Energy flow through marine ecosystems: confronting transfer efficiency

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Highlights

- Transfer efficiency is a key parameter describing ecosystem structure and function and is used to estimate fisheries production, however, it is also one of the most uncertain parameters.
- Questions remain about how habitats, food resources, fishing pressure, spatiotemporal scales, temperature, primary production, and other climate drivers impact transfer efficiency.
- Direct measurements of transfer efficiency are difficult, but observations of marine population abundances, diets, productivity, stable isotope analysis, and models integrating these constraints can provide transfer efficiency estimates.

- Recent estimates suggest that transfer efficiency is more variable than previously thought, compounding uncertainties in marine ecosystem predictions and projections.
- Increased understanding of factors contributing to variation in transfer efficiency will improve projections of fishing and climate change impacts on marine ecosystems.

Glossary

- Assimilation efficiency: proportion of ingested material that is broken down by digestive enzymes to fuel the organism's metabolic processes. Unassimilated material is egested.
- Energy flux model: a model that quantifies relationships between biodiversity and the flow of energy through ecosystems
- Food web: a system of interconnected feeding relationships or food chains. Illustrations depict resources and consumers with nodes linked by lines that symbolize a feeding relationship (e.g. Figure 1D). Nodes can represent predator and prey, species, trophic levels, functional groups or size classes.
- Food web model or ecosystem model: a mathematical representation of how energy or biomass flows from primary producers to primary consumers and then to secondary consumers and higher predators.
- Predator-prey mass ratio: the ratio of the average mass of an individual predator to that of its prey.
- Production: the generation of biomass or energy. Primary production refers to the synthesis of organic compounds from carbon dioxide most often via photosynthesis. Secondary production involves the generation of biomass through consumption of another organism.
- Productivity: the rate of production.
- Resilience: ability of a population or ecosystem to recover to its original state following a disturbance.

- Size spectrum model: a mathematical representation of a food web that groups individuals by their sizes.
- Trophic level model: a mathematical representation of a food web that groups individuals by their position in a food chain.
- Stable isotopes: naturally occurring, non-radioactive atoms of the same element that have different numbers of neutrons. The isotope with fewer neutrons is lighter in mass, which results in faster chemical reaction rates and may lead to a preference for its uptake by organisms. Comparing ratios of carbon and nitrogen stable isotopes in organismal tissues to ratios in their prey can elucidate the processes that formed these tissues and estimate the organism's trophic level.
- Transfer efficiency: the proportion of resource production converted into consumer production. Transfer efficiency is often calculated as the proportion of production passed from one node to another in a food web.
- Trophic level: the position of an individual within a food web based on the number of feeding links between it and the primary producer. Primary producers such as phytoplankton and plants have a trophic level of 1, herbivores have a trophic level of 2, carnivores have a trophic level of at least 3. Non-integer trophic levels result from mixed diets. Detritus is often also assigned a trophic level of 1.

Abstract

Transfer efficiency is the proportion of energy passed between nodes in food webs. It is an emergent, unitless property that is difficult to measure and responds dynamically to environmental and ecosystem changes. Because the consequences of changes in transfer efficiency compound through ecosystems, slight variations can have large effects on food availability for top predators. We review processes controlling transfer efficiency, approaches to estimate it, and known variations across ocean biomes. Both process-level analysis and observed macroscale variations suggest that ecosystem-scale transfer efficiency is highly

variable, impacted by fishing, and will decline with climate change. It is important that we more fully resolve the processes controlling transfer efficiency in models to effectively anticipate changes in marine ecosystems and fisheries resources.

Efficiency of energy transfer through food webs

Transfer efficiency (see Glossary) is an emergent, unitless property that quantifies the fraction of energy passed from one node to another in a **food web.** It is often estimated as the ratio of **production** at a **trophic level** relative to one trophic level below (Figure 1; [1-5]). A high transfer efficiency means that a greater proportion of production at lower trophic levels is converted to production at the upper trophic levels. Transfer efficiency is a critical factor shaping marine ecosystems, as even subtle shifts in transfer efficiency can compound across trophic levels and lead to profound differences in abundances of top predators (Boxes 1, 2; [2,6-10]) and sustainable fishing rates [4,5,11]. Fisheries catches, for example, vary by more than two orders of magnitude across heavily fished systems despite variations in primary production within a factor of four [8]. Cross-biome gradients in transfer efficiencies underlie these differences, with high transfer efficiencies accentuating fish biomass peaks in high primary production areas and low efficiencies deepening lows in oligotrophic (low primary production) systems [2,8]. As climate change affects ocean temperature and primary production [12], increased transfer efficiencies could compensate for changes in primary production. Alternatively, decreased transfer efficiencies could exacerbate declines in primary production, reducing potential fisheries harvest from the oceans [13,14].

