Correspondence

Global proliferation of cephalopods

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Human activities have substantially changed the world's oceans in recent decades, altering marine food webs, habitats and biogeochemical processes [1]. Cephalopods (squid, cuttlefish and octopuses) have a unique set of biological traits, including rapid growth, short lifespans and strong life-history plasticity, allowing them to adapt quickly to changing environmental conditions [2–4]. There has been growing speculation that cephalopod populations are proliferating in response to a changing environment, a perception fuelled by increasing trends in cephalopod fisheries catch [4,5]. To investigate long-term trends in cephalopod abundance, we assembled global time-series of cephalopod catch rates (catch per unit of fishing or sampling effort). We show that cephalopod populations have increased over the last six decades, a result that was remarkably consistent across a highly diverse set of cephalopod taxa. Positive trends were also evident for both fisheries-dependent and fisheries-independent time-series, suggesting that trends are not solely due to factors associated with developing fisheries. Our results suggest that large-scale, directional processes, common to a range of coastal and oceanic environments, are responsible. This study presents the first evidence that cephalopod populations have increased globally, indicating that these ecologically and commercially important invertebrates may have benefited from a changing ocean environment.

Our dataset spanned the last 61 years (1953 to 2013), with all major oceanic regions represented (69% northern hemisphere, 31% southern hemisphere), along with key taxa (52% squid, 31% octopuses, 17% cuttlefish and sepiolids; Figure 1; Supplemental information). We restricted these time-series data to cephalopod catch rates, which are a more reliable proxy of abundance than raw catch [6]. Our analyses revealed that cephalopod abundance has increased over the last six decades, a result consistently replicated across three distinct life history groups: demersal, benthopelagic, and pelagic (Figure 1; all effective degrees of freedom [edf] = 1, all p values ≤ 0.01). This is remarkable given the enormous life-history diversity exhibited across these groups, which were represented in this study by 35 species/genera and six families. Demersal species, for instance, have low dispersal capacity (tens of km) and occupy shelf waters. Benthopelagic species also occupy shelf waters, but have moderate dispersal capacity (hundreds of km) largely facilitated by a paralarval phase. Pelagic species inhabit open oceanic waters and have high dispersal capacity (thousands of km) facilitated by both a paralarval phase and a mobile adult

