

1 **Global proliferation of cephalopods**

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26 **eTOC Blurp**

27 Doubleday et al. compiled a global dataset of cephalopod abundance and demonstrate that
28 squid, octopus and cuttlefish populations have increased over the last six decades. This study
29 suggests that these ecologically and commercially important invertebrates have increased on
30 a global scale and may be benefiting from a changing marine environment.

31

32 **Main text**

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

50

51 Our dataset spanned the last 61 years (1953 to 2013), with all major oceanic regions
52 represented (69% northern hemisphere, 31% southern hemisphere), along with key taxa (52%
53 squid, 31% octopuses, 17% cuttlefish and sepiolids) (Figure 1, Table S1). We restricted these
54 time-series data to cephalopod catch rates, which are a more reliable proxy of abundance than
55 raw catch [6]. Our analyses revealed that cephalopod abundance has increased over the last
56 six decades, a result consistently replicated across three distinct life history groups: demersal,
57 benthopelagic, and pelagic (Figure 1, all effective degrees of freedom [edf] = 1, all p values \leq
58 0.01). This is remarkable given the enormous life-history diversity exhibited across these
59 groups, which were represented in this study by 35 species/genera and six families (Table
60 S1). Demersal species, for instance, have low dispersal capacity (tens of km) and occupy
61 shelf waters; benthopelagic species also occupy shelf waters, but have moderate dispersal
62 capacity (hundreds of km) largely facilitated by a paralarval phase; and pelagic species
63 inhabit open oceanic waters and have high dispersal capacity (thousands of km) facilitated by
64 both a paralarval phase and a mobile adult phase. Furthermore, our collated time-series
65 represented non-target, bycatch and target species, with target species being subject to
66 varying levels of fishing pressure that ranged from large-scale developed fisheries to
67 developing, artisanal and subsistence fisheries (Table S1). We also investigated trends by
68 data type, because fisheries-dependent time-series (as opposed to fisheries-independent time-
69 series derived from survey data) can be influenced by factors such as increasing catch
70 efficiency and the spatial expansion of fishing grounds. Significant positive trends for time-
71 series derived from both data sources were evident (all edf = 1, all p values < 0.05), which
72 suggests that the observed trends in catch rate are not an artefact of such factors (Figure 1).

73

74 Our results suggest that the proliferation of cephalopod populations has been driven by large-
75 scale processes that are common across a broad range of marine environments and facilitated

76 by biological characteristics common to all cephalopods. Numerous studies demonstrate that
77 cephalopod populations are highly responsive to environmental change, with anthropogenic
78 climate change, especially ocean warming, a plausible driver of the observed increase [4, 7].
79 Elevated temperatures, for instance, are thought to accelerate the life cycles of cephalopods,
80 provided the optimal thermal range of the species is not exceeded and food is not limited.
81 Further, it has been hypothesised that the global depletion of fish stocks, together with the
82 potential release of cephalopods from predation and competition pressure, could be driving
83 the growth in cephalopod populations [5]. It is relatively well documented that many fish
84 species have declined in abundance due to overfishing [e.g. 8], and several regional studies
85 have suggested that cephalopod populations have increased where local fish populations have
86 declined (albeit casual mechanisms have not been identified) [e.g. 5, 9, and S5, S11 in Table
87 S1]. However, a range of other environmental factors, such as changing current systems and
88 climatic cycles, increases in extreme weather events, eutrophication and habitat modification
89 [1], could also potentially confer a competitive advantage to cephalopods over longer-lived,
90 slower-growing marine taxa.