Transfer efficiency is often illustrated using a trophic pyramid (Figure 1A). The trophic pyramid presents a useful and conceptually simple depiction of trophodynamics – the thinning of the trophic pyramid at higher trophic levels is indicative of energy not transferred, resulting in decreasing production. Generally, a transfer efficiency of ~10%, based on early model estimates [4], is used as a characteristic value for marine ecosystems (Figure 1A).

Despite its recognized importance, transfer efficiency persists as a dominant source of uncertainty in our understanding of current marine ecosystems and projected changes. This reflects three challenges: 1) transfer efficiency is determined by diverse processes at multiple scales with potentially complex dependencies on environmental and ecosystem properties, 2) it is difficult to measure and estimate, and 3) current models used to predict marine resource trajectories generally have highly simplified representations of it. This contribution provides a synthesis of these challenges, our present understanding of transfer efficiency, and a summary of estimates of its value.

Processes controlling transfer efficiency

A complex set of processes control the distribution of production among trophic levels (Figure 1). We group this diversity of processes into three categories operating at different scales: metabolism at the individual organism scale (Figure 1B), life cycle at the species population scale (Figure 1C), and food webs at the ecosystem scale (Figure 1D). The integration of all these processes and scales ultimately determines the trophic organization of an ecosystem, the production of each level within it, and the efficiency of energy transfer through it.

Metabolism

At the individual level, numerous metabolic processes modulate the translation of ingested material to the production of new organic matter (Fig. 1B). Once material is ingested, a fraction of it is broken down by digestive enzymes to fuel the organism's metabolic processes. This fraction is referred to as the **assimilation efficiency**, with unassimilated material lost to egestion of dissolved and particulate organic material. Assimilated material is then partitioned between catabolic (energy producing) and anabolic (tissue building) processes, with anabolic processes only possible once catabolic needs are met. Catabolic metabolism is often further divided into basal (or maintenance) and active respiration, with the former costs incurred regardless of the organism's activity, and the latter increasing with movement and feeding levels. Only the anabolic investment is reflected in transfer efficiency, and each of the processes toward this final investment have complex environmental dependencies [15].

The metabolic theory of ecology [16] predicts that increasing temperature increases the rates of most biological processes to a point, including the rates at which organisms respire, [16-17], grow, and reproduce [18,19,22]. Metabolic and growth rates of primary producers are generally less temperature-sensitive than those of consumers [17] and can have different temperature dependencies [20]. This can lead to differential rates of consumer production relative to primary production as temperature changes [21], thus affecting transfer efficiency. In many cases, increasing ocean temperatures are associated with increasing stratification, decreased resource availability [19] or reduced food quality [22], complicating detection of direct temperature effects. Ecological stoichiometry has demonstrated theoretically and empirically that nutrition of prey relative to predator demands determines transfer efficiency [23]. Consumers feeding on high quality prey (i.e., rich in macronutrients and essential fatty acids) have higher growth rates [24] resulting in greater transfer efficiencies [25-28].

Life cycle

Life cycles (Fig. 1C) shape the translation of anabolic reproductive investments into production observed at each trophic level. The most volatile life cycle element for an individual species is survival through early life stages (i.e., recruitment in the fisheries context [29]). Subtle changes in food resources and metabolism have been implicated in large changes in early stage growth and survival at the species level [30-32]. Changes in timing of food availability due to climate change can have strong impacts on the reproductive success of a species [33]. Since volatility in survival is species-specific, food web structure can be maintained by having one species in a similar trophic position compensate for another, resulting in **resilience** in trophic structure and transfer efficiency at the ecosystem level. However, fluctuations in species abundances can control energy pathways through food webs, and systems dominated by a small number of species may have limited resilience, [34-35]. For example, a food web with multiple forage fish species will be more resilient to changes in abundance of a specific forage fish species due to reduced reproduction, as the other species can play the same trophic role and provide alternative energy pathways to higher trophic levels (Figure 1D). Furthermore, climate change is projected to affect the timing of consumer life cycles and critical resources, increasing the probability of extreme mismatches affecting species reproduction and growth, capable of restructuring food webs and reducing ecosystem level transfer efficiencies [36-40].

