The global contribution of forage fish to marine fisheries and ecosystems

Ellen K Pikitch[1,†], Konstantine J Rountos[1,†], Timothy E Essington[2], Christine Santora[1], Daniel Pauly[3], Reg Watson[3], Ussif R Sumaila[3], P Dee Boersma[4], Ian L Boyd[5], David O Conover[1], Philippe Cury[6], Selina S Heppell[7], Edward D Houde[8], Marc Mangel[9], Éva Plagányi[10], Keith Sainsbury[11], Robert S Steneck[12], Tess M Geers[1], Natasha Gownaris[1] & Stephan B Munch[1]

[1]School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY, 11794-5000, USA; [2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, 98195-5020, USA; [3]Fisheries Centre, University of British Columbia, Vancouver, BC, Canada, V6T 1Z4; [4]Department of Biology, University of Washington, Seattle, WA 98195-1800, USA; [5]NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 8LB, UK; [6]Institut de Recherche pour le Développement UMR EME-212, Centre de Recherche Halieutique Méditerranéenne et Tropicale, BP 171, 34203, Séte Cedex, France; [7]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-4501, USA; [8]University of Maryland, Center for Environmental Science, Cambridge, MD 21613, USA; [9]Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, USA; [10]CSIRO Marine and Atmospheric Research Hobart, Tasmania 7000, Australia; [11]Institute of Marine and Antarctic Science, University of Tasmania, Sandy Bay, Tasmania, Australia; [12]School of Marine Sciences, University of Maine, Walpole, ME, 04573, USA,

Abstract

Forage fish play a pivotal role in marine ecosystems and economies worldwide by sustaining many predators and fisheries directly and indirectly. We estimate global forage fish contributions to marine ecosystems through a synthesis of 72 published Ecopath models from around the world. Three distinct contributions of forage fish were examined: (i) the ecological support service of forage fish to predators in marine ecosystems, (ii) the total catch and value of forage fisheries and (iii) the support service of forage fish to the catch and value of other commercially targeted predators. Forage fish use and value varied and exhibited patterns across latitudes and ecosystem types. Forage fish supported many kinds of predators, including fish, seabirds, marine mammals and squid. Overall, forage fish contribute a total of about $16.9 billion USD to global fisheries values annually, i.e. 20% of the global ex-vessel catch values of all marine fisheries combined. While the global catch value of forage fisheries was $5.6 billion, fisheries supported by forage fish were more than twice as valuable ($11.3 billion). These estimates provide important information for evaluating the trade-offs of various uses of forage fish across ecosystem types, latitudes and globally. We did not estimate a monetary value for supportive contributions of forage fish to recreational fisheries or to uses unrelated to fisheries, and thus the estimates of economic value reported herein understate the global value of forage fishes.

Keywords Ecosystem service, ecosystem-based management, fisheries value, forage fish, supportive values, trade-offs

Introduction

'Forage fish' species are small or intermediate-sized pelagic species (e.g. sardine, anchovy, sprat, herring, capelin, krill) that are the primary food source for many marine predators, including mammals (Thompson *et al.* 1996; Pauly *et al.* 1998; Weise and Harvey 2008), seabirds (Crawford and Dyer 1995; Jahncke *et al.* 2004; Furness 2007; Daunt *et al.* 2008) and larger fish (Walter and Austin 2003; Butler *et al.* 2010; Logan *et al.* 2011; Magnussen 2011). Forage fish feed on zooplankton and phytoplankton and are important conduits of energy transfer in food webs for many marine ecosystems, from the tropics to the Earth's poles (Cury *et al.* 2000, 2003; Fréon *et al.* 2005; Bakun *et al.* 2010).

Fisheries for forage fish occur across broad latitudinal ranges (FAO 2010) and constitute a large and growing fraction of the global wild marine fish catch (Alder *et al.* 2008). In addition, five of the top ten fish species caught (by weight) in 2008 were forage fish species. Notably, the Peruvian anchoveta (*Engraulis ringens*, Engraulidae) supports the largest fishery in the world (FAO 2010). Nearly 90% of the global forage fish catch is used by reduction industries, which produce fish meal and fish oil (Alder *et al.* 2008). While economic studies of forage fish have focused primarily on their role as a directly harvested commodity (Herrick *et al.* 2009; Mullon

et al. 2009; Tacon and Metian 2009), few have attempted to quantify the indirect economic contributions that these species provide (Hannesson *et al.* 2009; Herrick *et al.* 2009; Hannesson and Herrick 2010). Accounting for the indirect or support service values that prey species provide to other fisheries is inherently more difficult (Hannesson *et al.* 2009; Hannesson and Herrick 2010; Hunsicker *et al.* 2010), but doing so can provide important information to assess the trade-offs between exploiting forage fish and other species in the same marine ecosystem.

There has been growing scientific consensus for the application of ecosystem-based management approaches (Pikitch *et al.* 2004; McLeod *et al.* 2005; McLeod and Leslie 2009) in contrast to traditionally applied single-species approaches (Beddington *et al.* 2007; FAO 2010). Single-species management generally seeks to maintain populations of a target species yet ignores most ecosystem factors. Even in cases where forage fish are well managed from a single-species perspective (i.e. overfishing is not occurring), a form of 'ecosystem overfishing' *sensu* Murawski (2000) can occur, whereby depleted abundance of forage fish may negatively affect the ecosystem (Gislason 2003; Coll *et al.* 2008). Implementing an ecosystem-based approach to the management of forage fisheries seems especially warranted (Pikitch *et al.* 2004; Richerson *et al.* 2010; Smith *et al.* 2011), as these

species exhibit strong trophic linkages and fluctuate in abundance along with seasonal, annual and inter-decadal variations in oceanographic forces (Barber and Chavez 1983; Francis *et al.* 1998; Polovina *et al.* 2001; Chavez *et al.* 2003).