91

92 The ecological and socio-economic ramifications associated with an increase in cephalopod
93 biomass are likely to be complex. Cephalopods are voracious and adaptable predators and
94 increased predation by cephalopods could impact many prey species, including commercially
95 valuable fish and invertebrates. Conversely, increases in cephalopod populations could
96 benefit marine predators which are reliant on them for food, as well as human communities
97 reliant on them as a fisheries resource. However, cephalopod population dynamics are
98 notoriously difficult to predict and human activities may have a deleterious effect on
99 cephalopod populations in the future. For example, early evidence suggests that ocean
100 acidification, due to increased CO₂ emissions, may impact cephalopod survival [4]. Further,

101 as fish stocks have declined, cephalopods have become an ever more important component of
102 global fisheries [10], with cephalopod fisheries catch peaking in recent years [4] and some
103 cephalopod fisheries showing signs of overexploitation (e.g. see S7, S22 in Table S1).
104 Therefore, as fisheries continue to refocus their efforts towards invertebrates [10], it will be
105 critical to manage cephalopod stocks appropriately so they do not face the same fate as many
106 of their longer-lived counterparts.

107

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117 **Supplemental Information**

118 Supplemental Information includes one table, experimental procedures and associated
119 references.

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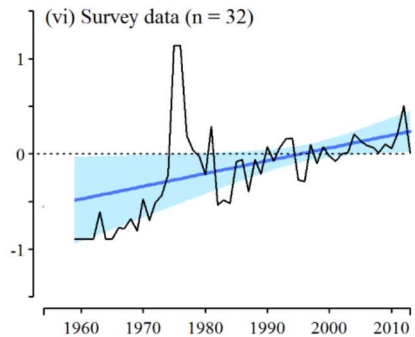
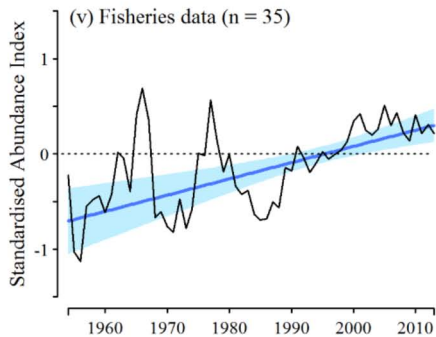
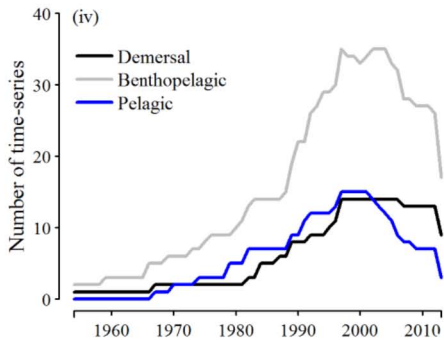
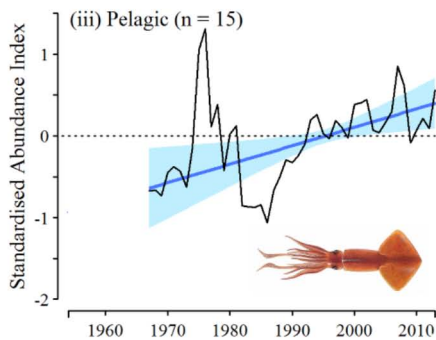
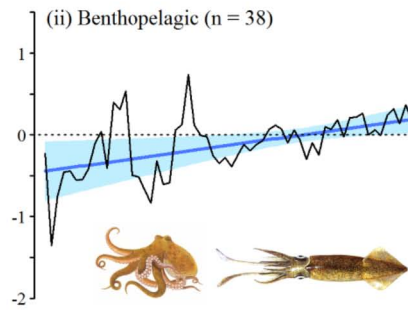
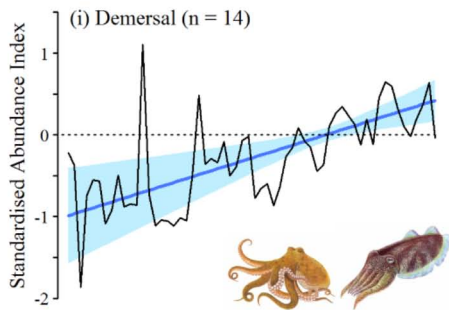
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149 **Figure Legend**

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151 **Figure 1.** Trends in cephalopod abundance