Food web structure

Transfer efficiency is further shaped at the ecosystem scale by a diversity of food web interconnections and non-predatory fluxes of organic material. Alternative pathways for primary production through food webs have different efficiencies and the emergent transfer efficiency integrates across these pathways. Prominent examples from the plankton food web are small phytoplankton dominated oligotrophic systems where multiple zooplankton consumer links are required to reach forage fish [2,41]. These systems are contrasted by productive coastal areas dominated by large phytoplankton, where forage fish are often only one trophic level removed from phytoplankton [2,41]. The partitioning between these pathways can be controlled by passing eddies and fronts leading to a time-varying trophic organization that does not always reflect the average state [42]. The spatial distribution or patchiness of prey can also influence transfer efficiency. Variation in phytoplankton abundances at the micro- to meso-scales has been suggested to enhance production, which is especially important for explaining high transfer efficiencies in oligotrophic regions [43].

Non-predatory loss mechanisms include any food web processes that prevent energy from reaching higher trophic (e.g., burial of organic matter that has sunk to the sea floor – Figure 1D). Viral lysis, for example, cycles bacterial and phytoplankton biomass back to dissolved organic material where detritivores such as bacteria are the consumers [44]. Exudation (leakage) of fixed organic carbon by phytoplankton [45] has similar trophic consequences. If viewed as external to the natural ecosystem, fishing also results in a removal of energy that reduces ecosystem-scale transfer efficiency between subsequent trophic levels. For pelagic ecosystems, the sinking of organic material as phytoplankton aggregates, fecal pellets, jelly falls or seasonal/diel migrations also present losses of energy losses that are ultimately reflected in transfer efficiency (Figure 1D); [2,41,46-48]. The environmental, physiological, and ecological dynamics governing each of these processes are as complex as those governing trophic linkages, and alternative assumptions about the form of these losses can have significant effects on emergent transfer efficiency [49].

Benthic and pelagic systems often have different energy pathways, which can lead to differential transfer efficiencies. In benthic ecosystems, the flux of detritus from surface waters and vertically migrating organisms provide the primary energy inputs [50-51]. Analysis of global marine catch data has provided modest evidence for higher transfer efficiencies associated with benthic food webs [8], where food resources are concentrated in a two-dimensional space requiring less foraging [52]. However, in lake ecosystems, there is no clear agreement whether benthic or pelagic food webs exhibit higher transfer efficiency [53-55]. In near-shore coastal ecosystems, benthic and pelagic ecosystems are frequently coupled, and dynamic linkages in energy transfer are a key component of how they function [50]. For example, in coral reef ecosystems – known to be nutrient limited yet paradoxically highly productive and biodiverse – sponges consume dissolved organic material and excrete their cells as detritus, providing a critical energy pathway to higher trophic levels that increases transfer efficiency [51]. Additionally, cryptobenthic fishes on coral reefs have been found to provide larvae in the near-reef pelagic zone accounting for almost 60% of consumed reef fish biomass, providing a key energy pathway to higher trophic levels, producing greater ecosystem-scale transfer efficiency [56].

Other food web factors impacting transfer efficiency include mixotrophs (capable of being producers and consumers) in planktonic food webs due to their ability to photosynthesize to compensate for respiratory losses or to reduce energy consumption by catabolic respiration [57]. Predator and prey size diversity have also been found to affect transfer efficiencies in planktonic communities, with transfer efficiency decreasing with increasing prey size diversity and conversely increasing with greater predator size diversity [42]. Additionally, growth in individual prey size drives declines in transfer efficiency [15]. The wide range of processes and scales that influence transfer efficiency result in challenges in its estimation.

Estimating transfer efficiency

While transfer efficiencies emerge from diverse metabolic, life cycle, and food web processes, estimating transfer efficiency requires knowledge of just two fundamental properties: the trophic level of organisms within an ecosystem determined by their diets, and the production at each trophic level. Neither of these, however, is easy to measure. Indirect transfer efficiency estimates thus rely on combining limited direct measurements, theory, and models. Although challenges exist to estimate transfer efficiency in aquatic ecosystems, there are several approaches that can been used, summarized below.