Human decision-making is often influenced by comparisons of monetary values or trade-offs between different products or services (Polasky and Segerson 2009). By quantifying the value of these ecosystem products and services, such trade-offs, and the impacts of degrading ecosystems, are made more explicit (Costanza *et al.* 1997; Balmford *et al.* 2002; Barbier *et al.* 2011). The majority of economic analyses conducted for forage fish fisheries have been one dimensional (Herrick *et al.* 2009), focusing on factors or management strategies affecting the direct value of these species as a landed commodity. Only a handful of studies have enumerated the indirect values that species targeted by fisheries provide (Hannesson *et al.* 2009; Hannesson and Herrick 2010; Hunsicker *et al.* 2010; Kamimura *et al.* 2011). Because of their key position in marine food webs, the overall global importance of forage fish to fisheries and ecosystems has likely been significantly understated.

This study provides the first global estimate of forage fish value to commercially important marine fisheries and enumerates the contributions of forage fish to ecosystem predator production. We synthesized data obtained from Ecopath models representing marine ecosystems around the world. This approach allowed for broad relationships to be detected and described by summarizing data from multiple independent studies (Gurevitch and Hedges 1999), including information on feeding habits, production and catch rates. We estimated the contribution that forage fish species make to: (i) the diets and production of all forage fish predators within each modelled ecosystem, (ii) forage fish fisheries, in terms of catch and catch value and (iii) the catch and value of other commercially targeted predator species (e.g. tunas, cod, striped bass), based on their diet dependence on forage fish. We compared and contrasted these contributions and values, and investigated the effects of model structure, ecosystem type and latitude (Table 1). Finally, we use the relationships and properties revealed by these models, together with estimates of catch values at the scale of economic exclusive zones (EEZ) and high seas areas (HSA), to estimate the total value that forage fish contribute to global marine fisheries.

Methods

Compilation and synthesis of Ecopath models

Of the more than 200 Ecopath models that have been published (Fulton 2010), 72 were obtained and selected for this synthesis. The requirements for inclusion in our analysis were that the Ecopath models had to represent a marine or estuarine ecosystem in a relatively recent state (within the last 40 years), include at least one forage fish model group, and have all the necessary data and parameters openly available. The majority of Ecopath models used (90%, 65 out of 72) represented ecosystems within the past 30 years. We obtained Ecopath models from peer-reviewed publications ($n = 33$), technical reports ($n = 36$) and theses/dissertations ($n = 3$) (Table 1). Ecopath models that were not included failed to have at least one forage fish model group, did not have data openly available, represented older time periods (>40 years old), or a combination of all three. Collected models spanned a wide geographical range and provided relatively good global coverage of most coastal ocean areas and marine ecosystem types, with the exception of the Indian Ocean, which is poorly studied compared with other ocean areas (De Young 2006) (Fig. 1). When available, we also obtained Ecopath pedigree index information (Christensen and Walters 2004; Christensen *et al.* 2005) to assess data quality of the models.

To examine the patterns in forage fish contributions and values, we grouped Ecopath models by latitude and by ecosystem type. Latitude groupings consisted of three categories: Tropical-Subtropical (less than 30° N – less than 30° S), Temperate (greater than or equal to 30° N – 58° N and greater than or equal to 30° S – 58° S) and High latitude (greater than 58° N and greater than 58° S). We separated upwelling ecosystem models from the latitude groupings due to the dominant roles forage fish catches play in these ecosystems. Ecosystem types included: upwelling ecosystems, semi-enclosed ecosystems, non-upwelling coastal ecosystems, tropical lagoon ecosystems, open ocean ecosystems, Arctic high latitude ecosystems, and Antarctic ecosystems. All models were categorized into only one ecosystem type and latitude group (Table 1).

In this analysis we define 'forage fish' as species that occupy an important intermediary trophic position and that retain that ecological role throughout their life. We thus excluded from our

Table 1 List of the 72 Ecopath models used in this synthesis. Full model references can be found in Appendix S1 (available in the online version of this article).

