

## The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too?

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### Abstract

Cephalopods are a key component of marine food webs, providing sustenance for myriad marine species. Cephalopods are also of increasing economic importance as evidenced by the rapid rise in their global landings over recent decades. If fisheries continue on this trajectory, conflicts may transpire among cephalopod and finfish fisheries, particularly in ecosystems where cephalopods are highly valuable both directly as a landed commodity and indirectly as prey for other harvested species. We provide the first measure of the ecosystem services that cephalopods contribute to fisheries in 28 marine ecosystems, both as a commodity and an ecological support service. We also evaluate how current demands on cephalopods compare to mid-20th century conditions. We find that cephalopod contributions to fisheries vary widely, but are substantial in many ecosystems. Commodity and supportive services provided by cephalopods contributed as much as 55% of fishery landings (tonnes) and 70% of landed values (\$USD). The contribution of cephalopods as a commodity was generally greatest in the coastal ecosystems, whereas their contribution as a supportive service was highest in open ocean systems. Further, the commodity and supportive services provided by cephalopods to fisheries landings increased in most of the coastal ecosystems between the mid-20th century (years 1960–70) and contemporary periods (years 1990–2004), indicating the rising demand for cephalopods. Current demands have no historical precedent and ecosystems in which cephalopods are highly exploited as a targeted resource and as an ecological support service should be further evaluated to prevent the unsustainable development of marine fisheries within them.

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**Introduction**

The premise for an ecosystem-based approach to fisheries management (EBFM) is that greater consideration of ecosystem structure and function will foster better management decisions and improve the sustainability of marine resources (Christensen *et al.* 1996; National Marine Fisheries Service 1999; National Research Council – NRC, 2006). One element of the EBFM that has long been recognized is the potential for conflicts to arise from the simultaneous targeting of food web components. When predators are forced to compete with fisheries for their forage base, management plans for one target stock can affect the productivity of other target or non-target species (Brodziak *et al.* 2004; Walters *et al.* 2005; NRC 2006). Failure to consider such conflicts can result in adverse consequences (Sumaila 1997; Hjerermann *et al.* 2004), thus some management agencies are now coordinating harvest regulations for predators and pivotal forage species (Kock 2000; Constable 2001). However, there are many prey species for which the effect of their removal on the resilience of marine fisheries and ecosystem dynamics is underappreciated or unknown. Because fisheries in most regions of the world now target multiple trophic levels (Essington *et al.* 2006), there is a need to identify the potential trade-offs between values of forage species as an extracted resource and an ecosystem support service.

Cephalopods, like many forage species, are an important component of both marine food webs and fisheries. Cephalopods are a major prey source for commercially important fishes (e.g. tunas and salmon), marine mammals, and seabirds in ecosystems worldwide (Smale 1996) and an increasingly valuable direct human resource. Their commercial importance has risen dramatically in recent decades (Caddy and Rodhouse 1998; Watson and Pauly 2001), and it has been suggested that cephalopods are one of the last marine resources capable of withstanding substantial expansion in fishery landings (Voss 1973; Boyle and Boletzky 1996; Clarke 1996). Thus, we may expect that increasing cephalopod harvests will persist as global fisheries continue to expand to lower trophic level species,

and presumably to species of lesser economic value, in response to the increasing demand for marine resources. An understanding of their value to marine ecosystems and the potential trade-offs associated with cephalopod fisheries is an important contribution towards the goal of more holistic, ecosystem-based management.

Potential trade-offs between the demands on cephalopods may be identified through a valuation approach that quantifies the commercial and ecological value of cephalopods to marine fisheries. Valuation studies are commonly being used to identify economic and ecological consequences of human practices (Costanza *et al.* 1997; Holmlund and Hammer 1999; Rönnbäck 1999; McArthur and Boland 2006; Hannesson *et al.* 2009). Although there are empirical and conceptual challenges in assigning values to ecosystem components, this approach makes apparent the range of potential values of a natural resource and identifies priorities for further research (Costanza *et al.* 1997). Value can be defined as a measure of the contribution of an ecosystem component to a particular goal or objective, such as the maximization of ecosystem sustainability or the optimization of fisheries yield and economic value (Lazo 2002). In this study, value refers to the bottom-up contribution of cephalopods to 'demand-derived ecosystem services' (Holmlund and Hammer 1999): the landings (tonnes) and landed values (\$USD) of commercial fisheries. Here, we measure the value of two types of ecosystem services that cephalopods provide, expressing them as the proportion of fisheries landings and landed value that each comprise. We define commodity services as the harvest and sale of cephalopods, and supportive services as the portion of the landings and landed value of other species that rely on cephalopods for their production. While cephalopods also hold value as prey items of conservation species (i.e. marine mammals), we restrict our analysis to fisheries landings and landed values because these metrics are amenable for making comparisons across ecosystems.

Our measures of value can provide insight into cephalopods, fisheries, and the potential conflicts between fisheries. First, we can use this information to determine whether cephalopods are more

valuable as a human grocery item or as forage for commercial fishes. When cephalopods are valuable as both, it implies a high demand for two potentially incompatible ecosystem services and may signal unsustainable fishery development. Second, we can determine if there are common attributes of ecosystems that have high or low contributions of cephalopods to fisheries. These attributes, if identified, can be helpful in developing fisheries because they may indicate ecosystems at risk of developing conflicting and thereby unsustainable fisheries. Third, we can evaluate the trajectory of the fisheries over time and ask whether there are historical precedents for the demand on ecosystem services that cephalopods presently provide to fisheries. If no precedent exists, it may be prudent to further evaluate whether contemporary fisheries which rely heavily on cephalopods as a commodity and support service may be unsustainable in the long term.

In this study, we quantified the commodity services and supportive services provided by cephalopods to global marine fisheries, identified the biophysical factors that may dictate the magnitude of their contributions, and determined whether the contributions of cephalopods to commercial fisheries has changed over historical and contemporary periods. This study is the first to quantify the ecosystem services provided by cephalopods in support of marine fisheries across global ecosystems. The findings from this work are valuable for identifying marine ecosystems that may be unable to support the further expansion of a cephalopod fishery without impairing the resilience of the finfish fisheries.

## Methods

To quantify the commodity and support services provided by cephalopods to marine fisheries landings and landed values we used commercial landings (tonnes) and ex-vessel prices (real price; \$USD per tonnes) reported for individual taxonomic groups, respectively. Diet data of these taxonomic groups were also used to estimate the contribution of cephalopods as a support service to marine fisheries. Here, we describe our data sources and analyses for many of the large marine ecosystems (LMEs) and open ocean ecosystems.

### Commercial landings and ex-vessel price data

Large marine ecosystems are units of ocean and coastal regions that are characterized by unique

bathymetry, hydrography and productivity (Griffis and Kimball 1996). These ecosystems cover areas >200 000 km<sup>2</sup> and collectively account for up to 90% of the annual catch of global marine fisheries (Sherman and Duda 2001; Garibaldi and Limongelli 2003). Reported landings and ex-vessel price data of commercial fishes captured in the delineated LMEs have been compiled by the *Sea Around Us Project* (SAUP; Watson *et al.* 2004; Sumaila *et al.* 2007). The data were consolidated from a variety of sources including the Food and Agricultural Organization (FAO), the International Council for the Exploration of the Sea (ICES) and regional agencies. Landings and price data are reported for individual species, although in a limited number of cases the data are aggregated by genus, family or higher taxonomic groups. In this study, our intent was to include myriad LMEs to represent a diverse set of 'coastal' ecosystem types, including continental shelves, gulfs, seas, major currents and upwelling zones over many regions of the world's oceans. For our analysis, we selected 22 of the 66 LMEs based on the taxonomic resolution of the fisheries data (i.e. majority of the catch was identified to species level) and the availability of food habits data (Table 1; Fig. 1). One potential bias with this method is that the selected ecosystems were mainly those characterized by well-developed industrialized fisheries and fishery management organizations (i.e. eastern Pacific Ocean, western and eastern Atlantic Ocean). These ecosystems had the best data in terms of catch resolution and diet data availability. The quality of the catch and (or) diet data for many ecosystems in the western Pacific Ocean and Indian Ocean were not amenable to our analysis, thus these systems were under-represented in our study. Collectively, the selected 22 coastal marine ecosystems contribute to 50% of the total fishery landings in the global LMEs. For each system, we used averaged landings and ex-vessel price data (real price adjusted to year 2000; \$USD per tonnes) for years 1990–2004 and 1960–70 to represent contemporary and historical periods, respectively.