Diet estimates

Accurate accounting of trophic level is challenging. Trophic level quantifies the number of feeding links between an organism and primary producers (Figure 1), and is a function of an organism's diet, and the diet of their prey, etc. Trophic level can be estimated from diets through direct observation of feeding behaviour and stomach content analysis. Alternatively, **stable isotope** ratios can reveal trophic level due to fractionation that occurs during assimilation of prey. However, estimating trophic level is highly dependent on how one chooses to resolve the relevant food web nodes (individuals, populations, species, functional groups, size classes). It is further complicated by temporal variation in the diet of individuals depending on the species, food availability, and life stages present at any given time (e.g. juveniles and adults of the same species often eat different prey). As the trophic level of each relevant food web unit is required to calculate transfer efficiency from one level to the next, any uncertainty in assigning trophic level to a single group will be propagated to calculations of transfer efficiency for the ecosystem.

Stable isotopes of nitrogen and carbon used jointly with biomass spectra can elucidate feeding relationships in food webs [58-60]. Due to differences in fractionation, the tissues of predators preferentially incorporate heavier nitrogen isotopes from their diet, resulting in a systematic enrichment in nitrogen-isotope ratio ($\delta^{15}N = {}^{15}N/{}^{14}N$) with increasing trophic level [61,62]. Size-fractionated stable isotope analysis is commonly used to quantify the flow of energy in **size spectrum models** and to inform **predator-prey mass ratios** (PPMR [58,63-64]). The slope (*b*) of $\delta^{15}N$, an indicator of trophic level, as a function of logarithmic body size class is first used to estimate *PPMR*: $PPMR = n^{(\square/b)}$, where $\square$ is the fractionation of $\delta^{15}N$ and n is the logarithmic base of the size classes [65]. Size spectra are often used in aquatic ecosystems to illustrate the relationship between abundance and/or biomass with size, again grouped in logarithmic classes. Biomass size spectra provide information about the amount of production in each size class, under the metabolic theory assumption that individual biomass production is a function of body size [66-67]. Combining the production per size class from the slope of biomass size spectra data (β), and the change in trophic level with size from PPMR, allows the estimation of transfer efficiency (TE): $TE = PPMR^{\beta+0.75}$ [17,59,68]. One caution, however, is that stable isotope estimates of PPMR have been shown to be particularly sensitive to the trophic enrichment factors used in analyses [62,69-71]. For example, using a trophic enrichment factor of 2 instead of 3.4 can yield PPMR estimates that are 1-3 orders of magnitude lower, and transfer efficiency estimates that are 2-4 times higher [69].

Production estimates

Productivity – the rate at which energy or biomass is generated – can be estimated by tracking population development through time by assessing mass-specific growth and mortality rates using size or age-structured observations [72]. Quantification of primary production in the oceans relies on ^{14}C measurements [73] and can be estimated by satellite – albeit with some uncertainty in deeper waters [74] – by leveraging diverse algorithms (e.g., [75]). Empirical production to biomass ratios from metabolic theory can be applied to abundance data to estimate productivity where it is not possible to make such observations of primary production or to estimate production of higher trophic levels [72]. These ratios are generally combined with other variables (e.g., biomass) to form an integrated picture of an ecosystem from which transfer efficiencies can be derived [48,76] .

Production-based transfer efficiency estimates for temperate Northern hemisphere marine ecosystems yielded an average transfer efficiency of 13% (ranging from 11-17%) for trophic levels 1-2 (phytoplankton to herbivorous mesozooplankton and benthic organisms) and an average transfer efficiency of 10% (ranging from 7-12%) for trophic levels 2-3 (zooplankton and benthic organisms to fish) [76]. Laboratory plankton feeding experiments have yielded higher transfer efficiencies than wild populations because wild populations often feed at suboptimal prey concentrations (which can be controlled in the lab) and lab conditions can prevent loss of production to the microbial loop that is not consumed in wild populations (Figure 1D; [76]). The impacts of energy fluxes through these different food web pathways highlight the importance of integrating processes at the ecosystem scale.