152 Trends in abundance from 1953 to 2013 for demersal (i), benthopelagic (ii) and pelagic (iii)
 153 cephalopods (all edf = 1, all p values ≤ 0.01), with number of time-series by life-history
 154 group (iv; total n = 67). Illustrations depict key taxa associated with each group. Demersal =
 155 species with no planktic paralarval stage, benthic eggs and benthic/demersal hatchlings and
 156 adults; benthopelagic = species with benthic eggs, planktic paralarvae and demersal adults;
 157 pelagic = planktic eggs and paralarvae and pelagic adults. Trends in abundance for time-
 158 series derived from fisheries data (v) and survey data (vi) (all edf = 1, all p values < 0.05).
 159 For all abundance plots, dark blue lines represent fitted values derived from generalised
 160 additive mixed models ($\pm 95\%$ CI) and black lines represent mean standardized time-series
 161 (z-scores). See Supplemental Experimental Procedures and Table S1 for categorisation of
 162 each time-series.



Supplemental Information: Global proliferation of cephalopods

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Table S1 (related to Figure 1 and Supplemental Experimental Procedures). Metadata for each time-series of cephalopod abundance (n = 67). All series are in units of catch or proportional catch per unit effort (catch rate) or lobster ‘kills’ per unit effort (predation rate). LH (life history group) = demersal (D), benthopelagic (B), pelagic (P); Data type = fisheries-independent survey data (S); fisheries data (F). * = series with 1 or 2 missing years, # = predation-based time series.

Family & species	LH	Country of origin	Latitude	Longitude	Time period	No. of Years	Data type	Source ¹
Loliginidae								
<i>Alloteuthis sp</i>	B	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Doryteuthis gahi</i>	B	Falkland Is	-51.700	-57.943	1989-2013	25	F	FD
<i>Loligo bleekeri</i>	B	Japan	39.929	134.176	1975-2006	32	F	[S2]
<i>Loligo forbesii</i>	B	UK	57.158	-1.921	1980-2012	33	S	MSS
<i>Loligo forbesii</i>	B	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Loligo opalescens</i>	B	USA	36.519	-121.884	1969-2006	38	F	[S3]
<i>Loligo pealeii</i>	B	USA	40.820	-70.952	1973-2001	29	S	[S4]
<i>Loligo pealeii</i>	B	USA	41.444	-71.420	1959-2005	47	S	[S5]
<i>Loligo vulgaris</i>	B	Morocco	23.887	-16.056	1990-2006*	17	S	[S6]
<i>Loligo vulgaris</i>	B	Portugal	39.764	-9.414	1953-2013*	61	F	IPMA
<i>Loligo vulgaris</i>	B	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Loligo vulgaris</i>	B	Spain	39.431	1.912	1966-2012	47	F	[S7] updates IEO
<i>Loligo sp, Alloteuthis sp</i>	B	UK	49.676	-9.065	1982-2004	23	S	Cefas
<i>Loligo sp, Alloteuthis sp</i>	B	UK	51.111	1.569	1989-2013	25	S	Cefas
<i>Loligo sp, Alloteuthis sp</i>	B	UK	53.723	-4.997	1988-2013	26	S	Cefas
<i>Loligo sp, Alloteuthis sp</i>	B	UK	55.783	0.965	1992-2013	22	S	Cefas
<i>Loligo sp, Uroteuthis sp</i>	B	Indonesia	-8.596	119.256	1976-2003	28	F	[S8]
<i>Sepioteuthis australis</i>	D	Australia	-34.843	138.209	1984-2013	30	F	SARDI
<i>Sepioteuthis australis</i>	D	Australia	-42.182	148.168	1996-2013	18	F	DPIPWE
<i>Uroteuthis sp</i>	B	Australia	-20.730	149.706	1990-2011	22	F	[S9]
Ommastrephidae								
<i>Dosidicus gigas</i>	P	Peru	-12.110	-77.385	1991-2002	12	F	[S10]
<i>Dosidicus gigas</i>	P	USA	45.988	-126.493	1991-2006	16	F	[S11]
<i>Illex argentinus</i>	P	Falkland Is	-51.700	-57.943	1989-2012	25	F	FD
<i>Illex coindetii</i>	P	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Illex illecebrosus</i>	P	USA	40.820	-70.952	1967-2005	39	S	[S12]