Although the selected LMEs account for coastal regions, substantial high seas fisheries operate for highly migratory species in open ocean regions that are not included in any of the LMEs. Thus, in addition to the LMEs, we designated six open ocean ecosystems for our analysis (Fig. 1). Similar to methods of Vasconcellos and Watson (2004), the latitudinal boundaries of the Atlantic ecosystems (north, central and south Atlantic) were selected in

**Table 1** List of ecosystems evaluated in our analysis, the number of species groups that compose the top fisheries landings, the percent of total fishery landings accounted for in the respective ecosystems, the averaged mean trophic levels (TL) of the ecosystems, the weighted average trophic levels of the fisheries and the diet data category. Results are reported for the contemporary and historical periods (in parentheses). \*Contemporary and historical values are the same.

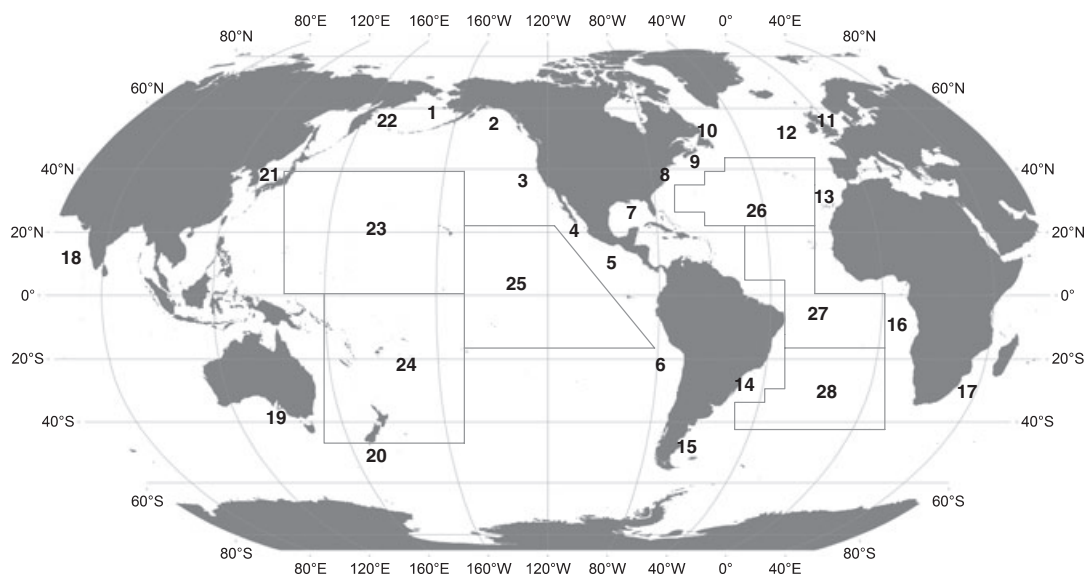
Ecosystem	Number of groups	Percent of catches	Ecosystem average TL	Fishery average TL	Category
Agulhas Current	25 (8)	92*	3.57 (3.05)	3.94 (3.12)	2
Arabian Sea	25 (25)	81 (90)	3.51 (3.40)	3.65 (3.47)	3
Benguela Current	14 (11)	95*	3.44 (2.98)	3.44 (2.96)	2
California Current	25 (25)	95*	3.43 (3.49)	3.48 (3.63)	2
Canary Current	25 (25)	95 (90)	3.27 (3.37)	3.11 (3.09)	2
Celtic-Biscay Shelf	25 (25)	90 (92)	3.50 (3.48)	3.63 (3.67)	2
Central Atlantic	9 (9)	–	–	4.41 (4.38)	2
Central North Pacific	12	–	3.60	3.94	2
East Bering Sea	12 (14)	95*	3.60 (3.57)	3.64 (3.65)	1
Eastern Tropical Pacific	14	–	4.16	4.70	2
Gulf of Alaska	15 (14)	95*	3.64 (3.59)	3.71 (3.65)	2
Gulf of California	21 (18)	95*	3.01 (2.94)	3.20 (3.83)	2
Gulf of Mexico	18 (9)	95*	2.40 (2.48)	2.42 (2.27)	2
Humboldt Current	6 (1)	95*	2.79 (2.73)	2.75 (2.70)	1
New Zealand Shelf	25 (17)	91 (95)	3.94 (3.11)	4.01 (3.46)	2
Newfoundland/Labrador Shelf	20 (8)	95*	3.05 (3.87)	3.76 (3.91)	2
North Atlantic	9 (9)	–	–	4.45 (4.46)	2
North Sea	12 (10)	95*	3.27 (3.43)	3.34 (3.52)	2
Pacific-Central American Coast	16 (8)	95*	2.84 (2.88)	2.80 (2.83)	2
Patagonian Shelf	15 (17)	95*	3.57 (3.50)	3.61 (3.69)	2
Scotian Shelf	18 (12)	95*	2.93 (3.69)	3.64 (3.76)	1
Sea of Japan	23 (25)	95 (94)	3.32 (3.31)	3.33 (3.39)	3
South Atlantic	9 (9)	–	–	4.45 (4.45)	2
South Brazil Shelf	25 (20)	89 (95)	3.21 (3.03)	3.42 (3.04)	2
South Pacific	8	–	–	4.36	2
Southeast Australian Shelf	25 (13)	86 (95)	3.78 (3.19)	3.99 (3.82)	2
US Northeast Continental Shelf	23 (23)	95*	2.51 (2.90)	2.97 (3.31)	1
West Bering Sea	13 (16)	95*	3.42 (3.36)	3.48 (3.43)	3

accordance with the biogeochemical provinces of the Atlantic Ocean. The longitudinal boundaries were chosen in a similar manner; however, we excluded areas that overlapped with the geographical boundaries of the LMEs. The boundaries of the central north Pacific (CNP) and eastern tropical Pacific (ETP) ecosystems were based on those designated in published ecosystem models for these systems (Cox *et al.* 2002; Olson and Watters 2003). The boundaries of the south Pacific ecosystem were chosen in accordance with the oceanographic features of the Pacific Ocean and with regions that do not overlap with the LMEs or the CNP and ETP ecosystems.

The delineated Atlantic and Pacific open ocean ecosystems also coincide with the jurisdictional boundaries of regional fishery organizations that are responsible for managing high seas resources. In this study, the landings data for the north, central,

and south Atlantic systems were obtained from the International Commission for the Conservation of Atlantic Tunas (ICCAT; 1990–2004). Fisheries landings data for the south Pacific were obtained from the Secretariat of Pacific Community (SPC). For this system, we used the catch data for those years with the highest geographical coverage (2000–05). Fisheries catch data for the CNP (avg. 1990–98) and ETP (avg. 1993–97) were taken from the aforementioned ecosystem models of these regions (Cox *et al.* 2002; Olson and Watters 2003). The catch data for all of open ocean systems were summarized by species, years and vessel gear type.

