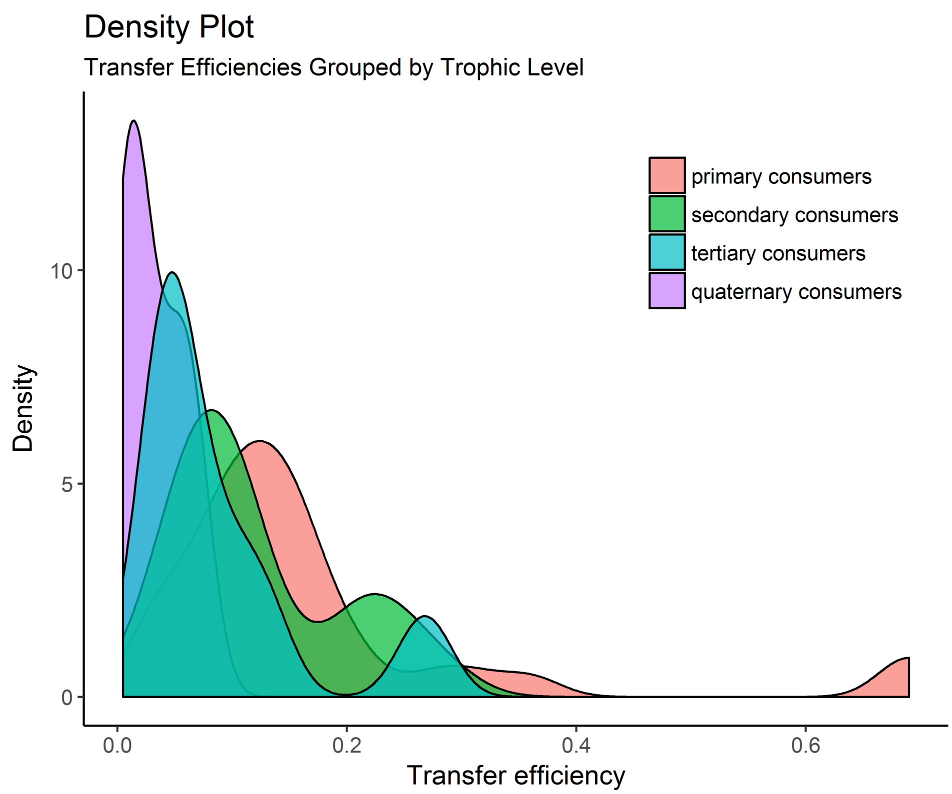

Figure 2.5: Density plot of transfer efficiencies grouped by trophic level. The data in this figure includes both ecosystem (i.e., freshwater and marine) and empirical and model-based transfer efficiency data. Plot created using R v.3.4.3 (R Core Team 2017) ggplot2 package v.2.2.1 (Wickham 2009).

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Akoglu et al. 2014	Black Sea	temperate seas	model	primary consumers	3
Akoglu et al. 2014	Black Sea	temperate seas	model	secondary consumers	3.8
Akoglu et al. 2014	Black Sea	temperate seas	model	tertiary consumers	7.4
Akoglu et al. 2014	Black Sea	temperate seas	model	quaternary consumers	0.5
Anjusha et al. 2013	Gulf of Mannar	tropical seas	empirical	primary consumers	13
Anjusha et al. 2013	Gulf of Mannar	tropical seas	empirical	primary consumers	12
Anjusha et al. 2013	Gulf of Mannar	tropical seas	empirical	primary consumers	14.6
Anjusha et al. 2013	Gulf of Mannar	tropical seas	empirical	primary consumers	9.1
Anjusha et al. 2013	Gulf of Mannar	tropical seas	empirical	primary consumers	6.8
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	27.2
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	17.6

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	9.39
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	7.19
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	3.12
Anjusha et al. 2013	Palk Bay	tropical seas	empirical	primary consumers	3.23
Baird et al. 2004	Sylt-Romo Bight	temperate seas	model	average	2.61
Baird et al. 2007	Sylt-Romo Bight: arenicola flats	temperate seas	model	average	3.47
Baird et al. 2007	Sylt-Romo Bight: dense zostera noltii beds	temperate seas	model	average	5.58
Baird et al. 2007	Sylt-Romo Bight: mud flats	temperate seas	model	average	6.13
Baird et al. 2007	Sylt-Romo Bight: muddy sand flats	temperate seas	model	average	7.31

