Getting to the bottom of global fishery catches

Éva Elizabeth Plagányi[a,1]

> When one tugs at a single thing in nature, he finds
> it attached to the rest of the world.
>
> John Muir, *The Yosemite*

Ecosystems are complex, interconnected systems fueled by primary production, from vegetation on land and phytoplankton in the sea. In the oceans, this energy moves from prey to predators, specifically from phytoplankton up the food chain to the species of marine fish that are harvested by fishers (1) (Fig. 1). However, despite some strong regional relationships between phytoplankton production and fish catch (2), these simple relationships do not exist in other places (3), perhaps due, in part, to uncertainties in catch estimates and fishing effort, as well as variable predation pressure from species at the top of the food chain. The total amount of the primary production that is appropriated by humans from both marine and terrestrial food webs is useful in understanding the limits to total food production (e.g., terrestrial crops, wild fisheries, aquaculture) on the planet as well as the consequences of this demand for other species (4–6). This cap on input energy has also led to the notion of food web competition whereby top predators such as marine mammals may compete indirectly with fisheries due to competition for energy from primary production (7).

This energy flow problem can be investigated with trophodynamic models that represent the cycling, and hence functioning, of mass, energy, and nutrients in marine ecosystems, and thus are the foundation of food web thinking (8). In PNAS, Stock et al. (3) consider four such models of increasing complexity and provide a compelling explanation for the observed differences in fisheries catch in apparently similar ecosystems. These findings also raise interesting questions for the future of ocean fisheries productivity under the influence of climate change.

The simplest model of Stock et al. (3) explains fisheries catch in global large marine ecosystems (LMEs) based on measures of net primary production (NPP) after adjusting for the trophic level of the catch (where phytoplankton are assumed to be trophic level 1). However, the fisheries–NPP relationship is more complex, and it is important to resolve the actual energy available from phytoplankton after accounting for lost material that sinks to the deep ocean and for the energy that passes through an important group of intermediate-sized plankton, the mesozooplankton (3) (Fig. 1). The importance of mesozooplankton, and specifically copepods such as *Calanus*, in linking phytoplankton variability to fisheries catch has previously been recognized (9) but, again, found not to hold universally. According to Stock et al. (3), the key to explaining cross-ecosystem catch differences better is to consider also how efficiently energy is transferred through the food web. Their calculations therefore reduce trophic transfer efficiencies in warm-water LMEs because of the higher metabolic demands in these regions. Finally, their most parsimonious model also accounts for differences in trophic efficiencies between ecological regions at the bottom of the ocean, so-called benthic systems, versus pelagic systems that inhabit the overlying water column. Higher trophic transfer efficiencies in benthic systems are ascribed to lower foraging costs compared with searching the 3D pelagic environment. In this way, Stock et al. (3) achieve a correlation that explains 79% of the variation between NPP and fish catch across most of the world's LMEs. This is notable, because reported fisheries catch across the LMEs varies by over five orders of magnitude, yet differences in catch are explained by the model to below a factor of 2.

One of the impediments to quantifying cross-ecosystem fisheries catch differences has been the difficulty in obtaining reliable total estimates of fishery catches, particularly from the artisanal and small-scale sectors, whose catches have not always been included in national landings statistics provided annually to the Food and Agriculture Organization of the United Nations (10). More recently, a catch reconstruction approach has been used to fill in the gaps in the official reported data (11), suggesting, for example, that the contribution from the small-scale sector and discards could be almost double the reported catches in the tropics (3). However, catch data alone are not

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[a]Commonwealth Scientific and Industrial Research Organization, Oceans and Atmosphere, Brisbane, QLD 4072, Australia

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[1]Email: eva.plaganyi-lloyd@csiro.au.

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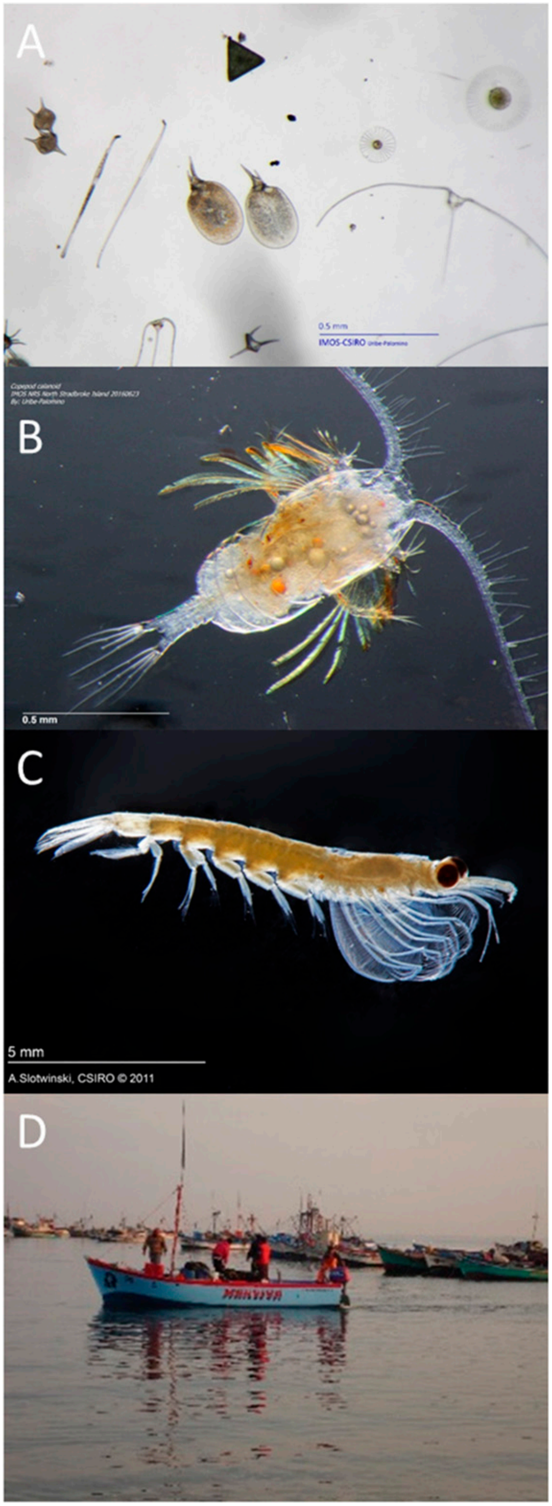