<i>Nototodarus gouldi</i>	P	Australia	-38.873	141.693	1996-2013	18	F	[S13]
<i>Nototodarus sloanii</i>	P	NZ	-48.070	166.424	1982-2008	27	F	[S14]
<i>Ommastrephes bartramii</i>	P	Japan	25.580	146.794	1974-2001	28	F	[S15]
<i>Todarodes pacificus</i>	P	Korea	39.929	134.176	1970-2005	36	F	[S16]
<i>Todarodes pacificus</i>	P	Japan	35.028	141.894	1979-2012	34	F	[S17]
<i>Todarodes pacificus</i>	P	Japan	39.929	134.176	1979-2012	34	F	[S18]
<i>Todaropsis eblanae</i>	P	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Todarodes sp, Illex sp, Todaropsis sp</i>	P	UK	49.676	-9.065	1982-2004	23	S	Cefas
<i>Todarodes sp, Illex sp, Todaropsis sp</i>	P	UK	55.783	0.965	1992-2013	22	S	Cefas
Thysanoteuthidae								
<i>Thysanoteuthis rhombus</i>	P	Japan	39.929	134.176	1989-2003	15	F	[S19]
Octopodidae								
<i>Eledone cirrhosa</i>	B	UK	55.783	0.965	1992-2013	22	S	Cefas
<i>Eledone cirrhosa</i>	B	UK	53.723	-4.997	1988-2013	26	S	Cefas
<i>Eledone cirrhosa</i>	B	UK	49.676	-9.065	1982-2004	23	S	Cefas
<i>Eledone cirrhosa</i>	B	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Eledone moschata</i>	D	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Enteroctopus dofleini</i>	B	Canada	49.274	-123.194	1983-1997	15	F	[S20]
<i>Enteroctopus megalocyathus</i>	B	Chile	-45.266	-72.820	2002-2013	12	F	IFOP
<i>Macroctopus maorum</i>	B	Australia	-34.843	138.209	1994-2013	20	F	SARDI
<i>Macroctopus maorum</i>	B	Australia	-42.182	148.168	1992-2013	22	F#	DPIPWE
<i>Macroctopus maorum</i>	B	Australia	-42.257	144.991	1992-2013	22	F#	DPIPWE
<i>Macroctopus maorum</i>	B	Australia	-43.017	147.921	1996-2013	18	F	DPIPWE
<i>Octopus (cf.) tetricus</i>	B	Australia	-30.319	114.911	1981-2012	32	F#	[S21]
<i>Octopus cynea</i>	B	Madagascar	-22.380	42.493	2004-2013	10	F	Blue Ventures
<i>Octopus cynea</i>	B	Mauritius	-19.610	63.377	1994-2006*	13	F	[S22]
<i>Octopus mimus</i>	B	Chile	-22.079	-70.288	2002-2013	12	F	IFOP
<i>Octopus pallidus</i>	D	Australia	-34.843	138.209	1987-2013	27	F	SARDI
<i>Octopus pallidus</i>	D	Australia	-40.513	145.297	1995-2013	19	F	DPIPWE
<i>Octopus vulgaris</i>	B	Morocco	20.969	-17.243	1990-2008	19	S	[S6]
<i>Octopus vulgaris</i>	B	Portugal	39.764	-9.414	1953-2013*	61	F	IPMA
<i>Octopus vulgaris</i>	B	Spain	36.990	-7.103	1997-2012	16	S	[S1]