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Baird et al. 2007	Sylt-Romo Bight: mussel beds	temperate seas	model	average	14.92
Baird et al. 2007	Sylt-Romo Bight: pelagic domain	temperate seas	model	average	1
Baird et al. 2007	Sylt-Romo Bight: sandy beaches	temperate seas	model	average	6.5
Baird et al. 2007	Sylt-Romo Bight: sandy shoals	temperate seas	model	average	3.3
Baird et al. 2007	Sylt-Romo Bight: sparse zostera noltii beds	temperate seas	model	average	5.06
Barnes et al. 2010	summary of 21 locations	-	model	average small sizes	13.8
Barnes et al. 2010	summary of 21 locations	-	model	average large sizes	5.8
Baumann 1995	general claim	-	empirical	average	15

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Bradford-Grieve et al. 2003	Southern Plateau, New Zealand	temperate seas	model	secondary consumers	23
Chassot et al. 2010	temperate	temperate seas	model	average	10
Chassot et al. 2010	tropical	tropical seas	model	average	14
Chassot et al. 2010	upwelling	upwelling ecosystems	model	average	5
Cornejo-Donoso and Antezana 2008	Antarctic Peninsula	temperate seas	model	primary consumers	21
Cornejo-Donoso and Antezana 2008	Antarctic Peninsula	temperate seas	model	secondary consumers	20
Cornejo-Donoso and Antezana 2008	Antarctic Peninsula	temperate seas	model	tertiary consumers	10
Cornejo-Donoso and Antezana 2008	Antarctic Peninsula	temperate seas	model	quaternary consumers	5
D'Alelio et al. 2016	Gulf of Naples	temperate seas	model	primary consumers	20
Duan et al. 2009	Pearl River Estuary	tropical seas	model	average	10.2

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Gamito and Erzini 2004	Ria Formosa lagoon, south Portugal	lagoons	model	primary consumers	4.8
Gamito and Erzini 2004	Ria Formosa lagoon, south Portugal	lagoons	model	secondary consumers	6
Gamito and Erzini 2004	Ria Formosa lagoon, south Portugal	lagoons	model	tertiary consumers	3.5
Gamito and Erzini 2004	Ria Formosa lagoon, south Portugal	lagoons	model	quaternary consumers	1.2
Gamito and Erzini 2004	Ria Formosa lagoon, south Portugal	lagoons	model	quinary consumers	0.2
Libralto et al. 2008	Atlantic coast of Morocco	temperate seas	model	average	10.9
Libralto et al. 2008	Azores archipelago	temperate seas	model	average	10.5
Libralto et al. 2008	Bali Strait	tropical seas	model	average	11.7
Libralto et al. 2008	Baltic sea	temperate seas	model	average	25.9

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Bay of Bengal	tropical seas	model	average	9
Libralto et al. 2008	Bay of Biscay	temperate seas	model	average	16.5
Libralto et al. 2008	Bay of Revellata, Corsica	temperate seas	model	average	18.8
Libralto et al. 2008	Bolinao reef flat	tropical seas	model	average	10.4
Libralto et al. 2008	Brunei Darussalam	tropical seas	model	average	12.9
Libralto et al. 2008	California upwelling	upwelling ecosystems	model	average	4
Libralto et al. 2008	Campeche Bank of Yucatan shelf	tropical seas	model	average	17.6
Libralto et al. 2008	Cantabric Sea	temperate seas	model	average	38.1
Libralto et al. 2008	Celestun lagoon, Mexico	lagoons	model	average	6.4
Libralto et al. 2008	Central North Pacific Ocean	temperate seas	model	average	4.4
Libralto et al. 2008	Chesapeake Bay	temperate seas	model	average	12.5

