

Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency

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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. Here, we review the processes controlling transfer efficiency, approaches to estimate it, and known variations across ocean biomes. Both process-level analysis and observed macro-scale 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.

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, as well as 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.

Keywords : trophic ecology, food web, trophic efficiency, energy transfer, climate change, fishing impacts

120 Efficiency of energy transfer through food webs

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

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

140 Despite its recognized importance, transfer efficiency persists as a dominant source of uncertainty
141 in our understanding of current marine ecosystems and projected changes. This reflects three challenges: 1)

142 transfer efficiency is determined by diverse processes at multiple scales with potentially complex
143 dependencies on environmental and ecosystem properties, 2) it is difficult to measure and estimate, and 3)
144 current models used to predict marine resource trajectories generally have highly simplified
145 representations of it. This contribution provides a synthesis of these challenges, our present understanding
146 of transfer efficiency, and a summary of estimates of its value.

147

148 **Processes controlling transfer efficiency**

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

155

156 *Metabolism*

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

167 The metabolic theory of ecology [16] predicts that increasing temperature increases the rates of
168 most biological processes to a point, including the rates at which organisms respire, [16-17], grow, and

169 reproduce [18,19,22]. Metabolic and growth rates of primary producers are generally less temperature-
170 sensitive than those of consumers [17] and can have different temperature dependencies [20]. This can
171 lead to differential rates of consumer production relative to primary production as temperature changes
172 [21], thus affecting transfer efficiency. In many cases, increasing ocean temperatures are associated with
173 increasing stratification, decreased resource availability [19] or reduced food quality [22], complicating
174 detection of direct temperature effects. Ecological stoichiometry has demonstrated theoretically and
175 empirically that nutrition of prey relative to predator demands determines transfer efficiency [23].
176 Consumers feeding on high quality prey (i.e., rich in macronutrients and essential fatty acids) have higher
177 growth rates [24] resulting in greater transfer efficiencies [25-28].

178

179 *Life cycle*

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

196

197 *Food web structure*

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

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

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

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

244

245 **Estimating transfer efficiency**

246 While transfer efficiencies emerge from diverse metabolic, life cycle, and food web processes,
247 estimating transfer efficiency requires knowledge of just two fundamental properties: the trophic level of
248 organisms within an ecosystem determined by their diets, and the production at each trophic level. Neither

249 of these, however, is easy to measure. Indirect transfer efficiency estimates thus rely on combining limited
250 direct measurements, theory, and models. Although challenges exist to estimate transfer efficiency in
251 aquatic ecosystems, there are several approaches that can be used, summarized below.

252

253 *Diet estimates*

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

265 Stable isotopes of nitrogen and carbon used jointly with biomass spectra can elucidate feeding
266 relationships in food webs [58-60]. Due to differences in fractionation, the tissues of predators
267 preferentially incorporate heavier nitrogen isotopes from their diet, resulting in a systematic enrichment in
268 nitrogen-isotope ratio ($\delta^{15}\text{N} = \frac{^{15}\text{N}}{^{14}\text{N}}$) with increasing trophic level [61,62]. Size-fractionated stable
269 isotope analysis is commonly used to quantify the flow of energy in **size spectrum models** and to inform
270 **predator-prey mass ratios** (PPMR [58,63-64]). The slope (b) of $\delta^{15}\text{N}$, an indicator of trophic level, as a
271 function of logarithmic body size class is first used to estimate PPMR: $\text{PPMR} = n^{(\square/b)}$, where \square is the
272 fractionation of $\delta^{15}\text{N}$ and n is the logarithmic base of the size classes [65]. Size spectra are often used in
273 aquatic ecosystems to illustrate the relationship between abundance and/or biomass with size, again
274 grouped in logarithmic classes. Biomass size spectra provide information about the amount of production

275 in each size class, under the metabolic theory assumption that individual biomass production is a function of
276 body size [66-67]. Combining the production per size class from the slope of biomass size spectra data
277 (β), and the change in trophic level with size from PPMR, allows the estimation of transfer efficiency (TE): TE
278 $= PPMR^{\beta+0.75}$ [17,59,68]. One caution, however, is that stable isotope estimates of PPMR have been
279 shown to be particularly sensitive to the trophic enrichment factors used in analyses [62,69-71]. For
280 example, using a trophic enrichment factor of 2 instead of 3.4 can yield PPMR estimates that are 1-3
281 orders of magnitude lower, and transfer efficiency estimates that are 2-4 times higher [69].