Ex-vessel price data for species captured in the open ocean systems were obtained from NOAA Fisheries–National Marine Fisheries Service (NOAA–NMFS). To be consistent with the LME ex-vessel prices, we utilized the ‘2000 Annual Trade Data by Product through Specific US Custom



**Figure 1** The approximate regions of the LMEs (# 1–22) and open ocean systems (# 23–28) that were included in the analysis of the contribution of cephalopods to marine fisheries. 1, East Bering Sea; 2, Gulf of Alaska; 3, California Current; 4, Gulf of California; 5, Pacific-Central American Coast; 6, Humboldt Current; 7, Gulf of Mexico; 8, US Northeast Continental Shelf; 9, Scotian Shelf; 10, Newfoundland/Labrador Shelf; 11, North Sea; 12, Celtic-Biscay Shelf; 13, Canary Current; 14, Southeast Brazil Shelf; 15, Patagonian Shelf; 16, Benguela Current; 17, Agulhas Current; 18, Arabian Sea; 19, Southeast Australian Shelf; 20, New Zealand Shelf; 21, Sea of Japan; 22, West Bering Sea; 23, Central North Pacific; 24, South Pacific; 25, Eastern Tropical Pacific; 26, North Atlantic; 27, Central Atlantic; 28, South Atlantic. The boundaries of individual LMEs can be viewed at <http://www.seaaroundus.org/lme/lme.aspx>.

Districts' provided by the Fisheries Statistics and Economic Division (NOAA–NMFS 2008a). For the Atlantic open ocean ecosystems, we used price data reported for the 'mid-Atlantic markets' and for the Pacific open ocean systems we used ex-vessel prices compiled for the 'Pacific markets.' Annual trade data were not available for marlins and sailfish; therefore, for these species we used the 2000 annual ex-vessel prices reported for the Hawaiian fish markets (NOAA–NMFS 2008b). To account for the difference in prices assigned to fresh and frozen products we made the simplifying assumption that fishes caught by longliners, baitboats, and pole and line vessels were sold as fresh products while those caught by purse seine were sold as frozen products. Lastly, historical landings and price data were not readily available for all of the open ocean systems, thus we limited our analysis of these systems to the contemporary period (within years 1990–2005).

### Modelling

The commodity contribution of cephalopods to fishery landings and landed values in an individual ecosystem were calculated as the summed tonnage

and monetary value (\$USD) of all cephalopods landed in that ecosystem, respectively. The supportive contribution of cephalopods to fishery landings and landed values in each ecosystem were estimated in the following manner. First, we focused our analysis on nekton that composed the top 95% of the total landings in a given ecosystem. For the few systems in which a high number of taxonomic groups composed the majority of landings, we limited our analysis to the top 25 landed groups (Table 1). Commercial fisheries in LMEs and pelagic regions often encompass tens to hundreds of species and data on feeding habits are not available for most of these. Because a few species contributed to the majority of landings and landed value of fisheries in most ecosystems, excluding those that collectively account for 5% of value would have little effect on our results. Typically, fewer than 25 taxonomic groups represented the top 95% of the total catch in each ecosystem and thus was an appropriate threshold for our analysis (Table 1).

Second, we obtained food habits data for each taxonomic group (by percent mass or volume) through an extensive literature search (see Appendix S1). To accomplish this task we used published



diet data from studies spanning a wide range of years and therefore applied the same diet data for our analysis of the contemporary and historical periods. For cases in which the landings and ex-vessel price data were grouped by broader taxonomic groups, i.e. genus or family, we included published diet estimates of species that are included in the respective group and that are known to inhabit the ecosystem as documented by Froese and Pauly (2009). When possible we included multiple estimates of the predators' diet composition. When estimates were available for multiple body sizes of a predator, we calculated a weighted average of the cephalopod component of the predator's diet: the diet estimates were weighted by  $m_i^{0.75}$ , where  $m_i$  is the predator body mass (g) and 0.75 is a common allometric scaling exponent of the relationship between food consumption and predator body mass (Essington *et al.* 2001). The data required to calculate the magnitude of feeding across multiple body sizes at the population level were not available for all predators, thus we used this simpler metric that more heavily weighted samples from adult over juvenile life history stages. We also categorized the quality of the diet data using the following criteria: (i) the majority of diet data were available for taxonomic groups in the specified ecosystem; (ii) the majority of diet data were available for the specified and/or adjacent ecosystems; and (iii) the majority of diet data were borrowed from non-specified and non-adjacent ecosystems.

Third, we developed a general model to combine these and additional data to estimate the supportive contribution of cephalopods to the fishery landings for each ecosystem. Our model recognizes that the total production of a predator species  $j$  is the summed product of consumption on each of  $i$  prey types ( $Q_i$ ) and the gross conversion efficiency of each ( $\gamma_i$ ):

$$P_j = \sum_i Q_i \gamma_i. \quad (1)$$

Consumption of prey group  $i$  is the product of the total mass consumed by the predator population ( $Q$ ) and the proportion of the predator's diet consisting of prey  $i$  ( $p_i$ ). Thus, the proportion of production of predator  $j$  that is attributable to feeding on prey  $i$  ( $P_{ji}$ ) does not depend on  $Q$ , and equals:

$$P_{ji} = \frac{\gamma_i \cdot p_i}{\sum p_i \gamma_i}. \quad (2)$$

The gross conversion efficiency of prey  $i$  can be broken down into those components that are prey

dependent and those that are not. We define  $A_i$  as the assimilation efficiency of prey (the fraction of energy absorbed through digestion),  $E_i$  as prey energy density,  $E_j$  as predator energy density, and  $M_j$  as the fraction of assimilated energy that is allocated to metabolism. Gross conversion efficiency for prey type  $i$  is therefore equal to:

$$\gamma_i = A_i \cdot \frac{E_i}{E_j} \cdot M_j. \quad (3)$$

Because only  $A_i$  and  $E_i$  depend on prey type, we define  $g_i$  as the product of the two, and substitute  $g_i$  into Equation (2) to derive an expression for the proportion of a predator's production dependent on prey species  $i$ :

$$P_{ji} = \frac{g_i \cdot p_i}{\sum g_i \cdot p_i}. \quad (4)$$

For each ecosystem, we first calculated a basic estimate of the supportive contribution of cephalopods to fisheries as the product of their contribution to each species' production ( $P_{j,ceph}$ ) and each species' landings ( $L_j$ ) or landed value ( $V_j$ ). The total supportive contribution of cephalopods was then derived by summing over all predators, i.e.  $\sum P_{j,ceph} L_j$  and  $\sum P_{j,ceph} V_j$ , respectively. We used a bootstrap method (1000 iterations) to incorporate the variance associated with the multitude of combinations of predators and estimates of  $p_{ceph}$ . The means of the runs were used as most likely point estimates of total cephalopod contribution to  $L$  and  $V$ . We then considered the extent to which these values of supportive contribution can be biased upwards or downwards due to differences in  $g_i$  among prey types. Because our focus was on cephalopods, we simplified the calculation by categorizing prey into two groups: cephalopod and other prey items. Thus, with these two categories, Equation (4) can be expanded to:

$$P_{j,ceph} = \frac{g_{ceph} \cdot p_{ceph}}{g_{ceph} \cdot p_{ceph} + g_{other} \cdot (1 - p_{ceph})}, \quad (5)$$

where  $p_{ceph}$  and  $g_{ceph}$  are the diet proportion comprised cephalopods and the assimilation efficiency for cephalopod prey, respectively, and  $g_{other}$  indicates the average quantity over all other prey types. If we define  $d$  as the ratio of  $g_{ceph}:g_{other}$ , then Equation (5) becomes

$$P_{j,ceph} = \frac{d \cdot p_{ceph}}{p_{ceph} \cdot (d - 1) + 1}. \quad (6)$$

It is not possible to generate independent estimates of  $d$  for each predator in every ecosystem

**Table 2** List of predator feeding groups, predator families which compose each group, and maximum and minimum estimates of prey energy densities ( $\text{KJ g}^{-1}$ ) used to determine the upper and lower bounds of the supportive contribution of cephalopods to marine fisheries.