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Chiku lagoon, Taiwan	lagoons	model	average	13.1
Libralto et al. 2008	Coast of Western Gulf of Mexico	tropical seas	model	average	16.2
Libralto et al. 2008	Coastal areas and reefs	-	model	average	13
Libralto et al. 2008	Continental shelf of southern Brazil	tropical seas	model	average	11.8
Libralto et al. 2008	Eastern Bering Sea	temperate seas	model	average	13.2
Libralto et al. 2008	Eastern Scotian shelf	temperate seas	model	average	11
Libralto et al. 2008	Eastern Tropical Pacific Ocean	temperate seas	model	average	20.4
Libralto et al. 2008	Etang de Thau, France	lagoons	model	average	10.8
Libralto et al. 2008	Faroe Islands	temperate seas	model	average	14.4
Libralto et al. 2008	Faroe Islands	temperate seas	model	average	15.4

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Floreana rocky reef Galapagos	tropical seas	model	average	13
Libralto et al. 2008	Georgia Strait	temperate seas	model	average	9.5
Libralto et al. 2008	Great Barrier Reef	tropical seas	model	average	11.5
Libralto et al. 2008	Gulf of Lingayen	tropical seas	model	average	13.5
Libralto et al. 2008	Gulf of Maine - Georges Bank	temperate seas	model	average	15.6
Libralto et al. 2008	Gulf of Mexico continental shelf	tropical seas	model	average	9.7
Libralto et al. 2008	Gulf of Thailand	tropical seas	model	average	10.4
Libralto et al. 2008	Hong Kong	tropical seas	model	average	9.1
Libralto et al. 2008	Icelandic fisheries	temperate seas	model	average	14.2
Libralto et al. 2008	Kuala Trengganu	tropical seas	model	average	17.8
Libralto et al. 2008	Laguna de Bay, Philippines	lagoons	model	average	12.4

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Lancaster Sound Region	temperate seas	model	average	8.2
Libralto et al. 2008	Maputo Bay	temperate seas	model	average	7.6
Libralto et al. 2008	Newfoundland	temperate seas	model	average	14.3
Libralto et al. 2008	North Benguela upwelling	upwelling ecosystems	model	average	7.9
Libralto et al. 2008	North Coast of Central Java	tropical seas	model	average	11.8
Libralto et al. 2008	North Sea	temperate seas	model	average	11.6
Libralto et al. 2008	Northern British Columbia	temperate seas	model	average	14.2
Libralto et al. 2008	Northern Gulf of Saint Lawrence	temperate seas	model	average	12
Libralto et al. 2008	Northern-central Adriatic Sea	temperate seas	model	average	10
Libralto et al. 2008	Norwegian and Barents Sea	temperate seas	model	average	10.5
Libralto et al. 2008	NW Africa upwelling	upwelling ecosystems	model	average	6.1

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Open oceans	open oceans	model	average	12
Libralto et al. 2008	Orbetello lagoon	lagoons	model	average	9.6
Libralto et al. 2008	Peru upwelling	upwelling ecosystems	model	average	6.6
Libralto et al. 2008	Prince William Sound, Alaska	temperate seas	model	average	14.1
Libralto et al. 2008	San Miguel Bay	tropical seas	model	average	20.6
Libralto et al. 2008	San Pedro Bay	tropical seas	model	average	9.4
Libralto et al. 2008	Schlei Fjord	temperate seas	model	average	7.4
Libralto et al. 2008	Shallow areas of Gulf of Thailand	tropical seas	model	average	6.8
Libralto et al. 2008	South Catalan Sea	temperate seas	model	average	12.6
Libralto et al. 2008	South China Deep Sea	tropical seas	model	average	10.6
Libralto et al. 2008	Southern Brazil	tropical seas	model	average	6.3
Libralto et al. 2008	Southwest coast of India	tropical seas	model	average	14

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Libralto et al. 2008	Tampa Bay	tropical seas	model	average	8.6
Libralto et al. 2008	Temperate shelves	temperate seas	model	average	14
Libralto et al. 2008	Tropical shelves	tropical seas	model	average	10
Libralto et al. 2008	Upwellings	upwelling ecosystems	model	average	5
Libralto et al. 2008	Venezuela northeastern shelf	tropical seas	model	average	7.3
Libralto et al. 2008	Venice lagoon	lagoons	model	average	14.5
Libralto et al. 2008	Vietnam-China shelf	tropical seas	model	average	7.5
Libralto et al. 2008	West Coast of Vancouver Island	temperate seas	model	average	13.7
Libralto et al. 2008	West Greenland coast	temperate seas	model	average	12.1
Libralto et al. 2008	West Greenland trawling area	temperate seas	model	average	7.1