Model based estimates

Given the wide range of processes controlling, and factors affecting transfer efficiency at multiple scales, models can be used as an integration tool, to test hypotheses, and to make predictions. **Food web models** provide a means of integrating all available diet and production data. Transfer efficiency values can be estimated from food web models by calculating how much energy or biomass production is transferred between species, functional groups, size classes or trophic levels (e.g. [77-79]). However, *a priori* estimates of transfer efficiency have often directly or indirectly influenced the choice of model parameters and processes that modellers consider to describe energy flows. For example, the 10% transfer efficiency estimated by Pauly and Christensen [4] and the 5%, 10%, and 15% efficiencies for upwelling, temperate, and tropical ecosystems respectively, estimated by Coll et al. [80] and Libralato et al. [5] often guide the choice of parameters in the well-established and commonly-used food web and fisheries modelling framework, Ecopath with Ecosim [77]. However, if all other model parameters are fixed, the mass-balancing of Ecopath with Ecosim models can be used to estimate transfer efficiencies within food webs.

The emergence of regularities in observation-based estimates provides a foothold for modellers simulating the flow of energy through marine ecosystems using theoretical approaches. Early models of biomass spectra lack mechanistic details, but can resolve patterns emerging from transfer efficiency estimates [67,81,82]. **Energy flux models** aim to find relationships between biodiversity and the flow of energy through ecosystems and include efficiency terms, however have not yet been applied to estimate transfer efficiency [83-84]. **Size spectrum models** are based on allometric principles that predators tend to be bigger than their prey, so that species can be ignored, and size classes of organisms can be used to track energy flow instead. Size spectrum models have been used to derive transfer efficiency by scaling up from individual level principles of how consumption, search rate, prey choice, and assimilation efficiency vary with body size [15,48,85]. As the number of observational studies reporting these properties grows, it is becoming possible to examine how transfer efficiency differs with both size and functional group – e.g. small versus large zooplankton, filter feeders versus mobile predatory benthic invertebrates, fishes of different sizes and feeding modes, ectotherms versus endotherms – and to add these trait-specific properties to models [52,86].

Process-based plankton food web models from global Earth system models produce primary and secondary production estimates that can be used to calculate transfer efficiency and global fisheries catches at the large marine ecosystem (LME) scale [8]. Using this approach, empirical model predictions best matched observed catches when the microbial loop and benthic and pelagic compartments were included in the formulation [8]. The ecosystem transfer efficiencies needed to reconcile simulated primary production with observed fish catches were 14% on average, with tropical and subtropical systems reduced at 74% of temperate values, and benthic transfer efficiencies greater than pelagic values [8].

FEISTY is a spatially explicit, mechanistic model of three fish functional types based on allometric scaling principles, basic life cycles, trophic interactions between fishes and their benthic and pelagic food resources, and fisheries [78]. When coupled with a global Earth system model to provide environmental conditions and plankton abundances as model inputs, FEISTY recreated general historical patterns of global fisheries catches [78]. The ecosystem-scale transfer efficiency values estimated by FEISTY ranged from 5-18% in oceanic, 5-27% in coastal, and 4-23% in upwelling provinces (Box 2).

The EcoTroph model quantifies the fraction of secondary production transferred between trophic levels using taxon-specific consumption to production rates based on life history traits [82,87], thermal habitat [82,88], and also accounts for respiration, excretion, accumulation, and transfer to detritus. Using fisheries catch data as an indicator of fish biomass by trophic level, EcoTroph estimated coastal ecosystem transfer efficiency from secondary production to trophic level 4 that varied as 5.9% in upwelling, 6.5% in tropical, 8.1% in temperate, and 10.4% in polar regions [79]. This transfer efficiency from trophic levels 2–4 increased from 7.1% to 7.6% from 1950-2010, a finding that was consistent across all coastal ecosystem types and may be explained by increased fishing exploitation [79,89]. Using sea surface temperature projections to 2100, EcoTroph projected global transfer efficiency in coastal ecosystems to decline by 0.1% until 2040 under both low and high emissions scenarios (RCP2.6 and 8.5 respectively; [79]). From 2040-2100, transfer efficiencies were projected to remain stable under low emissions and decrease from 7.7% to 7.2% under high emissions – with smaller average declines in tropical ecosystems [79]. Overall, fishing pressure was positively correlated with transfer efficiency [89], while sea surface temperature was negatively correlated [79].