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
1	Western Bering Sea[1]	1980s–1990s	High latitude	Arctic high latitude	254 000	–	48	22	3	Yes	Yes	Aydin et al. (2002)
2	Eastern Bering Sea (1)	1980s	High latitude	Arctic high latitude	484 508	–	25	14	1	Yes	No	Trites et al. (1999)
3	Eastern Bering Sea (2)	1980s–1990s	High latitude	Arctic high latitude	485 000	–	38	19	2	Yes	No	Aydin et al. (2002)
4	Prince William Sound, Alaska (1)[2]	1980–89	High latitude	Arctic high latitude	8800	0.351	19	6	2	Yes	No	Dalsgaard and Pauly (1997)
5	Prince William Sound, Alaska (2)[3]	1994–96	High latitude	Arctic high latitude	9000	0.675	48	20	5	Yes	No	Okey and Pauly (1999)
6	Hecate Strait, Northern British Columbia	2000	High latitude	Non-upwelling coastal	70 000	–	50	34	5	Yes	Yes	Ainsworth et al. (2002)
7	Northern California Current	1990	Upwelling	Upwelling	69 176	–	63	38	3	Yes	Yes	Field et al. (2006)
8	Gulf of California	1978–79	Tropical-Subtropical	Semi-enclosed	27 900	–	25	8	1	Yes	No	Arreguín-Sánchez et al. (2002)
9	Huizachi-Caimanero lagoon complex, Mexico	1970–2000	Tropical-Subtropical	Tropical lagoon	175	0.750	26	6	1	Yes	No	Zetina-Rejón et al. (2003)
10	Golfo de Nicoya, Costa Rica	1980s–1990s	Tropical-Subtropical	Tropical lagoon	1530	–	20	10	1	Yes	No	Wolff et al. (1998)
11	Golfo Dulce, Costa Rica	1960–90s	Tropical-Subtropical	Tropical lagoon	750	–	20	9	1	No	No	Wolff et al. (1996)
12	Eastern Subtropical Pacific Ocean[4]	1993–97	Tropical-Subtropical	Open ocean	32 800 000	–	40	31	2	Yes	No	Olson and Watters (2003)
13	Northern Humboldt Current[5]	1995–96	Upwelling	Upwelling	165 000	0.638	32	15	3	Yes	No	Tam et al. (2008)
14	Northern Humboldt Current[6]	1997–98	Upwelling	Upwelling	165 000	0.638	32	16	3	Yes	No	Tam et al. (2008)
15	Sechura Bay, Peru	1996	Upwelling	Upwelling	400	0.462	22	5	1	Yes	No	Taylor et al. (2008)
16	Central Chile	1998	Upwelling	Upwelling	50 042	–	21	8	5	Yes	Yes	Neira et al. (2004)
17	Tongoy Bay, Chile	1980s–1990s	Upwelling	Upwelling	60	–	17	5	1	No	No	Wolff (1994)
18	Falkland Islands	1990s	Temperate	Non-upwelling coastal	527 000	–	44	32	2	Yes	Yes	Cheung and Pitcher (2005)
19	South Brazil Bight	1998–99	Tropical-Subtropical	Non-upwelling coastal	97 000	–	25	6	2	Yes	No	Gasalla and Rossi-Wongtschowski (2004)

Table 1 Continued.

| Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
20	Caeté Estuary, Brazil	1999	Tropical-Subtropical	Non-upwelling coastal	220	–	18	4	1	Yes	No	Wolff *et al.* (2000)
21	Gulf of Paria	1980s–1990s	Tropical-Subtropical	Tropical lagoon	7600	–	23	11	1	No	No	Manickchand-Heileman *et al.* (2004)
22	Northeastern Venezuela shelf	1970s–1980s	Tropical-Subtropical	Non-upwelling coastal	30 000	–	16	10	1	Yes	No	Mendoza (1993)
23	Gulf of Salamanca	1997	Tropical-Subtropical	Tropical lagoon	955	0.743	18	6	1	Yes	No	Duarte and García (2004)
24	Celestun lagoon, Mexico	2001	Tropical-Subtropical	Tropical lagoon	28	0.362	19	1	2	Yes	No	Vega-Cendejas and Arreguin-Sánchez (2001)
25	Terminos lagoon, Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	2500	–	20	5	1	No	No	Manickchand-Heileman *et al.* (1998a)
26	Southwestern Gulf of Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	65 000	–	19	9	1	No	No	Manickchand-Heileman *et al.* (1998b)
27	Laguna Alvarado, Mexico	1991–94	Tropical-Subtropical	Tropical lagoon	62	0.500	30	9	2	Yes	No	Cruz-Escalona *et al.* (2007)
28	Tampamachoco lagoon, Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	15	–	23	6	1	No	No	Rosado-Solórzano and Guzmán del Próo (1998)
29	Gulf of Mexico	1950–2004	Tropical-Subtropical	Non-upwelling coastal	1 530 387	–	61	23	6	No	No	Walters *et al.* (2008)
30	West Florida shelf	1980s–1990s	Tropical-Subtropical	Non-upwelling coastal	170 000	–	59	18	2	No	No	Okey *et al.* (2004)
31	Chesapeake Bay	2000	Temperate	Non-upwelling coastal	10 000	0.450	45	17	5	Yes	No	Christensen *et al.* (2009)
32	Gulf of Maine	1977–86	Temperate	Non-upwelling coastal	90 700	–	30	12	2	Yes	No	Heymans (2001)
33	Northern Gulf of St. Lawrence	1985–87	Temperate	Non-upwelling coastal	103 812	0.651	31	19	3	Yes	No	Morissette *et al.* (2003)
34	Newfoundland	1995	Temperate	Non-upwelling coastal	495 000	0.396	50	30	4	Yes	No	Heymans and Pitcher (2002)
35	Lancaster Sound region, Canada	1980s	High latitude	Arctic high latitude	97 698	–	32	2	1	No	No	Mohammed (2001)
36	West Greenland	1991–92	High latitude	Arctic high latitude	63 500	0.439	12	4	1	Yes	No	Pedersen (1994)

Table 1 Continued.