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Lin et al. 2006	Tapong Bay, southwestern Taiwan	tropical seas	model	average	5.5
Liu et al. 2009	Nanwan Bay, southern Taiwan	tropical seas	model	primary consumers	13.9
Liu et al. 2009	Nanwan Bay, southern Taiwan	tropical seas	model	secondary consumers	6.6
Liu et al. 2009	Nanwan Bay, southern Taiwan	tropical seas	model	tertiary consumers	5.2
Liu et al. 2009	Nanwan Bay, southern Taiwan	tropical seas	model	quaternary consumers	2
Manickchand-Heileman et al. 2003	Gulf of Paria, Venezuela and Trinidad	tropical seas	model	average	12.2
Neira and Arancibia 2004	upwelling Central Chile	upwelling ecosystems	model	primary consumers	8.1
Neira and Arancibia 2004	upwelling Central Chile	upwelling ecosystems	model	secondary consumers	27.4
Neira and Arancibia 2004	upwelling Central Chile	upwelling ecosystems	model	tertiary consumers	26.8
Neira and Arancibia 2004	upwelling Central Chile	upwelling ecosystems	model	quaternary consumers	6.7

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Neira and Arancibia 2004	upwelling Central Chile	upwelling ecosystems	model	quinary consumers	7.4
Pauly and Christensen 1995	general claim	NA	empirical	average	10.13
Rybarczyk and Elkaim 2003	Bay of Somme	temperate seas	model	primary consumers	15.6
Rybarczyk and Elkaim 2003	Chesapeake Bay	temperate seas	model	primary consumers	31
Rybarczyk and Elkaim 2003	Delaware Bay	temperate seas	model	primary consumers	69
Rybarczyk and Elkaim 2003	Narragansett Bay	temperate seas	model	primary consumers	69
Rybarczyk and Elkaim 2003	Seine Estuary	temperate seas	model	primary consumers	36.05
Sheldon et al. 1977	ocean pelagic	open oceans	model	primary consumers	15
Tsagarakis et al. 2010	N. Aegean	temperate seas	model	average	17.4
Tsagarakis et al. 2010	N.C. Adriatic	temperate seas	model	average	10
Tsagarakis et al. 2010	S. Catalan	temperate seas	model	average	12.6
Villaneuva et al. 2006	Ebrie lagoon	lagoons	model	average	15.5

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency
Ware 2000	Georges Bank	temperate seas	model	primary consumers	15.9
Ware 2000	Gulf of Maine	temperate seas	model	primary consumers	11.9
Ware 2000	Gulf of Maine	temperate seas	model	secondary consumers	10.5
Ware 2000	Mid-Atlantic Shelf	tropical seas	model	primary consumers	10.2
Ware 2000	Mid-Atlantic Shelf	tropical seas	model	secondary consumers	10.1
Ware 2000	Nova Scotia Shelf	temperate seas	model	primary consumers	12.1
Ware 2000	Nova Scotia Shelf	temperate seas	model	secondary consumers	12.3
Ware 2000	Oyashio current model	temperate seas	model	primary consumers	17
Ware 2000	Oyashio current model	temperate seas	model	secondary consumers	7.9
Ware 2000	SW Britisth Columbia model	temperate seas	model	primary consumers	11.1
Ware 2000	SW Britisth Columbia model	temperate seas	model	secondary consumers	8

Articles	Region	Clustered Region	Method	Trophic Level	Transfer Efficiency

Table 2.2: Marine transfer efficiency data

Discussion

Overall, these studies show similarities between the two systems. The results give visual evidence that although the average transfer efficiency does not differ greatly from 10%, there is substantial variation in transfer efficiency in both systems (Figure 2.3). Additionally our study was able to identify that trophic level and the general geographic location of the ecosystem impacts the variability of the transfer efficiency. Some of this large variation seems to have predictable patterns, but the potential sources of this variation can only be explored for the larger sample sizes from marine systems. Thus in the absence of data, the distributions generated in the current study are good starting points to model the variation in transfer efficiency.