Estimated transfer efficiencies across ocean biomes

Our summary of transfer efficiency estimates indicates that it is highly variable and can range from less than 1% - 27% in upwelling regions, from 2% - 34% in temperate regions, and from 8% - 52% in tropical and subtropical regions (Box 1). This large amount of variation in transfer efficiency estimates means that fish production could vary by one order of magnitude in upwelling provinces, two orders in coastal, and up to three orders of magnitude in oceanic provinces (Box 2). Transfer efficiency has been observed to be highly variable at the ecosystem scale, influenced by ecosystem type (Box 1 & 2) [90,91], trophic level [1,78], size [69], and is affected by fishing pressure [89], climate change [92-96] temperature [79,97], and varies through time [6,79,89]. Both process-level analysis and observed macroscale variations suggest that transfer efficiency increased due to fishing exploitation in the last half of the 20th century and will decline with increasing temperatures due to climate change [79]. Globally, fishing exploitation has tended to target large and long-living species leading to declines in abundance compared to smaller species with faster life histories affecting transfer efficiency [98-101]. These fishing-induced changes in species assemblages may have contributed to the past observed increase in transfer efficiency [79]. The large variation in transfer efficiency estimates highlights the need for more explicit consideration, rather than the tradition of relying on average values (Boxes 1, Outstanding Questions).

Concluding remarks

More than 50 years after Ryther's [2] seminal paper highlighting the potential for fisheries production to be influenced by transfer efficiency variability (Boxes 1,2), it remains a key uncertainty in marine ecosystem, fisheries, and climate change research. Early observational and modelling evidence suggests that processes (e.g. metabolism, life cycle, and food web structure) and factors (e.g. ecosystem properties) influencing transfer efficiency are sensitive to environmental conditions and fisheries exploitation. Though there are key sources of uncertainty, these processes have received less research attention than other efforts to estimate future changes in temperature, primary production, and fish distribution and biomass.

At this stage, it is unclear if transfer efficiency is truly highly variable in space and time or if there is large measurement error around estimates. Improving transfer efficiency estimates by reducing uncertainty in empirically based estimates and more fully resolving transfer efficiency-controlling processes in predictive models is a priority for effectively anticipating changing marine resource baselines in response to climate change to avoid overexploitation (see Outstanding Questions). This may be possible as new technologies emerge that enable us to better observe biomass, productivity, and species interactions. Crucially, it is important to not limit transfer efficiency values in models, but allow the potential range of transfer efficiency to emerge from other constraints. The transfer efficiency field of research is ripe for further inquiry to build confidence in our understanding of how energy flows through marine ecosystems.

Boxes

Box 1. How variable are transfer efficiency estimates and how do they vary according to biome?

Summary of three studies evaluating transfer efficiency values with Ecopath with Ecosim (EwE) [77] models by oceanographic biome [79,102,103]. Values from [102] were estimated from 234 published EwE models. Values from [103] were estimated from the EcoTroph database of EwE models from 1950-2010. Values from [79] were estimated from the EcoTroph database of EwE models 2000-2010.

Biome	Trophic level	Low	Mean	High

Polar/Subarctic-Boreal	2 to 3 & 3 to 4	3.5%	12.0%	25.5%
Temperate	2 to 3 & 3 to 4	1.9%	9.6%	34.4%
Tropical/Subtropical	2 to 3 & 3 to 4	0.8%	8.6%	52.0%
Upwelling	2 to 3 & 3 to 4	0.3%	8.0%	27.1%

Methods

Transfer efficiency values from [102] were extracted from the boxplot in their Figure 19. Values for their trophic level groups III and IV, which represent transfers from trophic level 2 to 3, and trophic level 3 to 4 respectively, were both used.

Transfer efficiency values from Maureaud et al. [103] reflect mean values published in the main text. Regional minima and maxima were estimated from the table of efficiency cumulated indicator (ECI) values by large marine ecosystem (LME) in the supplementary materials. The LME figure in [79] was used to assign each LME to a biome and only those LMEs that were entirely of one biome type were used. Minimum and maximum ECI per region were found over the complete time range (1950-2010). Transfer efficiency (TE) was then calculated from ECI using: TE = $ECI^{1/2}$. ECI is transfer efficiency from trophic level 2 to trophic level 4, thus these values of transfer efficiency reflect mean transfer efficiency from trophic levels 2 to 3 and from trophic levels 3 to 4.