<i>Octopus vulgaris</i>	B	Spain	39.431	1.912	1966-2012	47	F	[S7] updates IEO
Sepiidae								
<i>Sepia apama</i>	D	Australia	-34.843	138.209	1984-2013	30	F	SARDI
<i>Sepia elegans</i>	D	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Sepia officinalis</i>	D	UK	51.111	1.569	1989-2013	25	S	Cefas
<i>Sepia officinalis</i>	D	Portugal	39.764	-9.414	1953-2013*	61	F	IPMA
<i>Sepia officinalis</i>	D	Spain	36.990	-7.103	1997-2012	16	S	[S1]
<i>Sepia officinalis</i>	D	Spain	39.431	1.912	1966-2012	47	F	[S7] updates IEO
<i>Sepia sp.</i>	D	UK	53.723	-4.997	1988-2013	26	S	Cefas
<i>Sepia sp.</i>	D	UK	55.783	0.965	1992-2013	22	S	Cefas
<i>Sepia sp.</i>	D	Morocco	20.969	-17.243	1982-2006	25	S	[S6]
Sepiolidae								
Unknown	B	UK	53.723	-4.997	1988-2013	26	S	Cefas
Unknown	B	UK	55.783	0.965	1992-2013	22	S	Cefas

¹ Source acronyms: MSS = Marine Scotland Science (Scotland); Cefas = Centre for Environment, Fisheries & Aquaculture Science (England); IPMA = Instituto Português do Mar e Atmosfera (Portugal); IFOP = Instituto de Fomento Pesquero (Chile); SARDI = South Australian Research and Development Institute, Aquatic Sciences (South Australia); IEO = Instituto Español de Oceanografía (Mallorca); DPIPWE = Department of Primary Industries, Parks, Water and Environment (Tasmania); FD = Fisheries Department (Falkland Islands). Numbers in square brackets refer to published sources (see Supplemental References).

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Supplemental Experimental Procedures

We searched extensively for available published and unpublished long-term (≥ 10 years) annual time-series of cephalopod abundance (catch rate) (Table S1). Where necessary, graph scanning software (*Plot Digitizer 2.6.6*) was used to extract data from published graphs. We obtained 67 time-series of cephalopod catch rates (catch data standardised to fishing or survey-sampling effort) from both fisheries-dependent (54%) and fisheries-independent (46%) sources. Time-series ranged from 10 to 61 years in length (mean: 26 years), spanning the time period from 1953 to 2013 (Figure 1). Series that could not be identified to the family level were omitted, as well as series with > 2 missing years. A small number of time-series ($n = 3$) were based on octopus predation rates in rock lobster fisheries (i.e. number of lobster ‘kills’ per unit of fishing effort), as opposed to the standard catch rate. To account for different measures of catch and predation rate within the dataset, each catch-rate series was standardised to a mean of 0 and standard deviation of 1 (i.e. z-scores). Casewise deletion was applied to those time-series ($n = 5$) with one or two years of missing data. Time-series were categorised into three life-history groups (demersal, benthopelagic, and pelagic; see Figure 1 for definitions) and two data types (fisheries-dependent data and fisheries-independent survey data) (see Table S1).

We used generalised additive mixed models (GAMMs) to investigate temporal trends in cephalopod abundance, which we fitted within the *R* computing environment (version 3.2.0) using functions within the package *mgcv* [S23]. Generalised additive models provide a data-driven method of accounting for non-linear relationships between response and predictor variables by including smoothing functions of those predictors [S24, 25]. We controlled for serial dependence through time by assuming a within time-series autoregressive moving-average (ARMA) process with $p=1$ and $q=1$ (i.e. temporal lags of one year for both the autoregressive and moving-average terms), which was pre-selected over alternative temporal autocorrelation structures based on Akaike’s Information Criterion (AIC) [S26]. We used GAMMs to estimate trends in abundance for species with different life histories. To determine if trends were influenced by possible biases associated with fisheries-dependent data, we also investigated abundance trends by data type. We reported the effective degrees of freedom for each fitted smooth term (edf, where a linear fit is indicated by an edf of 1) and its approximate significance (p value).

Author Contributions

Funding acquisition, BMG; Conceptualisation, BMG, MS, TAAP, ZAD; Data provision, AA, AQ, GJP, JS, MS, SL, SCL, WS; Data collection and curation, ZAD; Development of methodology, concepts and paper content, AA, BMG, GJP, JS, MS, TAAP, ZAD; Formal analysis and software, TAAP; Writing – Original Draft, ZAD; Writing – Review & Editing, all authors; Visualisation, TAAP, ZAD; Project supervision and administration, BMG, ZAD.