We hypothesize the difference in transfer efficiency between trophic levels could be partially attributed to the composition of the taxa. Additionally, the differences could be due to the mobility of the organisms at each trophic levels and the amount of energy expedited to capture their prey. Both of these points highlight the need for additional research that can distinguish between the different mechanisms that influence transfer efficiency (e.g., endotherms vs. ectotherms).

We encountered two main difficulties in this study due to the different naming conventions in the early states (Figure 2.1 and 2.2) and the different efficiencies of interest amongst different fields. We bring this point up to highlight the challenges in conducting interdisciplinary work. We found freshwater studies report either assimilation and consumption efficiencies or transfer efficiency, while the majority of marine papers focused on transfer efficiency. As previously mentioned, we found very few terrestrial studies that reported results on transfer efficiency. It is intriguing that the focus on transfer efficiency is an aquatic phenomenon. While we are unable to say with certainty why this is, we can speculate that in aquatic systems, and especially marine systems, it is extremely difficult to gather data on most species in an ecosystem. As a result, it is challenging to calculate the assimilation and consumption efficiencies in these systems. The great ease in counting terrestrial populations means the studies do not need to rely on more inferential, trophic level wide, techniques.

Despite the aforementioned limitations, we are able to demonstrate the 10% value is problematic given the substantial variation that exists in the transfer efficiency. Even though the average and median values that emerge from the synthesis are not dramatically different from 10%–which may suggest that an assumption of 10% would be reasonable–by continuing to use a 10% transfer efficiency researchers are eschewing the large variation and predictable patterns within this variation, which will impact a food web model?s ability to provide realistic results. From here on, we explore implications of applying a fixed 10% transfer efficiency in ecology, fisheries, and aquaculture.

Applications in ecology

When it comes to ecology, the transfer efficiency is used to understand food web dynamics and how various species interact and influence one another. Most commonly, it is used in size spectrum studies that explore predator-prey relationships (Barnes et al. 2010). In general though, the more detailed and species-specific assimilation efficiency is used more frequently in such analyses. Since many issues within ecology and conservation biology focus on individual species patterns, it is valuable to be able to calculate species-specific efficiencies. The transfer efficiency is perhaps too broad of a metric for many questions. While using a 10% transfer efficiency value can have drastic underrepresentation and lead to severely mismanaged systems, given the preference for the assimilation efficiency the implications of a 10% transfer efficiency most likely has not been directly measured in many cases in ecology. Previous research has shown distinct transfer efficiencies between trophic levels and for terrestrial (i.e., temperate forests, deciduous forests, and grasslands) and freshwater (i.e., lakes) systems (Hairston 1993). Even though the assimilation and consumption efficiencies are different measures, there is comparable variation in them as there is in the transfer efficiency data, and therefore the implications of applying fixed values for these efficiencies could be the same as those for the transfer efficiency.

Applications in fisheries

In fisheries, transfer efficiency is mostly used to determine the impact of fishing on a population. It can be used to estimate various metrics, such as biomass and the primary production required (PPR) given fisheries catch. Primary production required estimates the amount of net primary production needed to replace the biomass removed by fisheries landings. The idea is that primary production is a major limiting factor of fisheries catch. If biomass or the primary production required is incorrectly estimated, we risk the potential of under- or overfishing.

What is the cost of ignoring variability in transfer efficiencies for fisheries applications? To explore this question, we reexamined the analyses by Chassot et al. (2010) and Watson et al. (2014) of the primary production required to produce the biomass of fish that were caught. As an exploration, we recreated the analysis for one marine region, the California Current. We gathered annual catch data from Sea Around Us (`http://www.seaaroundus.org/`) from 1950 to 2014, trophic level data on fishes from Fishbase data base (`http://www.fishbase.org/`), and net primary production data on SeaWiFS from the Ocean Productivity web site (`http://www.science.oregonstate.edu/ocean.productivity/`). Watson et al. (2014) also included trophic level data on invertebrates from SeaLifeBase; however, SeaLifeBase does not include trophic level data for the California Current. We first replicated the previously published results using a fixed 10% transfer efficiency using the following equation[1].

$$PPR_t = \sum_{i=1}^{n} \frac{C_{i,t}}{CR} * \frac{1}{TE}^{TL_i - 1} \tag{2.1}$$

PPR_t is the primary production required in year t to produce the observed catch, $C_{i,t}$ is the biomass of catch for species i in year t, CR is the conversion rate of carbon to wet weight, TE is the transfer efficiency, TL_i is trophic level for species i, and n is the number of species within a region.