282

283 *Production estimates*

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

293 Production-based transfer efficiency estimates for temperate Northern hemisphere marine
294 ecosystems yielded an average transfer efficiency of 13% (ranging from 11-17%) for trophic levels 1-2
295 (phytoplankton to herbivorous mesozooplankton and benthic organisms) and an average transfer
296 efficiency of 10% (ranging from 7-12%) for trophic levels 2-3 (zooplankton and benthic organisms to fish)
297 [76]. Laboratory plankton feeding experiments have yielded higher transfer efficiencies than wild
298 populations because wild populations often feed at suboptimal prey concentrations (which can be
299 controlled in the lab) and lab conditions can prevent loss of production to the microbial loop that is not

300 consumed in wild populations (Figure 1D; [76]). The impacts of energy fluxes through these different food
301 web pathways highlight the importance of integrating processes at the ecosystem scale.

302

303 *Model based estimates*

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

317 The emergence of regularities in observation-based estimates provides a foothold for modellers
318 simulating the flow of energy through marine ecosystems using theoretical approaches. Early models of
319 biomass spectra lack mechanistic details, but can resolve patterns emerging from transfer efficiency
320 estimates [67,81,82]. **Energy flux models** aim to find relationships between biodiversity and the flow of
321 energy through ecosystems and include efficiency terms, however have not yet been applied to estimate
322 transfer efficiency [83-84]. **Size spectrum models** are based on allometric principles that predators
323 tend to be bigger than their prey, so that species can be ignored, and size classes of organisms can be
324 used to track energy flow instead. Size spectrum models have been used to derive transfer efficiency by
325 scaling up from individual level principles of how consumption, search rate, prey choice, and assimilation

326 efficiency vary with body size [15,48,85]. As the number of observational studies reporting these
327 properties grows, it is becoming possible to examine how transfer efficiency differs with both size and
328 functional group – e.g. small versus large zooplankton, filter feeders versus mobile predatory benthic
329 invertebrates, fishes of different sizes and feeding modes, ectotherms versus endotherms – and to add
330 these trait-specific properties to models [52,86].

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

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

344 The EcoTroph model quantifies the fraction of secondary production transferred between trophic
345 levels using taxon-specific consumption to production rates based on life history traits [82,87], thermal
346 habitat [82,88], and also accounts for respiration, excretion, accumulation, and transfer to detritus. Using
347 fisheries catch data as an indicator of fish biomass by trophic level, EcoTroph estimated coastal ecosystem
348 transfer efficiency from secondary production to trophic level 4 that varied as 5.9% in upwelling, 6.5% in
349 tropical, 8.1% in temperate, and 10.4% in polar regions [79]. This transfer efficiency from trophic levels
350 2–4 increased from 7.1% to 7.6% from 1950-2010, a finding that was consistent across all coastal
351 ecosystem types and may be explained by increased fishing exploitation [79,89]. Using sea surface

352 temperature projections to 2100, EcoTroph projected global transfer efficiency in coastal ecosystems to
353 decline by 0.1% until 2040 under both low and high emissions scenarios (RCP2.6 and 8.5 respectively;
354 [79]). From 2040-2100, transfer efficiencies were projected to remain stable under low emissions and
355 decrease from 7.7% to 7.2% under high emissions – with smaller average declines in tropical ecosystems
356 [79]. Overall, fishing pressure was positively correlated with transfer efficiency [89], while sea surface
357 temperature was negatively correlated [79].