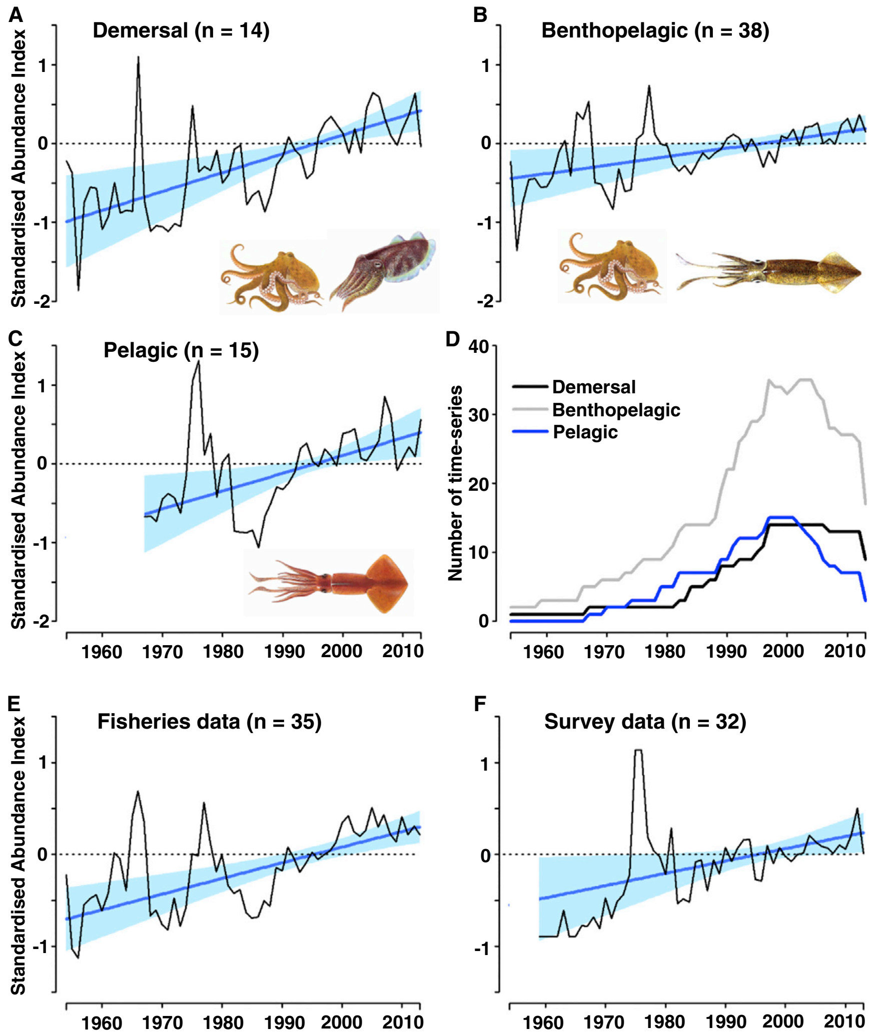

Figure 1. Trends in cephalopod abundance.
Trends in abundance from 1953 to 2013 for demersal (A), benthopelagic (B) and pelagic (C) cephalopods (all edf = 1, all p values ≤ 0.01), with number of time-series by life-history group (D; total n = 67). Illustrations depict key taxa associated with each group. Demersal = species with no planktic paralarval stage, benthic eggs and benthic/demersal hatchlings and adults; benthopelagic = species with benthic eggs, planktic paralarvae and demersal adults; pelagic = planktic eggs and paralarvae and pelagic adults. Trends in abundance for time-series derived from fisheries data (E) and survey data (F) (all edf = 1, all p values < 0.05). For all abundance plots, dark blue lines represent fitted values derived from generalised additive mixed models (± 95% CI) and black lines represent mean standardized time-series (z-scores). See supplemental information.

phase. Furthermore, our collated time-series represented non-target, bycatch and target species, with target species being subject to varying levels of fishing pressure that ranged from large-scale developed fisheries to developing, artisanal and subsistence fisheries (Supplemental information). We also investigated trends by data type, because fisheries-dependent time-series — as opposed to fisheries-independent time-series derived from survey data —can be influenced by factors such as increasing catch efficiency and the spatial expansion of fishing grounds. Significant positive trends for time-series derived from both data sources were evident (all edf = 1, all p values < 0.05), which suggests that the observed trends in catch rate are not an artefact of such factors (Figure 1).

Our results suggest that the proliferation of cephalopod populations has been driven by large-scale processes that are common across a broad range of marine environments and facilitated by biological characteristics common to all cephalopods. Numerous studies demonstrate that cephalopod populations are highly responsive to environmental change, with anthropogenic climate change, especially ocean warming, a plausible driver of the observed increase [4,7]. Elevated temperatures, for instance, are thought to accelerate the life cycles of cephalopods, provided the optimal thermal range of the species is not exceeded and food is not limited. Further, it has been hypothesised that the global depletion of fish stocks, together with the potential release of cephalopods from predation and competition pressure, could be driving the growth in cephalopod populations [5]. It is relatively well documented that many fish species have declined in abundance due to overfishing [8], and several regional studies have suggested that cephalopod populations have increased where local fish populations have declined (albeit casual mechanisms have not been identified; Supplemental Information) [5, 9]. However, a range of other environmental factors, such as changing current systems and climatic cycles, increases in extreme weather events, eutrophication and habitat modification [1], could also potentially confer a competitive advantage to cephalopods over longer-lived, slower-growing marine taxa.

The ecological and socio-economic ramifications associated with an increase in cephalopod biomass are likely to be complex. Cephalopods are voracious and adaptable predators and increased predation by cephalopods could impact many prey species, including commercially valuable fish and invertebrates. Conversely, increases in cephalopod populations could benefit marine predators which are reliant on them for food, as well as human communities reliant on them as a fisheries resource. However, cephalopod population dynamics are notoriously difficult to predict and human activities may have a deleterious effect on cephalopod populations in the future. For example, early evidence suggests that ocean acidification may impact cephalopod survival [4]. Further, as fish stocks have declined, cephalopods have become an ever more important component of global fisheries [10], with cephalopod fisheries catch peaking in recent years [4] and some cephalopod fisheries showing signs of overexploitation (Supplemental information). Therefore, as fisheries continue to refocus their efforts towards invertebrates [10], it will be critical to manage cephalopod stocks appropriately so they do not face the same fate as many of their longer-lived counterparts.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and one table can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.04.002.

AUTHOR CONTRIBUTIONS

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