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
37	Icelandic shelf	1997	High latitude	Arctic high latitude	115 000	0.295	21	10	2	No	No	Mendy (1999)
38	Barents Sea (1)	1990	High latitude	Arctic high latitude	1 400 000	—	41	18	5	Yes	No	Blanchard et al. (2002)
39	Barents Sea (2)	1995	High latitude	Arctic high latitude	1 400 000	—	41	18	5	Yes	No	Blanchard et al. (2002)
40	Baltic Sea	1974–2000	Temperate	Semi-enclosed	396 838	—	16	5	4	Yes	No	Harvey et al. (2003)
41	North Sea	1981	Temperate	Non-upwelling coastal	570 000	—	25	8	4	Yes	Yes	Christensen (1995)
42	English Channel	1995	Temperate	Non-upwelling coastal	89 607	—	48	15	4	Yes	No	Stanford and Pitcher (2004)
43	Western English Channel	1994	Temperate	Non-upwelling coastal	56 452	—	52	20	4	Yes	No	Araújo et al. (2005)
44	Bay of Mont. St. Michel, France	2003	Temperate	Non-upwelling coastal	250	—	19	1	1	Yes	No	Arbach Leloup et al. (2008)
45	Cantabrian Sea shelf	1994	Temperate	Non-upwelling coastal	16 000	0.669	28	9	2	Yes	No	Sánchez and Olaso (2004)
46	Azores Archipelago	1997	Temperate	Non-upwelling coastal	584 000	0.409	44	15	1	Yes	No	Guénette and Morato (2001)
47	Northwestern Mediterranean Sea	1994	Temperate	Semi-enclosed	4500	—	23	10	3	Yes	No	Coll et al. (2006)
48	Orbetello lagoon, Italy	1996	Temperate	Non-upwelling coastal	27	—	9	4	1	Yes	No	Brando et al. (2004)
49	Northern & Central Adriatic Sea	1990s	Temperate	Semi-enclosed	55 500	0.657	40	16	3	Yes	No	Coll et al. (2007)
50	Black Sea	1989–91	Temperate	Semi-enclosed	423 000	—	11	4	1	Yes	No	Örek (2000)
51	Atlantic coast of Morroco	1984	Upwelling	Upwelling	586 900	0.382	38	19	2	Yes	No	Stanford et al. (2004)
52	Banc d'Arguin, Mauritanie	1988–98	Tropical-Subtropical	Non-upwelling coastal	10 000	0.537	22	7	1	Yes	No	Sidi and Diop (2004)
53	Cape Verde Archipelago	1981–85	Tropical-Subtropical	Non-upwelling coastal	5394	—	31	9	1	Yes	No	Stobberup et al. (2004)
54	Central Atlantic Ocean	1997–98	Temperate	Open ocean	18 419 191	—	39	14	1	Yes	No	Vasconcellos and Watson (2004)
55	Gambian continental shelf	1995	Tropical-Subtropical	Non-upwelling coastal	4000	—	23	7	2	No	No	Mendy (2004)

Table 1 Continued.

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
56	Guinea-Bissau continental shelf	1990–92	Tropical-Subtropical	Non-upwelling coastal	40 816	–	32	12	2	Yes	No	Amorim *et al.* (2004)
57	Senegambia	1990	Tropical-Subtropical	Non-upwelling coastal	27 600	–	18	7	2	Yes	No	Samb and Mendy (2004)
58	Guinean continental shelf	2005	Tropical-Subtropical	Non-upwelling coastal	42 969	–	35	21	2	Yes	No	Gascuel *et al.* (2009)
59	Southern Benguela Current	1990	Upwelling	Upwelling	220 000	–	32	15	4	Yes	No	Shannon *et al.* (2003)
60	South Orkneys/South Georgia	1990s	High latitude	Antarctic	1 880 000	–	30	22	2	Yes	Yes	Bredesen (2004)
61	Antarctic Peninsula	1991–2001	High latitude	Antarctic	3400	–	39	20	2	Yes	Yes	Erfan and Pitcher (2005)
62	Kerguelen Archipelago EEZ	1987–88	Temperate	Non-upwelling coastal	575 100	–	23	15	2	Yes	Yes	Pruvost *et al.* (2005)
63	Maputo Bay, Mozambique	1980s–1990s	Tropical-Subtropical	Non-upwelling coastal	1100	–	10	4	1	Yes	No	Paula e Silva *et al.* (1993)
64	Great Barrier Reef, Australia	2000	Tropical-Subtropical	Tropical lagoon	325 848	–	30	12	2	No	No	Gribble (2005)
65	Darwin Harbour, Australia	1990–2000	Tropical-Subtropical	Non-upwelling coastal	250	0.375	21	5	1	No	No	Martin (2005)
66	Brunei Darussalam	1989–90	Tropical-Subtropical	Tropical lagoon	7396	–	13	4	1	Yes	No	Silvestre *et al.* (1993)
67	Terengganu, Malaysia	1980s	Tropical-Subtropical	Tropical lagoon	1050	–	13	2	2	Yes	No	Liew and Chan (1987)
68	Hong Kong, China	1990s	Tropical-Subtropical	Non-upwelling coastal	1680	–	37	12	1	No	No	Buchary *et al.* (2002)
69	Tapong Bay, Taiwan	1999–2001	Tropical-Subtropical	Tropical lagoon	4	0.820	18	1	2	No	No	Lin *et al.* (2006)
70	East China Sea	1997–2000	Tropical-Subtropical	Open ocean	770 000	0.636	45	19	6	Yes	No	Jiang *et al.* (2008)
71	Bohai Sea	1982–83	Temperate	Non-upwelling coastal	77 000	–	13	5	1	Yes	No	Tong *et al.* (2000)
72	Central North Pacific	1990s	Tropical-Subtropical	Open ocean	9 888 350	–	25	20	2	No	No	Cox *et al.* (2002)