Transfer efficiency values from [79] reflect mean values published in their Figure 4a. Minima and maxima per region were extracted from the violin plots in Figure 4a. These values of transfer efficiency reflect the mean transfer efficiency from trophic levels 2 to 3 and from trophic levels 3 to 4 over the years 2000-2010.

Box 2. How does estimated fish production vary considering variation in transfer efficiency estimates?

Impact of transfer efficiency variability on estimated fish production based on Ryther's ocean provinces [2] calculated using primary productivity and mean number of trophic levels. Observed fisheries catches also included for reference.

Province	Area-integrated primary production (tons organic C per year)	Mean # trophic levels	Transfer efficiency range		Estimated fish production (tonnes wet weight)		Actual catch (tonnes wet weight)
			low	high	low	high	
Oceanic	4.08E+10	6	0.05	0.18	7.82E+04	6.04E+07	8.80E+06
Coastal	9.00E+09	4	0.05	0.27	1.25E+07	1.63E+09	8.14E+07
Upwelling	2.50E+08	2.5	0.04	0.23	1.89E+07	2.55E+08	1.98E+07
Total	5.00E+10						1.10E+08

Methods

1. Provinces were taken directly from [2]. For FEISTY model output [47] and Sea Around Us fisheries catch data [97] they were defined as upwelling: LMEs 3, 13, 27, 29; coastal: all non-upwelling LMEs; oceanic: the remaining ocean.
2. Ryther [2] had a total estimate of area-integrated primary production (APP) of $2x10^{10}$ tonnes organic carbon per year. Modern estimates are 50 Pg carbon per year = $5x10^{16}$ g C = $5x10^{10}$ tonnes [104]. To update Ryther's estimates, a total of 50 Pg C was used with his proportional distribution of APP across the three provinces. These proportions were oceanic = 81.5%, coastal = 18.0%, upwelling = 0.5%.
3. Mean number of trophic levels equals Ryther's [2] trophic level +1 because his Table 3 listed the number of trophic levels between primary producers and human consumers, whereas the number here includes primary producers.
4. Low and high transfer efficiency values were the 5th and 95th percentiles of FEISTY model [78] output of TEeff_ATL (transfer efficiency from trophic level 1 - 5) from each province, which were then converted to transfer efficiency. It is calculated as the production of all large fishes (trophic level 5) divided by the net primary production (trophic level 1) in each model grid cell. It is

converted to one transfer efficiency estimate by raising to the power of 1 over the number of transfer steps (trophic level 5 – trophic level 1 = 4), TEeff_ATL$^{1/4}$.

5. Low and high estimates of fish production use the low and high estimates of transfer efficiency combined with the area-integrated primary production (APP) and mean number of trophic levels to calculate fish production as 9 * APP * transfer efficiency ^ (trophic level-1), where 9 is the constant wet weight to carbon ratio of 9:1 of Pauly & Christensen [4].
6. Actual catch is based on global average annual reported and reconstructed catches from 2005-2014 [105] multiplied by the proportion of catch in each of Ryther's [2] provinces. The global total catch average over this 10 year time period was 110 tonnes wet weight with the following proportions: oceanic = 8%, coastal = 74%, and upwelling = 18%.

Outstanding questions

1. What new data acquisition methods are needed to improve transfer efficiency estimates?
2. Over what spatial and temporal scales do transfer efficiencies vary for different species and functional groups? What mechanisms explain this variation?
3. What are the impacts of reduced oxygen and increased ocean acidification on transfer efficiency?
4. How do individual level processes integrate into community level dynamics and affect transfer efficiency response to environmental change?
5. How does transfer efficiency respond to changes in species distributions that essentially create new ecosystems (i.e., new interactions, disrupted feeding patterns, differing adaptation rates) and what processes are fundamental for models to capture in order to accurately explain observed variation in transfer efficiency?

Figures

Figure 1. Processes controlling transfer efficiency. A – A trophic pyramid depicts the classic view of production flowing from primary producers to secondary consumers. Roman numerals indicate trophic level. A 10% transfer efficiency of production is indicated by lighter grey in the pyramid, highlighting how little primary production gets transferred to the top of the food web. B – At the individual scale, metabolic processes determine growth efficiency. C – At the species population scale, maturation, reproduction, and survival of individual life cycles influence transfer efficiency. D – At the ecosystem scale, complex energy pathways, including the microbial loop (depicted middle left which includes dissolved organic carbon (DOC)) and differing paths through benthic and pelagic communities, influence transfer efficiency. Food web diagram after [106].