To explore the impact of ignoring variability in transfer efficiencies, we used the data we gathered on marine transfer efficiencies to test for sensitivities to transfer efficiency variability. We fit an approximate distribution to the marine transfer efficiency data using goodness-of-fit criterion so that we could randomly sample a value from the observed distribution instead of using a fixed 10% value in the above equation (See supporting information for details). This approach allowed us to incorporate variability in the transfer efficiency. While the time span of the Sea Around Us catch data ran for over 60 years, we explored the distribution at 20 year intervals to get a sample of the changes in transfer efficiency. We constructed Monte Carlo simulations and ran 10,000 simulations

[1] Chassot et al. (2010) specified ecosystem specific transfer efficiencies.

for the years 1950, 1970, 1990, and 2010. Although it is difficult to compare our results directly to Watson et al. (2014), since their results are broken up by continental fishing fleets, we found that when transfer efficiency is allowed to vary, the projected PPR varies dramatically. Although the majority of the time the PPR is a sustainable fraction of the total production of the California Current, on average 47.18% of the time (i.e., 46.93% in 1950, 47.21% in 1970, 47.35% in 1990, and 47.22% in 2010) the simulations suggest annual landings could exceed total primary production (Figure 2.6). Therefore, the application of a 10% transfer efficiency in fisheries management has a high chance of leading to unsustainable fishing practices.

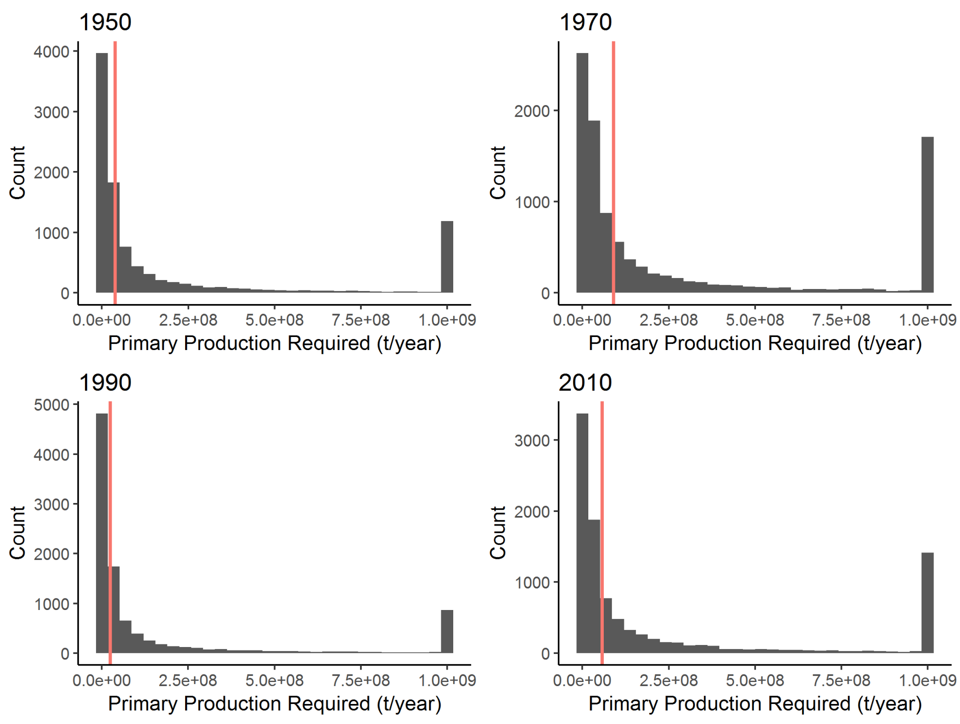

Figure 2.6: Histogram of simulated primary production required given catch divided by the average primary production in 1950, 1970, 1990, and 2010 in the California Current using a random transfer efficiency. The vertical red line indicates the primary production required divided by primary production using a fixed 10% transfer efficiency in the calculations. We adjusted the far right bin width due to rare events. The original range extends out further. Plot created using R v.3.4.3 (R Core Team 2017) ggplot2 package v.2.2.1 (Wickham 2009).