[1]48 group model, [2]pre-oil spill model, [3]post-oil spill model, [4]ETP7 model, [5]La Niña model, [6]El Niño model. MG = Model groups, PMG = Predator model groups, FFMG = Forage fish model groups.
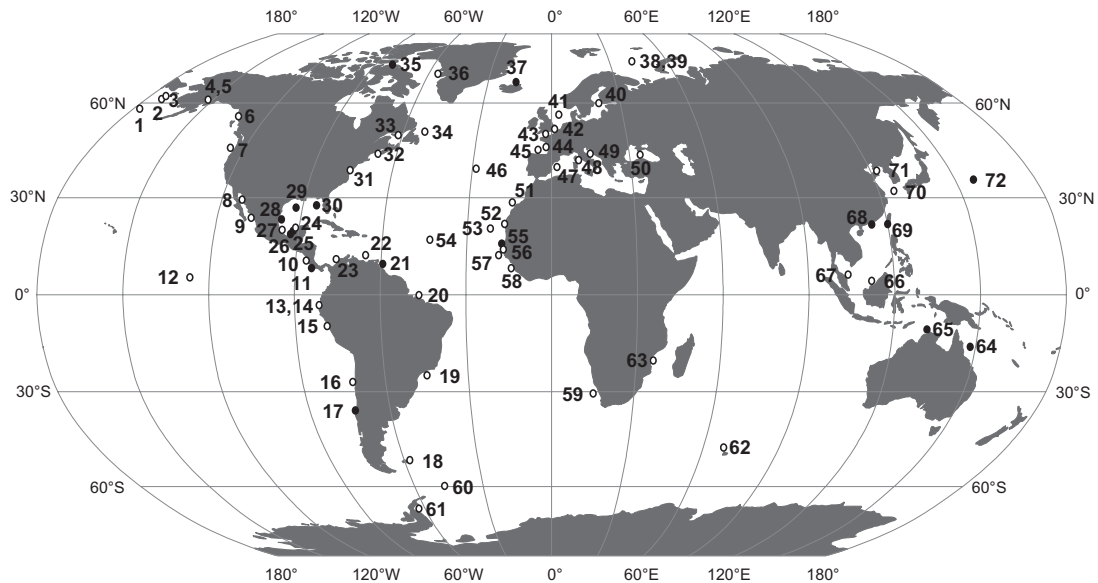
Figure 1 Approximate locations of the 72 Ecopath models used in this synthesis. Ecopath models where monetary value could (white circles) and could not (black circles) be calculated. Model numbers correspond to Table 1.

definition species that assume this role early in life but later move into higher trophic categories as they age (e.g. North Pacific hake, Blue whiting, Alaska pollock).

Data extraction

We extracted model groups, catch data, diet composition matrices, biomass data, production-to-biomass ratios and model area (km^2) from tables in Ecopath model publications and transferred them into separate Microsoft$^©$Excel spreadsheets. When necessary, we converted all Ecopath catch and biomass data not conforming to the standard Ecopath units for catch (tonne km^{-2} year^{-1}) and biomass (tonne km^{-2}).

The majority (83%) of Ecopath models in this analysis had data on total catch (landings plus discards). The remaining 17% (12 out of 72) of the models only published landings data with no estimates of discards. For these 12 models we assumed that discards were zero in our analysis. Discards represent approximately 8% of the marine fisheries catch by weight globally but vary greatly among species and ecosystems (Kelleher 2005).

Ecopath models contain interactive 'groups' which can be composed of either single or multiple species that share similar life histories or ecological functions (Polovina 1984). We used the Ecopath models assembled with the original model groups as specified by the model authors. The published models generally included a list of species or taxa constituting each model group. When such taxonomic information was provided, we used this information to create an inventory of all species. In this study, we classified a model group as a forage fish group whenever at least one forage fish species was included. For instance, if an anchovy species was a component of a larger model group called 'Small Pelagics', along with gobies and juvenile mackerels, then we considered this group as a forage fish group, even though other species in that group may not necessarily meet our definition of forage fish. The majority (65% or 105 out of 161) of forage fish model groups consisted entirely of forage fish species. Of the remaining 56 forage fish model groups, 30 were discerned to be dominated by forage fish species, while information on the preponderance of forage fish species was lacking for the other 26 model groups. The one exception to our classification of forage fish model groups applied to krill (Order: Euphausiaea), which were only represented as separate model groups in 9 of the 72 Ecopath models in this analysis (Table 1). In the few remaining Ecopath models where krill were present in the ecosystem but not as a separate model group, they were grouped into various 'Zooplankton' groups. We chose to exclude these 'Zooplankton' model groups as forage fish groups in this analysis and only included contributions of krill from models

with defined krill model groups. We acknowledge that this modelling approach may cause differences between ecosystems in terms of forage fish contributions (i.e. those that have a separate krill group and those that do not) but assumed in this analysis that if model authors grouped krill separately it was due to their perceived importance in the ecosystem. We considered it was more appropriate to include krill groups as forage fish in this analysis when present than to completely exclude them.

Importance of forage fish to ecosystem predators

We identified forage fish predators in all models and their dependence on forage fish (percent of forage fish in diet) from the respective model diet matrix. We defined forage fish predators as model groups whose diets contained any fraction of one or more forage fish model groups (i.e. diet of >0% forage fish). This definition allowed for forage fish species to be included as forage fish predators, if their diet consisted of forage fish. This rarely occurred, with only 3.9% (35 out of 895) of forage fish predators also included as forage fish. Forage fish predators were then categorized into the following dependence groups: (i) low dependence on forage fish (>0 to <25%), (ii) moderate dependence (≥ 25 to <50%), (iii) high dependence (≥ 50 to <75%) and (iv) extreme dependence on forage fish ($\geq 75\%$).