Predator groups	Families	Min. $E_i$	Max. $E_i$
Gadids	Anoplopomatidae, Gadidae, Merluccidae, Moridae, Phycidae	1.56	5.93
Flatfishes	Cynoglossidae, Paralichthidae, Pleuronectidae, Rajidae, Scophthalmidae, Soleidae	1.42	4.64
Salmon	Salmonidae	1.61	5.09
Sharks	Carcharinidae, Triakidae, Pristidae	2.32	6.33
Small pelagics	Atherinidae, Carangidae, Centrolophidae, Chirocentridae, Clupeidae, Engraulidae, Osmeridae, Scomberesocidae	1.33	6.24
Tunas/marlins	Scombridae, Istiophoridae	2.18	6.00
Mackerels	Scombridae	1.80	7.07
Perch-likes/Scorpionfishes	Ammodytidae, Ariidae, Balistidae, Centropomidae, Cheilodactylidae, Gerreidae, Haemulidae, Hexagrammidae, Lethrinidae, Lutjanidae, Moronidae, Percophidae, Pinguipedidae, Platycephalidae, Scianidae, Scorpaenidae, Sebastidae, Sparidae, Trigillidae	1.21	6.15
Eels/Anglers	Congeridae, Ophiidae, Lophiidae, Zeidae	1.39	6.10
Other fishes	Oreosomatidae, Nototheniidae, Trachichthyidae	1.74	6.51
Cephalopods	Loliginidae, Ommastrephidae, Octopodidae, Sepiidae	1.83	5.56

because values of  $E_i$  and  $A_i$  are unknown for many prey species. Instead, we generated minimum and maximum estimates of  $d$  for 10 predator feeding groups and applied these estimates to all ecosystems to essentially generate lower and upper bounds of  $P_{j,\text{ceph}}$ . We classified predators into feeding groups according to similarities in habitat types (as documented by Froese and Pauly 2009), taxonomy and prey types (Table 2). The taxon of cephalopod and non-cephalopod prey items were identified from the food habits literature (see Appendix S1), and values of  $E_i$  and  $A_i$  for prey items for each predator feeding group were found through a separate literature search (see Appendix S2). By combining the data synthesis of Glaser (2009) and this study, we compiled approximately 600 prey energy density values for a total of 328 prey groups (see Appendix S2). When multiple estimates of  $E_i$  were available for a single species we selected the median value for our analysis. When published estimates of energy density values were unavailable for a prey species we used values from species within the same genus or family. Lastly, for each predator feeding group, the representative minimum and maximum  $E_i$  values were determined by  $\pm 1$  standard deviation of the prey energy density values identified for the respective group.

In our search for published estimates of  $A_i$  for marine prey species, we found that most estimates were derived from marine mammal and seabird

studies: there is a scarcity of data on prey assimilation efficiencies for fish predators. Given the limited data, we estimated a viable range of  $A_i$  values from the minimum and maximum values of  $A_i$  presented in marine mammal studies, approximately 0.60–0.90 (Miller 1978; Ashwell-Erickson and Elsner 1981; Keiver *et al.* 1984; Ronald *et al.* 1984; Fisher *et al.* 1992; Fadley *et al.* 1990, 1994; Rosen 1996; Lawson *et al.* 1997a,b; Rosen *et al.* 2000; Rosen and Trites 2000). We realize that prey assimilation efficiencies vary in a predator-specific manner and are also affected by numerous factors, including nutrition state, age, season and prey type (Rosen and Trites 2000). However, our estimated range of  $A_i$  is based on biologically plausible values. Also, the estimated range is quite wide and therefore is likely to capture the maximum extent to which our point estimates could vary due to uncertainty of assimilation efficiency of prey items. The marine mammal studies also indicate that the  $A_i$  values of cephalopods as prey are near the upper range of estimated  $A_i$  values, and therefore we used values of 0.80 and 0.90 as the minimum and maximum estimates  $A_i$  for cephalopods, respectively.

Similar to the point estimates, the lower and upper bounds of the total supportive contribution of cephalopods to fisheries was quantified as the product of each predator's landings ( $L_j$ ) or landed value ( $V_j$ ) and the minimum or maximum estimate of  $P_{j,\text{ceph}}$  from Equation (6) summed over the top

landed predator groups. As before, these were calculated using a bootstrap method (1000 iterations) to incorporate uncertainty in  $p_{\text{ceph}}$ . We note that these estimates are of first order contributions obtained through one trophic feeding level. Preliminary analyses that considered multiple trophic levels revealed that the vast majority (>99%) of the supportive contributions to fisheries landings were attributed to first order contributions.

### Comparisons within and among ecosystems

To identify potential biophysical factors associated with differences in the contribution of cephalopods, we regressed the estimated percent contributions (point, minimum and maximum) of cephalopods as commodity and supportive services against the primary production rates reported by the Inland and Marine Waters Unit (IMW), Institute for Environment & Sustainability, EU Joint Research Center (JRC), Ispra, Italy and posted online by the SAUP. We also regressed the percent contributions estimated for all ecosystems on the average trophic levels of the ecosystems. For the LMEs, we averaged the mean trophic levels reported for each ecosystem by the SAUP for the historical and contemporary periods. We consider the trophic levels generated by the SAUP to be un-biased or at least uniformly biased across all LMEs; the same methodology was used to generate estimates of species trophic levels in each ecosystem (see [http://www.seararoundus.org/doc/SAUP\\_Manual.htm#8](http://www.seararoundus.org/doc/SAUP_Manual.htm#8) for methods). Estimates of mean trophic levels were not available for open ocean systems. We used the reported trophic levels (SAUP) of landed species to estimate the mean trophic levels of Atlantic and south Pacific ecosystems over the contemporary period. We calculated the mean trophic levels of the CNP and ETP ecosystems using the species-specific trophic levels published in the Ecopath models (Cox *et al.* 2002; Olson and Watters 2003). Further, we evaluated whether the nature of the fishery dictated the observed trends. We compared the estimated percent contributions of cephalopods to the average trophic levels of the catches. The trophic levels of the top landed taxonomic groups in each system were weighted by the reported landings of respective group. We were unable to account for predator body sizes in our estimates of trophic levels because body sizes were not available for the taxonomic groups.