Applications in aquaculture

Aquaculture already cultivates hundreds of different marine and freshwater species. The relevance of transfer efficiencies to production decisions depends on whether the species requires additional feed or not. Non-fed aquaculture includes either primary producers or primary consumers that are not provided additional feeds by the aquaculturist. Fed aquaculture, on the other hand, involves consumer species that are typically fed compound feeds designed to meet their specific nutritional requirements. Consumption of autotrophs, usually phytoplankton by filter feeders, is studied extensively in non-fed aquaculture to track carrying capacity of ecosystems with added aquaculture (Banas et al. 2007). These carrying capacities are estimated using assimilation efficiencies of a specific target species (Rosland et al. 2009, Irisarri et al. 2013, Srisunont and Babel 2016) or as broader estimates of transfer efficiencies (Simenstad and Fresh 1995, Sommer 1998, Byron et al. 2011, Han et al. 2017).

More and more fed species are given specialized compound feeds rather than whole organisms in order to increase efficiency and sustainability of feed resources. To assess the sustainability of feeds, the field has begun to track transfer efficiencies by dissecting the feed into its compositional parts and estimating the efficiencies for each of the components using the method devised by Pauly and Christensen (1995). While a 10% transfer efficiency was initially employed to estimate the primary production requirements or biotic resource use in environmentally-based aquaculture assessments (e.g., Papatryphon et al. 2004, Pelletier and Tyedmers 2007, Pelletier et al. 2009), more recent studies have incorporated species-specific efficiencies in their analyses to better understand the environmental tradeoffs between different feed compositions (Cashion et al. 2016). Additionally, Cashion et al. (2016) found that the use of a 10% transfer efficiency has led to an underestimation of the impacts of salmon aquaculture on natural marine biomass resources. Actual impacts are likely three times greater. As with the case for wild fisheries, ignoring the variability in transfer efficiencies can have negative impacts on the conservation of limited resources and management of human activities.

Concluding remarks

Our results raise the question why the use of an assumed transfer efficiency value of 10% is still so prevalent despite widespread evidence of substantial variability and examples of where the consequences of ignoring such variability have been documented? One issue is clearly convenience. The overall mean of observed values is not dramatically different from the assumed 10% value. Nonetheless, given the scope of observed variation and uncertainty, using a 10% value for the sake of arithmetic convenience carries large risks. Our study is not the first to raise this point, but synthesizing the full scope of evidence around the levels of variability and its potential consequences for decisions will hopefully highlight the costs of ignoring variability in this key ecosystem parameter.

Another reason for the continued assumption of a constant value is the lack of relevant data for most systems. But our synthesis of the distributions of observed values for trophic efficiency in freshwater and marine ecosystems provides an opportunity to draw from this synthetic distribution rather than assuming a constant value. In cases where locally relevant data are infeasible to collect, this synthetic distribution may provide a better platform for decisions.

Finally, one other issue is that the studies that have addressed the variability in transfer efficiency specifically have typically been in the context of narrower questions (e.g., aquaculture feeds). These narrower studies may not catch the attention of people using transfer efficiencies in other ways. By pulling together information from diverse studies from different fields, we hope this synthesis will generate a broader discussion.

In the absence of specific data for a broader array of systems, instead of using a fixed 10% constant, we suggest using simulations or Bayesian models drawing on these synthetic distributions, which are great tools for incorporating variation and uncertainty. This approach would take us a long ways towards creating more valid food web models, and as such, improve our understanding on how food web dynamics impact community structure.

Chapter 3

Chapter 2 Title

3.1 Section Title

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Chapter 4

Chapter 3 Title

4.1 Section Title

add..

Appendix A

Appendix Title

A.1 Section Title

Appendicitis

Bibliography

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