We estimated the portion of each forage fish predator's production supported by forage fish across all ecosystem models using equations modified from Hunsicker *et al.* (2010). First, we calculated the total annual production (P_j, units: tonne km^{-2} $year^{-1}$) of each forage fish predator group j in each Ecopath model using Equation (1), in which predator group j's biomass (B_j, units: tonne km^{-2}) was multiplied by that respective predator group's production-to-biomass ratio ($P\ B^{-1}$, units: $year^{-1}$).

$$P_j = B_j \left(\frac{P}{B}\right)_j \qquad (1)$$

Second, we found the portion of each predator group's total annual production ($P_{i,j}$) supported by forage fish prey groups (i), by multiplying predator group j's respective diet dependence on forage fish ($D_{i,j}$) by P_j using Equation (2).

$$P_{i,j} = D_{i,j} P_j \qquad (2)$$

The total support service contribution of forage fish to ecosystem predator production (S_z) therefore can be found using Equation (3), as the product of

($D_{i,j}$) and (P_j) summed over all forage fish groups (i) and predator groups (j) in an ecosystem.

$$S_z = \sum_j \sum_i D_{i,j} P_j \qquad (3)$$

Hunsicker *et al.* (2010) showed that $D_{i,j}$ is equivalent to the contribution of prey group i to predator group j's production ($P_{i,j}$) when assimilation and energy content of prey items are roughly equivalent. In the absence of detailed data on these variables, we assumed they were equal to one another but note that our analysis underestimates $P_{i,j}$ because of the generally high energy content of forage fish species (Van Pelt *et al.* 1997; Anthony *et al.* 2000) compared to most predators. Thus, our estimates for the support service contribution of forage fish to ecosystem predator production can be considered conservative in this regard.

Direct and support service contributions of forage fish to commercial fisheries

We calculated the contributions of forage fish to fisheries in terms of catch (tonne km^{-2} $year^{-1}$) for all 72 Ecopath models and catch value (2006 USD km^{-2} $year^{-1}$) for a subset of models that had adequate taxonomic information ($n = 56$). Ecopath models were grouped into categories based on ecosystem type and latitude of the model (Table 1). We used a global ex-vessel price database, developed by Sumaila *et al.* (2007) to obtain ex-vessel 'real' price data for all fished species in our Ecopath models. Ex-vessel 'real' price is defined as the actual prices that fishermen receive for their products before processing and is hereafter simply referred to as price. In this analysis, we use 'value' to refer to ex-vessel fish price times quantity (gross returns) and not economic profit (net returns).

We obtained total catch data for every country participating in fisheries in a respective Large Marine Ecosystem (LME) in year 2006 from the Sea Around Us project LME database (Watson *et al.* 2004; www.seaaroundus.org), and used the ex-vessel price database to compile country specific ex-vessel price data for every species in the 56 models. Information on every fishing country in each LME and their respective total catch can be accessed on the Sea Around Us project LME database website (www.seaaroundus.org). To account for differences in prices between countries operating in a given LME, we calculated a weighted average based on the total catch in 2006 of all participating countries within that LME. When

model groups consisted of two or more species, the ex-vessel price for the model group was found by averaging the ex-vessel prices for all respective species within, which were each weighted by the catches of participating countries. We used these averaged ex-vessel model group prices to calculate fisheries value (2006 USD km^{-2} year^{-1}) for each respective model group in all 56 Ecopath models.

For small geographic areas (e.g. estuaries, lagoons, and small coastal areas), we assumed that only the country surrounding these waters fished them. We made this assumption because detailed information about which specific countries fish within an Ecopath model area is not usually published. For the few Ecopath models that were located outside a defined LME area (e.g. Central North Pacific Ocean, Central Atlantic Ocean and Eastern Subtropical Pacific Ocean), we assumed participating fishing countries to be those nearest to, and surrounding, the model locations. Ecopath models of island countries and territories that fell outside of LME boundaries (e.g. the Azores Archipelago) were assumed to be fished only by that country, or the country of which it is a territory.

We estimated forage fish catch by summing the catch of all forage fish model groups in each respective ecosystem model. Catch value (2006 USD km^{-2} year^{-1}) was estimated for each respective forage fish model group by multiplying the catch (tonne km^{-2} year^{-1}) by the respective ex-vessel price (2006 USD tonne^{-1}) (Sumaila *et al.* 2007). Similarly, we summed catch values for all forage fish model groups to find the total forage fish catch value (2006 USD km^{-2} year^{-1}) for each Ecopath model. We estimated the support service contributions of forage fish to the catch (S_C) and catch value (S_V) of other commercially targeted model groups by using Equation (3), except that the predator group's total annual production (P_j) was replaced by the catch (C_j, Equation 4) and catch value (V_j, Equation 5) of each predator group *j*.