Lastly, to determine whether there is evidence of change in the value of cephalopods over time we

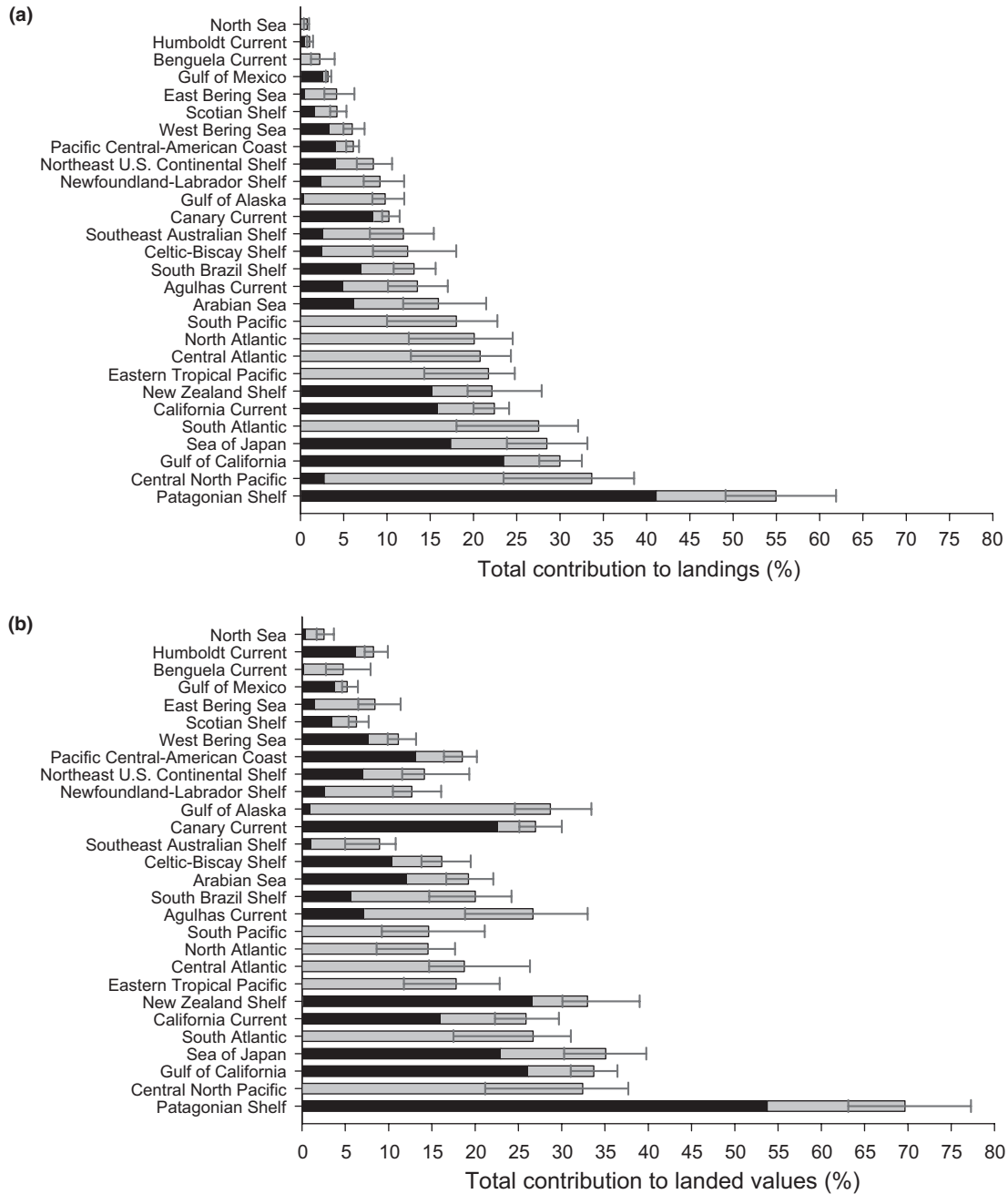
evaluated their historical and contemporary contributions to landings and landed values within in each LME in terms of metric tons and \$USD, respectively. We also compared the contemporary ex-vessel prices of cephalopods and fishes within each system to evaluate whether the rise in cephalopod landings lends support to the notion that fisheries are replacing high value fish predators with low value species as they fish down or through marine food webs. For this analysis, we used the contemporary average value per metric ton (\$USD per tonnes) of cephalopods and of the top landed fishes in which cephalopods represented >20% of their diet composition.

### Results

The ecosystems evaluated in our study varied with respect to their oceanographic features and fisheries characteristics. They included continental shelves, major currents and upwelling zones, gulfs, seas, and open oceans. The number of taxonomic groups that composed the top 95% of the fisheries landings in the various ecosystems was typically <25 groups, but ranged from 1 to >25 (Table 1). For seven LMEs, this number ranged from 26 to 56 groups, thus we limited our analyses of these LMEs to the top 25 groups, which allowed us to account for 80–95% of the total tonnage of fishery landings in these systems (Table 1). Fisheries in the coastal LMEs generally had a larger number of taxonomic groups than those in the open ocean ecosystems. The quality of the diet data for most ecosystems was assigned to the second rank: the majority of the data for the taxonomic groups were available either for the specified or adjacent ecosystems (Table 1). In a few cases, diet data were available for the majority of the top landed species within the specified system, e.g. Humboldt Current, East Bering Sea, Scotian Shelf, and US Northeast Continental Shelf. Diet data were less readily available for the Sea of Japan and the West Bering Sea ecosystems. To summarize the main findings of our analyses, we present our results in terms of the point estimates of the commodity and supportive contributions of cephalopods to marine fisheries.

Our results show that the contribution of cephalopods as an ecosystem service to marine fisheries is substantial in many marine systems. The total contribution (commodity and supportive) of cephalopods to fishery landings and landed values was as high as 55% and 70% in the Patagonian Shelf





**Figure 2** The total percent contribution of cephalopods to contemporary fishery landings (a) and landed values (b) in 22 LMEs and six open ocean ecosystems. Commodity contribution, black bars; Point, minimum, and maximum estimates of supportive contribution, grey bars.

ecosystem, respectively (Fig. 2a,b). The average point estimates of the total contribution to fishery landings and landed values across the studied ecosystems were 15% and 20%, respectively.

The relative importance of commodity vs. supportive contributions of cephalopods varied widely

among the LMEs (Fig. 2a). In eight of the LMEs, the contribution of cephalopods as a direct fishery landing was greater than their ecological support to predator landings. Their commodity contribution exceeded their supportive contribution by a factor of two in the California Current, Gulf of California, and

New Zealand Shelf and by a factor of three in the Patagonian Shelf. The opposite relationship was also observed in eight of the LMEs. In the Celtic-Biscay Shelf, Gulf of Alaska, and southeast Australian shelf the supportive contributions were twice as large as the commodity contributions. In six of the LMEs, including the North Sea, Scotian Shelf, and the Northeast US Continental Shelf, the value of cephalopods as a commodity service and as a supportive service were relatively equal.

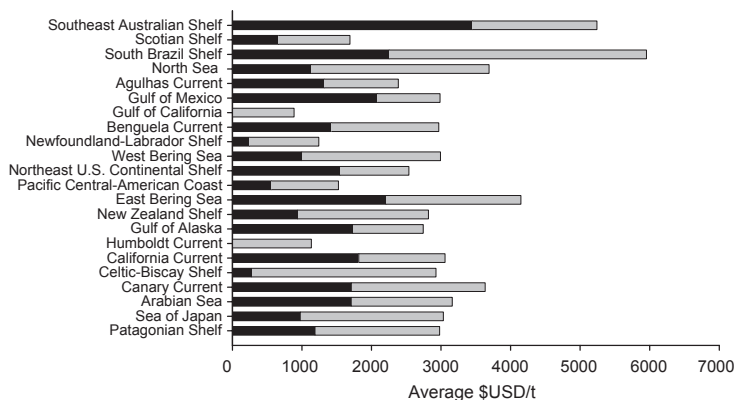
The LMEs differed from the open ocean systems with respect to the value of the two ecosystem services provided by cephalopods. In general, the estimated contributions of cephalopods as commodity to fishery landings were typically highest in the LMEs and the relative importance of their supportive contributions was greatest in the open ocean systems (Fig. 2a). Only the CNP had direct landings of cephalopods and the supportive contribution of cephalopods to fishery landings in this system exceeded their commodity contribution by a factor of 10. A similar pattern was observed for the contribution of cephalopods to fishery landed values (Fig. 2b). The commodity contributions to landed values were greatest in the LMEs whereas the supportive contributions were higher in the open ocean systems. The Gulf of Alaska was the only LME in which the supportive contribution of cephalopods to landed values was on par with the open ocean ecosystems. This is likely an effect of the large contribution of cephalopods to the diet contents of high priced fishes harvested in this region, i.e. Pacific salmon (*Oncorhynchus* spp., Salmonidae).