358

359 **Estimated transfer efficiencies across ocean biomes**

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

375

376 **Concluding remarks**

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

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

395

396 Boxes

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

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

402

Biome	Trophic level	Low	Mean	High
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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%

403

404 *Methods*

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

408 Transfer efficiency values from Maureaud et al. [103] reflect mean values published in the main
409 text. Regional minima and maxima were estimated from the table of efficiency cumulated indicator (ECI)
410 values by large marine ecosystem (LME) in the supplementary materials. The LME figure in [79] was used
411 to assign each LME to a biome and only those LMEs that were entirely of one biome type were used.
412 Minimum and maximum ECI per region were found over the complete time range (1950-2010). Transfer
413 efficiency (TE) was then calculated from ECI using: $TE = ECI^{1/2}$. ECI is transfer efficiency from trophic level
414 2 to trophic level 4, thus these values of transfer efficiency reflect mean transfer efficiency from trophic
415 levels 2 to 3 and from trophic levels 3 to 4.

416 Transfer efficiency values from [79] reflect mean values published in their Figure 4a. Minima and
417 maxima per region were extracted from the violin plots in Figure 4a. These values of transfer efficiency
418 reflect the mean transfer efficiency from trophic levels 2 to 3 and from trophic levels 3 to 4 over the years
419 2000-2010.

420

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

423 Impact of transfer efficiency variability on estimated fish production based on Ryther's ocean provinces [2]
424 calculated using primary productivity and mean number of trophic levels. Observed fisheries catches also
425 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

426

427 **Methods**

- 428 1. Provinces were taken directly from [2]. For FEISTY model output [47] and Sea Around Us fisheries
429 catch data [97] they were defined as upwelling: LMEs 3, 13, 27, 29; coastal: all non-upwelling
430 LMEs; oceanic: the remaining ocean.
- 431 2. Ryther [2] had a total estimate of area-integrated primary production (APP) of 2×10^{10} tonnes
432 organic carbon per year. Modern estimates are 50 Pg carbon per year = 5×10^{16} g C = 5×10^{10}
433 tonnes [104]. To update Ryther's estimates, a total of 50 Pg C was used with his proportional
434 distribution of APP across the three provinces. These proportions were oceanic = 81.5%, coastal
435 = 18.0%, upwelling = 0.5%.
- 436 3. Mean number of trophic levels equals Ryther's [2] trophic level +1 because his Table 3 listed the
437 number of trophic levels between primary producers and human consumers, whereas the number
438 here includes primary producers.
- 439 4. Low and high transfer efficiency values were the 5th and 95th percentiles of FEISTY model [78]
440 output of TEeff_ATL (transfer efficiency from trophic level 1 - 5) from each province, which were
441 then converted to transfer efficiency. It is calculated as the production of all large fishes (trophic
442 level 5) divided by the net primary production (trophic level 1) in each model grid cell. It is

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

445 5. Low and high estimates of fish production use the low and high estimates of transfer efficiency
446 combined with the area-integrated primary production (APP) and mean number of trophic levels
447 to calculate fish production as $9 * APP * transfer\ efficiency^{(trophic\ level-1)}$, where 9 is the
448 constant wet weight to carbon ratio of 9:1 of Pauly & Christensen [4].

449 6. Actual catch is based on global average annual reported and reconstructed catches from 2005-
450 2014 [105] multiplied by the proportion of catch in each of Ryther's [2] provinces. The global
451 total catch average over this 10 year time period was 110 tonnes wet weight with the following
452 proportions: oceanic = 8%, coastal = 74%, and upwelling = 18%.

453

454 Outstanding questions

455 1. What new data acquisition methods are needed to improve transfer efficiency estimates?

456 2. Over what spatial and temporal scales do transfer efficiencies vary for different species and
457 functional groups? What mechanisms explain this variation?

458 3. What are the impacts of reduced oxygen and increased ocean acidification on transfer
459 efficiency?

460 4. How do individual level processes integrate into community level dynamics and affect transfer
461 efficiency response to environmental change?

462 5. How does transfer efficiency respond to changes in species distributions that essentially create new
463 ecosystems (i.e., new interactions, disrupted feeding patterns, differing adaptation rates) and what
464 processes are fundamental for models to capture in order to accurately explain observed
465 variation in transfer efficiency?

466

467 Figures

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

477

478

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