$$S_c = \sum_j \sum_i D_{i,j} C_j \qquad (4)$$

$$S_V = \sum_j \sum_i D_{i,j} V_j \qquad (5)$$

Forage fish contribution to global fisheries value

Forage fish species contribute to the value of global fisheries in two important ways: (i) by their direct catch value and (ii) by their support service as prey to the value of other commercially targeted species. Using forage fish value estimates for these contributions from each Ecopath model, we extrapolated to Exclusive Economic Zone (EEZ) or High Seas Area (HSA) regions to derive global estimates. We worked at the scale of EEZs and HSAs because independent estimates of forage fish catch values were available at this scale (Sumaila *et al.* 2007) to complement the values we estimated in Ecopath models. We assumed that a single Ecopath model representing an area within an EEZ or HSA region provided a reasonable depiction of the relationship between the support service value of forage fish and the total fisheries value for the entire region. A breakdown of the actual area covered by our Ecopath models as a percentage of the total EEZ/HSA area or the total Inshore fishing area (IFA) can be found in Table S1 (see Appendix S2). The IFA is defined by the Sea Around Us Project database (www.seaaroundusproject.org) as the area between the shoreline and whichever comes first, either the 200 m bathycline or a distance of 50 km from the shoreline. The majority of the global marine fisheries catch value (78%) and forage fish catch value (97%) is derived from IFAs (Sumaila *et al.* 2007)(www.seaaroundusproject. org). A summary of Ecopath model coverage in terms of EEZ/HSA or IFA area and fisheries value is provided in Table S2 (see Appendix S2). When multiple Ecopath models were available for a given EEZ or HSA region, we used average values weighted by the geographic area covered by each ecosystem model. We quantified global forage fisheries value by summing the value of forage fish across all EEZs and HSAs in the Sea Around Us project database. The majority of forage fish species in these databases were separated into two commercial groups, 'Herring-likes' and 'Anchovies'. We assumed that the total direct forage fish catch value for each respective EEZ and HSA was the sum of these two commercial groups. When data on 'Herring-likes' and 'Anchovies' were missing from this database, we used data available for forage fish categorized by species group. This method may slightly underestimate forage fisheries value, as it did not include some forage fish species that were grouped into other non-forage fish commercial groups.

To estimate the global support service value of forage fish to other commercially targeted species, we extrapolated the values estimated for each

Ecopath model to each corresponding EEZ and HSA region. To do this, we used Ecopath models with value data available and calculated an Ecopath value ratio (EVR) using Equation (6). In Equation (6), the catch value of forage fish predators supported by forage fish (*Sv*) was divided by the total fishery catch value (*y*) of the Ecopath model, excluding non-cephalopod, non-krill invertebrates (e.g. other decapods, bivalves). By assuming that EVRs found in our Ecopath models are representative of the larger EEZs or HSAs in which they are located, we calculated the total support service value ($Supportive) of forage fish in each EEZ and HSA. Using Equation (7) we multiplied the respective EVR for an EEZ or HSA by the total fishery catch value (excluding non-cephalopod, non-krill invertebrates) for that area calculated from the Sea Around Us database ($SAUP).

$$EVR = \frac{Sv}{y} \qquad (6)$$

$$\$Supportive = EVR \times \$SAUP \qquad (7)$$

Ecopath models were available for 25% (64 out of 257) of the world's EEZs and HSAs, which represents 33% of the total EEZ/HSA area (Table S2, Appendix S2). In the majority (36 out of 64) of these EEZ/HSA areas, Ecopath model coverage was >50% of the respective EEZ/HSA area (see Appendix S2, Tables S1 and S2). These EEZ/HSAs constitute 39% of the global marine catch value (2006 $USD) excluding non-cephalopod and non-krill invertebrates (i.e. other decapods, bivalves) and 53% of the global forage fish catch value (2006 $USD) (Table S2, Appendix S2). Ecopath model coverage of IFAs was even greater, representing 47% of the total area (km^2) (Table S2, Appendix S2). An additional 86 EEZs and HSAs (see Table S1, Appendix S2), which did not have Ecopath models, were included under the assumption that the Ecopath model in the EEZ or HSA immediately adjacent was representative of that neighbouring EEZ or HSA. These EEZs and HSAs represented an additional 28% of the global forage fish catch value to fisheries. The remaining 107 EEZs or HSAs did not have Ecopath models or an adjacent neighbour with an Ecopath model (e.g. isolated islands) and represented only 19% of the global forage fish value to fisheries. In these EEZ/HSA areas, we applied an EVR based on the average of EVRs from other Ecopath models in the same latitudinal group. We calculated all values

as ex-vessel price values in 2006 $USD and summed all support service values and forage fisheries catch values across all EEZs and HSAs. This produced our estimate of forage fish contribution to global fisheries value.

Results

Quality of Ecopath models

Ecopath pedigree indices (Christensen and Walters 2004) were available for 22 models (Table 1). The Ecopath pedigree index varies with the quality of data within Ecopath models, and values can range from 0 (not reliable) to 1 (highly reliable) (Christensen and Walters 2004; Christensen *et al.* 2005). Ecopath pedigree indices in this analysis ranged from 0.295 to 0.820 with the majority (55%, 12 out of 22) exceeding 0.5 (Table 1). Differences were observed in pedigree indices of models published in peer-reviewed journals (Ecopath pedigree mean = 0.625, median = 0.638, *n* = 11) and technical reports (Ecopath pedigree mean = 0.450, median = 0.408, *n* = 11). None of our indices were in the poorest quality level grouping, wherein data are considered to be no better than guesses (<0.2; Christensen and Walters 2004; Christensen *et al.* 2005). Moreover, the average and median pedigree indices observed in this study (0.518 and 0.537, respectively) were substantially higher than those for other studies (0.441 and 0.439, respectively) (Morissette *et al.* 2006; Morissette 2007).