In two ecosystems, the commodity and supportive contributions of cephalopods were particularly high. In the Patagonian Shelf, the supportive contribution of cephalopods to fishery landings was 14% and their commodity contribution was

approximately 40%. Similar results were found when comparing their contribution to landed values: 15% and 54% of the fishery's monetary value was based on the supportive and commodity services provided by cephalopods, respectively. In the Sea of Japan, supportive and commodity contributions of cephalopods to landings were 11% and 17%, and their supportive and commodity contributions to landed values were 12% and 23%. Overall, the percent contribution of cephalopods to the landed values of the contemporary fisheries followed similar trends as those described for the fisheries landings, although the estimated contributions to landed values were often higher (Fig. 2b).

The trends in the percent contribution of cephalopods as a support service to marine fisheries among ecosystems were robust to uncertainty in our calculations. For example, the ecosystems with the highest point estimates for supportive contribution typically exhibited the highest minimum and maximum estimates of supportive contribution, and vice versa (Fig. 2a,b). This is not surprising because the extent to which the point estimates were inaccurate due to uncertainty in prey energy content and assimilation efficiencies was relatively small in comparison to the differences among ecosystems. In general, the difference between the point estimates of the percent contribution of cephalopods as a support service and the upward or downward deviation was <5%. The range between the upper and lower bounds was typically <10% (Fig. 2a,b).

The average \$USD per tonnes of cephalopods in many of the LMEs was greater than or near the average \$USD per tonnes of major fish predators of cephalopods (Fig. 3). The average price per tonnes of cephalopods exceeded that of the major predators by \$115–2500 in many of the ecosystems. For most

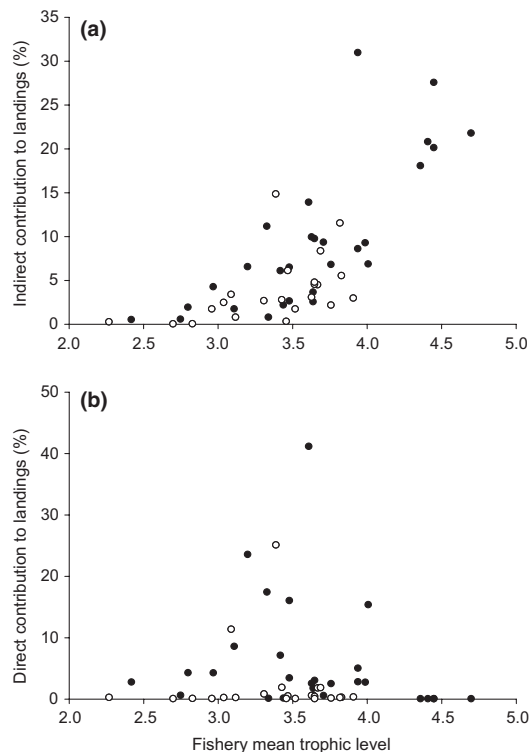


**Figure 3** The average contemporary ex-vessel prices (\$USD tonnes<sup>-1</sup>) of cephalopods (grey bars) and major fish predators of cephalopods (black bars) estimated for each large marine ecosystem. Fishes in which cephalopods comprise ≥20% of the diet composition were considered major predators.

of the systems in which the average prices of cephalopods were less than those of their fish predators, the differences in prices were relatively minor. This finding is counter to the notion that high trophic level species have a higher value per unit mass and it suggests that the recognized expansion of fisheries to lower trophic level species is not necessarily the equivalent of an expansion to lesser value species. The Gulf of Mexico and Southeast Australian Shelf were the only ecosystems in which the average price of fish predators was much greater than the cephalopods (>\$1200). However, in the Gulf of Mexico the average price of cephalopods increased by approximately \$400 USD per tonnes between the two periods. In the Southeast Australian Shelf ecosystem, the major predators of cephalopods included bigeye (*Thunnus obesus*, Scombridae), yellowfin (*Thunnus albacares*, Scombridae) and southern bluefin (*Thunnus maccoyii*, Scombridae) tunas, which had much higher ex-vessel prices than cephalopods. The average price per ton of fish predators were not shown for the Humboldt Current and the Gulf of California system because the top landed fishes were not major predators of cephalopods, i.e. cephalopods composed <20% of their diet. Thus, only the ex-vessel prices of cephalopods are shown (Fig. 3).

The average trophic level of marine fisheries was the best predictor of the magnitude of cephalopod contributions. Estimates of the supportive contribution to fishery landings increased with the average trophic level targeted by the fisheries (Fig. 4a). Fisheries with low average trophic levels are generally dominated by landings of smaller fishes that are unable to consume cephalopods due to size constraints, whereas the landings of fisheries with higher average trophic levels are mostly comprised larger bodied fishes and cephalopods that are less limited by size constraints. Fisheries with average trophic levels within the range of cephalopod trophic levels (3.2–4.0) exhibited the highest contributions of cephalopods to landings (Fig. 4b). The estimates of commodity contributions were lowest in those fisheries with average trophic levels that were not within this range. In other words, the trophic level of the fishery and the commodity contributions to cephalopods are not numerically independent, as the latter is used in the calculation of the former.

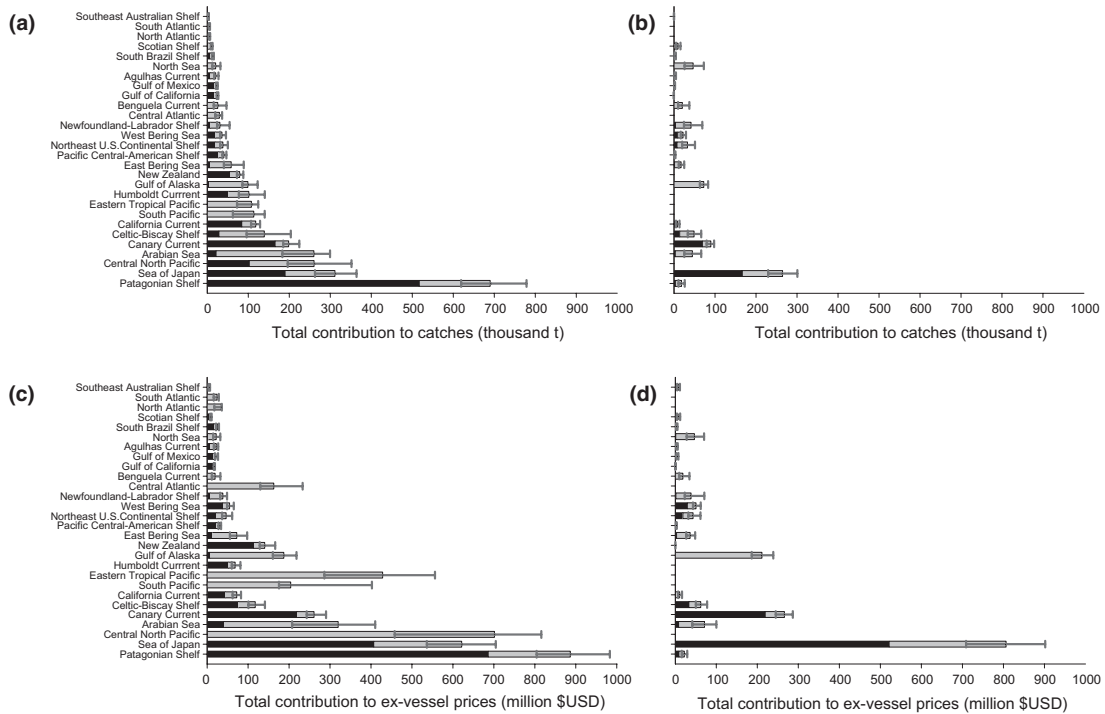
The additional biotic and abiotic factors evaluated in this study were not good predictors of the magnitude of cephalopod contributions. We found