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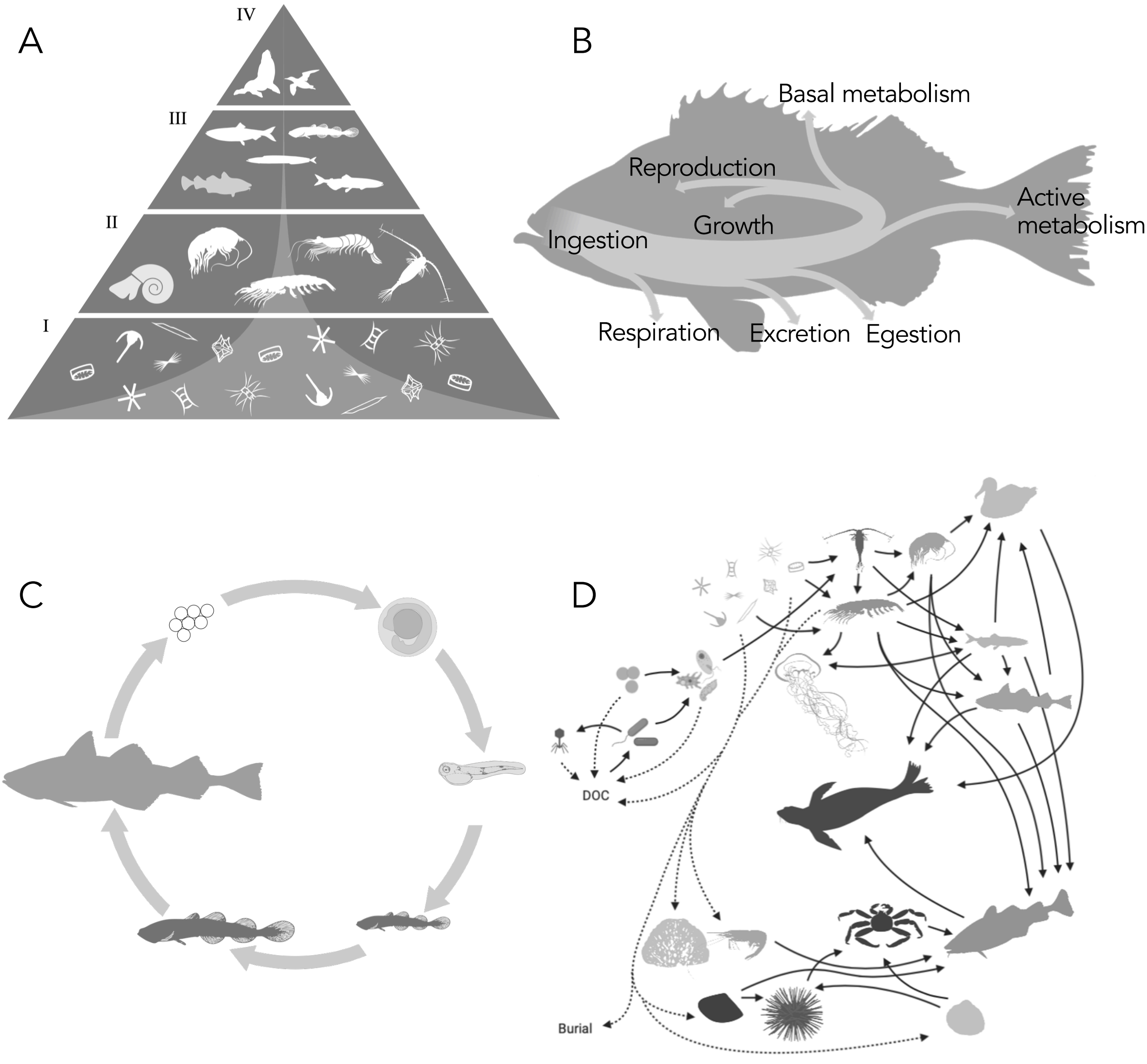
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Basal metabolism
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Ingestion
Active metabolism
Respiration
Excretion
Egestion
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