Fig. 1. **Food web pathways to fisheries catches. (*A*) Phytoplankton species, including *Tripos* sp. (*B*) Mesozooplankton copepod example *Acrocalanus sp.*, which channels primary production to higher trophic levels. (*C*) *Nyctiphanes australis*, a euphausiid and important prey species. (*D*) Fisheries catch landed in different marine ecosystems depends on fishing effort and the structure of the underlying food web as well as the efficiency with which energy is transferred between trophic levels in each system. Images courtesy of the Commonwealth Scientific and Industrial Research Organization (Canberra, Australia).**

necessarily a reliable indicator of actual fish biomass; factors such as management actions and largely unexploited mesopelagic fish biomass might bias the reliability of using catch to infer total fish biomass (12, 13). Stock et al. (3) account crudely for this possibility by excluding lightly fished outlier systems (e.g., Australia, which has conservative quota-based regulations) as well as unusual systems such as the polar regions and Hawaiian system. Moreover, they use the average of the top 10 annual total catches as an index of each system's productivity.

In recent years, understanding of global patterns and projections of the future of the world's oceans have been greatly facilitated by the use of complex interconnected models made possible by the rapid advances in computing power and physical modeling (14). The worldwide move toward ecosystem-based management approaches has provided further impetus for broadening modeling approaches and better integration of modeling and empiricism to address food security while sustaining ecosystems and biodiversity despite rapid changes (15). In PNAS, Stock et al. (3) use state-of-the-art approaches to blend empiricism effectively with a more theoretically based and mechanistic global earth system model. The latter high-resolution (10 km) model is coupled with the carbon, ocean, biogeochemistry, and lower trophics planktonic ecosystem model. Despite some shortcomings (as assessed through comparison with satellite information), the model outputs credible representations of broad-scale differences in planktonic web carbon and energy flows. Accurate representation of zooplankton in end-to-end models is broadly considered a linchpin in future model development, given the key role of this group in linking lower and upper trophic levels (14). However, our macroecological understanding of energy transfer through global food webs is still maturing, as is evident from the slightly ad hoc addition of parameters to account for the influence of temperature on trophic efficiencies as well as fundamental differences between pelagic and benthic systems.

The rapid improvements in models and improved integration away from the more traditional discipline-specific approaches (with separate climate, plankton, and fisheries models, for example) have created an ideal platform for using models to investigate the influence of changing climate on ecosystems, fisheries, and human systems (15, 16). Understanding of the impacts of anthropogenic climate change on marine ecosystems has lagged behind understanding of terrestrial ecosystems, in part, due to the complexity of the ocean and difficulties in measuring it (17). Whereas considerable progress has been made in documenting responses of marine organisms to climate change such as shifting species distributions, phenology, and calcification (18), there is still considerable uncertainty as to overall impacts of large-scale and local processes on marine food webs and system productivity. Stock et al. (3) shed further light on this question by modeling plausible changes in trophodynamic mechanisms under a climate change scenario. Their prediction that climate change will greatly amplify catch differences, by up to 50% in some regions, is worth heeding. Fully understanding, and hence predicting, marine responses to climate change is complex, as is evident from the differences in predictions from different models. For example, Cheung et al. (19) also explored the large-scale redistribution of global catch potential and, contrary to Stock et al. (3), predicted large future catch decreases in the United States, Chile, and China.

Clearly, more work is needed to prepare for the major ramifications as some regions benefit from growing catches and others are further stressed. Indeed, this prediction adds to a growing recognition of the need to limit global warming to the Paris Agreement target of 1.5 °C (relative to the preindustrial level) to minimize impacts on food security and resilience (20). Cheung et al. (21) underscore the need to mitigate climate change, predicting that each additional degree Celsius of warming will cost the planet some 3 million metric tons of potential fish catches. Ultimately, understanding the drivers of the productivity of marine ecosystems has the potential to help improve how we manage fisheries production both currently and into the future (22). If climate change alters the productivity of terrestrial and marine food webs, this change in productivity will challenge attempts to manage natural resources sustainably and conserve biodiversity.

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