**Figure 4** The supportive (a) and commodity (b) contributions of cephalopods to fishery landings in large marine ecosystems and pelagic marine ecosystems plotted against the mean trophic level of the fisheries in the respective ecosystems. Estimates are based on contemporary data (solid circles) and historical data (open circles; open ocean ecosystems not included).

no relationship between contribution of cephalopods and the primary production rate or the mean trophic level of the ecosystems. Further, we did not find a relationship between the types of LMEs and the cephalopod contributions. For example, the estimated range of the commodity and supportive contributions was relatively similar for the continental shelves, major currents and upwelling zones, gulfs and seas.

Comparisons between the historical and contemporary data revealed that in many LMEs the support service provided by cephalopods increased concomitantly with the rise in cephalopod landings. This pattern was also repeatable when either the point, minimum or maximum estimates were used as an index of their relative contribution (Fig. 5a,b). The supportive contribution to landings increased in 18 of the 22 LMEs and the direct landings increased in all of the LMEs. The estimated increase in the supportive contribution to landings ranged from



**Figure 5** The total contribution of cephalopods to contemporary (a) and historical (b) fishery landings (tonnes) and contemporary (c) and historical (d) fishery landed values (\$USD) for the selected large marine ecosystems and open ocean ecosystems. Commodity contribution, black bars; Point, minimum, and maximum estimates of supportive contribution, grey bars. Note: Historical landings and ex-vessel prices were not readily available for the open ocean ecosystems, thus there are no data presented for these ecosystems in figures (c) and (d).

2000 to 58 000 tonnes between the two periods. The greatest increases were observed in the Patagonian Shelf, Arabian Sea, Celtic-Biscay Shelf, and the Humboldt Current. Decreases in the supportive contributions were only observed in Northeast US Continental Shelf, Newfoundland-Labrador Shelf, Scotian Shelf and North Sea. In contrast to the historical period, contemporary fisheries in these regions were dominated by lower trophic level fishes, such as Atlantic herring (*Clupea harengus*, Clupeidae), Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae) and American sand lance (*Ammodytes americanus*, Ammodytidae), which do not consume cephalopods. Increases in the direct landings observed in all of the ecosystems ranged from 396 to 515 000 tonnes (Fig. 5a,b). The greatest increase was observed in the Patagonian Shelf ecosystem, but the Arabian Sea, Canary Current and California Current exhibited large increases in direct landings as well.

The commodity and supportive services provided by cephalopods to landed values increased over time

(Fig. 5c,d). The supportive contribution to landed values increased in over half of the ecosystems by a range of \$410 thousand USD to \$215 million USD. The direct landed values increased in all of the systems, except the Sea of Japan, by a range of \$730 thousand USD to \$680 million USD.

### Discussion

Our analysis of the contribution of cephalopods to global marine fisheries produced three main findings. First, cephalopods provide substantial ecosystem services in support of fisheries. On average, cephalopods support 15% and 20% of all marine fisheries landings and landed values in the studied ecosystems, respectively. The contributions of cephalopods as a targeted resource were greatest in the coastal LMEs whereas their contributions as sustenance for other commercial nekton were generally highest in the open ocean systems. In the Patagonian Shelf, cephalopods were highly valuable as both a commodity and a supportive service. Second,

the magnitude of estimated contributions among ecosystems appeared to be influenced by the nature of the fisheries, i.e. the species targeted by the fisheries. The contributions of cephalopods as a commodity were highest in ecosystems in which fisheries mainly harvested mid-trophic level species and their supportive contributions were greatest in the systems in which the fisheries targeted apex predators. Third, the commodity and supportive services provided by cephalopods to fisheries landings increased concomitantly in many of the LMEs between historical and contemporary periods. This is an indication of the rising demand of cephalopod resources as well as the lack of a historical precedent of cephalopods withstanding heavy fishing pressure while simultaneously acting as an ecosystem support service. Overall, ecosystems in which cephalopods were found to be valuable to fisheries, both as a targeted resource and an ecological support service, deserve further scrutiny of the trade-offs associated with a potential expansion of cephalopod fisheries.

The contribution of cephalopods in the high seas or open ocean fisheries is clearly different from the LMEs. This is primarily because the high seas fisheries mostly target high trophic level species (e.g. tunas and billfishes) and there is little directed harvesting for cephalopods. This was not always the case for these fisheries: in the 1980s squid were a major target of fisheries across the North Pacific Ocean until a drift netting ban was implemented. However, the priority in the high seas fisheries is currently on the large pelagic fishes, and these fisheries are quite lucrative, particularly in the Pacific Ocean. Thus, an appropriate trade-off for these fisheries may be to set pre-emptive limits on the allowable harvests of squid to protect the productivity of the high seas finfish fisheries that are more economically valuable. This trade-off is in contrast to those potentially faced by fisheries managers in the LMEs. In many LMEs, the value of cephalopods as a commodity was greater than their value as an ecological support service. Thus, from an economic standpoint it may advantageous to increase cephalopod landings in these systems despite the risk of a negative impact on the less valuable cephalopod predators.

The Patagonian Shelf LME is unique in comparison to the other ecosystems because it currently supports the high demands of both cephalopod fisheries and fisheries for cephalopod predators. As a consequence, this ecosystem may be nearing

its threshold of sustaining these simultaneous demands. The average estimate of contemporary cephalopod landings in this system greatly exceeds the estimated landings for the other studied ecosystems. The cephalopod landings are dominated by a single species, the Argentine squid (*Illex argentinus*, Ommastrephidae), which is the most valuable harvested species in this region in terms of both tonnage and monetary value. Cephalopods also compose approximately 38% of the food of the fish in this ecosystem (Haimovici *et al.* 1998), which includes the commercially valuable species Argentine hake (*Merluccius hubbsi*, Merlucciidae), southern blue whiting (*Micromesistius australis*, Gadidae) and hoki (*Macruronus magellanicus*, Merlucciidae). Our analyses of historical fisheries suggest that the high demand on cephalopods in the Patagonian Shelf ecosystem is unprecedented and it remains to be seen whether this situation is sustainable. It is possible that fishery managers in this region may soon be forced to make decisions regarding which fisheries are most desirable and to implement harvest strategies that reflect those decisions.

Confounding the attempts to effectively manage squid fisheries in all marine ecosystems are the climate and environmental conditions that govern their populations (McInnis and Broenkow 1978; Rasero 1994; Pierce 1995; Agnew *et al.* 2005). Fishery removals coupled with climatic changes have had severe effects on the productivity of some commercial fish stocks (Cushing 1995; Parsons and Beckett 1997; Schwartzlose *et al.* 1999), and there is increasing evidence that climate impacts commercial squid stocks as well (Falkland Islands Government 2005). For example, the historically high catch record (1 144 988 tonnes) of *I. argentinus* in the southwest Atlantic in the year 1999 was followed by one of the lowest catch records (511 807 tonnes) in the fishery's history only 4 years later (Chen *et al.* 2007). Recruitment in squid populations is influenced by oceanographic variability (Waluda *et al.* 1999, 2001), and climate change is likely to drive more variability within the environment. Dramatic declines in their landings, and the ensuing impact on their predators, could be potentially avoided by considering environmental factors in the development of management strategies for increasingly targeted squid stocks.

Cephalopods command relatively high ex-vessel prices and are highly available to marine fisheries. These two attributes could explain the rise in the



global cephalopod landings evidenced in recent decades. Our analysis revealed that the contemporary ex-vessel prices of cephalopods are greater than or similar to their major fish predators. Thus, it may have been strategic from an economic standpoint for many fisheries to expand their efforts to targeting cephalopods directly as the landings or availability of cephalopod predators started to level off or decline (Caddy and Rodhouse 1998). In many ecosystems, cephalopod fisheries have expanded gradually; however in other systems, such as the Patagonian Shelf, there has been a rapid development of cephalopod fisheries. The ex-vessel prices of cephalopods also suggest that fisheries do not necessarily replace highly valuable fishes with species of lesser value as they fish down or through marine food webs for more available species (Pauly *et al.* 1998). The rise in the supportive contribution of cephalopods to fisheries landings in many of the studied ecosystems may also be a consequence of the expansion of fisheries over time. In some ecosystems, the rise in supportive contributions could be confounded by the increase in direct landings of cephalopods due to their cannibalistic behaviour. We observed decreases in supportive contributions of cephalopods in only four ecosystems: the Northeast US Continental Shelf, Newfoundland–Labrador Shelf, Scotian Shelf and North Sea. This is likely an effect of the shift in fishing effort towards smaller bodied, lower trophic fishes following declines in the upper trophic level fishes, including groundfish and flatfish (Pauly and Maclean 2003; Essington *et al.* 2006).

Our measures of the contribution of cephalopods to marine fisheries are valuable for making broad-scale comparisons among global ecosystems. We consider our point estimates of their value as a support service to be an index of the relative contribution of cephalopods to the landings and landed values of their predators and not the actual cephalopod biomass required to generate their portion of predator biomass. Similarly, the increase in cephalopod supportive contributions between the historical and contemporary period do not imply increased abundance, biomass, or production of cephalopods, but reflect differences in exploitation patterns by fisheries which they support either directly or indirectly. An accurate account of cephalopod biomass would require further analyses based on species- and (or) ecosystem specific production: biomass ratios, consumption: biomass ratios, trophic efficiencies, growth efficiencies, and

bioenergetics or ECOPATH modelling. However, we consider our minimum and maximum estimates of the relative supportive contribution to be an accurate representation of the deviation surrounding the point estimates. The values of energy density and assimilation efficiencies used to estimate the lower and upper bounds of supportive contribution were reasonable. Thus, the estimated range of supportive contribution within a given ecosystem is likely to capture the maximum extent to which our point estimates could vary due to uncertainty in the energetic content and assimilation efficiency of prey items.

In this study, our efforts focused on the contribution of cephalopods to commercial fisheries and did not include the value of cephalopods as a forage item for conservation species. Consideration of these species could greatly increase the value of cephalopods to marine ecosystems. Past diet studies have shown that cephalopods are a major component in the stomach contents of marine mammals and seabirds (Clarke 1996; Croxall and Prince 1996; Klages 1996). For example in the eastern Bering Sea (EBS), cephalopods may comprise up to 85% of the diet of sperm whales, 16–25% of the diet of baleen and other toothed whales, and 8% of the stellar sea lion diet composition (Aydin *et al.* 2002). Our estimates of the supportive contribution of cephalopods to EBS commercial fisheries were low in comparison to other ecosystems, but their contribution to non-market species is indeed invaluable. Their importance as an ecosystem support service in this region is recognized and reflected in the North Pacific Fisheries Management Council's (NPFMC 2008) decision to consider moving squid from the non-target species management category to the forage fish category. This amendment would prohibit any directed harvesting of squid in the EBS, Aleutian Islands, and/or Gulf of Alaska ecosystems ([http://www.fakr.noaa.gov/npfmc/current\\_issues/non\\_target/non\\_target.htm](http://www.fakr.noaa.gov/npfmc/current_issues/non_target/non_target.htm), accessed June 2008). The importance of cephalopods to the production of conservation species is not unique to the EBS, but is a global phenomenon. Models of the potential competition between marine mammal/seabird populations and commercial fisheries may provide valuable insight into the implications of increased cephalopod landings on these populations in marine ecosystems worldwide.

The predatory role of cephalopods may also need to be considered in a valuation of their contribution to some marine fisheries. The low estimates of

supportive contributions for LMEs compared to the open ocean systems suggest that cephalopods may be more important as a predator than as a prey item in some coastal ecosystems. Cephalopods consume a wide variety of prey, including the juvenile stages of fishes and cephalopods (Clarke 1996; Klages 1996; Rodhouse and Nigmatullin 1996; Smale 1996; Hunsicker and Essington 2006; Field *et al.* 2007), and their voracious feeding behaviour has raised concern over their trophic impact on commercially valuable fishes (Maurer and Bowman 1985; Field *et al.* 2007; Hunsicker and Essington 2008). The predatory and competitive interactions of cephalopods could lessen their value as support service if they have a negative effect on commercial fish production.

An important issue that we do not address in this study is the potential for cephalopod predators to shift their diets in response to prey availability. Prey switching is common among predators (Smale 1996), yet, any effort to improve the accuracy of our estimates by quantifying the effects of prey switching would be overshadowed by the limitations of the diet data. Also, due to the limited number of available diet studies and the paucity of information on predator body sizes, we could not accurately account for how predator diet composition changed among seasons, with ontogeny, or between historical and contemporary periods. We therefore view our estimates as being relatively imprecise and emphasize the large contrasts between ecosystems or periods.

In conclusion, this work represents the first attempt to quantify the ecosystem services provided by cephalopods in support of marine fisheries and to identify potential conflicts between alternative demands. Management agencies are beginning to consider these ecological support services of low-trophic level components of food webs and fisheries in management plans to prevent detrimental impacts on predator populations due to prey harvesting. For example, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) considers the trophic interactions of krill in the development of their fisheries management plans for the Southern Ocean (Kock 2000; Constable 2001, 2004). Krill is a valuable fishery resource in the Antarctic ecosystem and is also the most important prey species in this system (Constable 2004). To ensure the sustainability of commercial fishes and species of conservation concern, CCAMLR uses a precautionary approach when setting catch

limits for krill (Constable 2004). It has been suggested that the trophic relationships of other commercially important forage species, such as herring, should also be considered in fisheries management strategies due to their importance in supporting the production of higher trophic levels (Read and Brownstein 2003; Brodziak *et al.* 2004). Our results lend further support to this notion by identifying numerous ecosystems in which cephalopods were a direct target of fisheries and valuable as a prey for other commercial species. Increased recognition by management agencies of the interconnectedness of commercial cephalopods and fishes may help promote sustainable fishing in these ecosystems under current and increased levels of exploitation.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Energy density values (KJ/g) were identified for the following list of prey items and were used to estimate the supportive contribution of cephalopods to fishery landings and landed values in 28 global marine ecosystems. References for the energy density values can be identified by their source code at the bottom of the appendix.

**Appendix S2.** List of peer-reviewed publications, reports, and theses from which predator food habits data were obtained for each ecosystem analyzed in the present study.

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