Extent of predator dependence on forage fish

Seventy-five percent (54 out of 72) of the Ecopath models used in this analysis had at least one model group that was highly ($\geq$ 50% but <75% of diet) or extremely dependent ($\geq$ 75% of diet) on forage fish. Twenty-nine percent (21 out of 72) of the models included at least one extremely dependent predator group. We found extremely dependent predators present across all latitude groups and ecosystem types, with the exception of open ocean ecosystems. Extremely dependent predators accounted for only 5.8% (52 out of 895) of all forage fish predators and consisted of fishes (*n* = 30), seabirds (*n* = 12), marine mammals (*n* = 9) and one species of squid (*Loligo gahi*, Loliginidae). Amongst conspecific predator groups, however, seabirds had the highest percentage of extremely dependent predators, with

19% (12 out of 62) of all seabird predators having diets ≥ 75% forage fish. Extremely dependent predators groups were most commonly found in upwelling and Antarctic ecosystem types, with an average of two and five extremely dependent predators per model, respectively. Many of these extremely dependent predator species were also listed on the IUCN Red List (Table 2).

We evaluated the relative frequency of various levels of forage fish dependencies and how they varied across ecosystem types by combining data from all models. Pooled data across all ecosystem models

indicated that on average, 49% of all predator groups in our models relied on forage fish for at least 10% of their dietary requirements (Fig. 2). Forage fish predators that are highly or extremely dependent on forage fish account for 16% of all predator groups in marine ecosystem models on average. Predators with diets consisting of more than 90% forage fish were also found but represented fewer than 5% of all predator groups in this analysis.

When comparing across ecosystem types, Antarctic ecosystem models generally had the greatest

Table 2 Extremely dependent forage fish predators (≥ 75% forage fish in their diets) found in this synthesis that have taxonomic information and are evaluated by the International Union for Conservation of Nature (IUCN) Red List. Model numbers correspond to model names in Table 1.

Common name	Scientific name	Family	IUCN Status[1]	Population trend	Model No(s)
Marine Mammals					
Sei Whale	*Balaenoptera borealis*	BALAENOPTERIDAE	Endangered	Unknown	(1, 60)
Blue Whale	*Balaenoptera musculus*	BALAENOPTERIDAE	Endangered	Increasing	(1, 60)
Fin Whale	*Balaenoptera physalus*	BALAENOPTERIDAE	Endangered	Unknown	(1, 60)
Common Minke Whale	*Balaenoptera acutorostrata*	BALAENOPTERIDAE	Least Concern	Stable	(1, 60)
Southern Right Whale	*Eubalaena australis*	BALAENIDAE	Least Concern	Increasing	60
Grey Seal	*Halichoerus grypus*	PHOCIDAE	Least Concern	Increasing	40
Crabeater Seal	*Lobodon carcinophagus*	PHOCIDAE	Least Concern	Unknown	60
Humpback Whale	*Megaptera novaeangliae*	BALAENOPTERIDAE	Least Concern	Increasing	(1, 60)
Ringed Seal	*Phoca hispida*	PHOCIDAE	Least Concern	Unknown	40
Seabirds					
Black-browed Albatross	*Thalassarche melanophrys*	DIOMEDEIDAE	Endangered	Decreasing	18
Macaroni Penguin	*Eudyptes chrysolophus*	SPHENISCIDAE	Vulnerable	Decreasing	(60, 62)
Humboldt Penguin	*Speriscus humboldtii*	SPHENISCIDAE	Vulnerable	Decreasing	17
Peruvian Pelican	*Pelecanus thagus*	PELECANIDAE	Near Threatened	Decreasing	(13–14, 15, 17)
Guanay Cormorant	*Phalacrocorax bougainvillii*	PHALACROCORACIDAE	Near Threatened	Decreasing	(13–14, 15)
Sooty Shearwater	*Puffinus griseus*	PROCELLARIIDAE	Near Threatened	Decreasing	1
Gentoo Penguin	*Pygoscelis papua*	SPHENISCIDAE	Near Threatened	Decreasing	(60, 62)
King Penguin	*Aptenodytes patagonicus*	SPHENISCIDAE	Least Concern	–	62
Rhinoceros Auklet	*Cerorhinca monocerata*	ALCIDAE	Least Concern	–	1
Southern Rockhopper Penguin	*Eudypte schrysocome*	SPHENISCIDAE	Least Concern	Decreasing	62
Tufted Puffin	*Fratercula cirrhata*	ALCIDAE	Least Concern	–	1
Southern Giant-petrel	*Macronectes giganteus*	PROCELLARIIDAE	Least Concern	Decreasing	18
Cassin's Auklet	*Ptychoramphus aleuticus*	ALCIDAE	Least Concern	–	1
Peruvian Booby	*Sula variegate*	SULIDAE	Least Concern	–	(13–14, 15, 17)
Common Guillemot	*Uria aalge*	ALCIDAE	Least Concern	–	1
Fish					
Yellowfin Tuna	*Thunnus albacares*	SCOMBRIDAE	Near Threatened	Decreasing	(13–14, 56)
Common Dolphinfish	*Coryphaena hippurus*	CORYPHAENIDAE	Least Concern	Stable	(13–14)
West African Ladyfish	*Elops lacerta*	ELOPIDAE	Least Concern	Unknown	56
Skipjack Tuna	*Katsuwonus pelamis*	SCOMBRIDAE	Least Concern	Stable	56
North Pacific Hake	*Merluccius productus*	MERLUCCIIDAE	Least Concern	Unknown	7
Sockeye Salmon	*Oncorhynchus nerka*	SALMONIDAE	Least Concern	Stable	(4–5)
Pacific Bonito	*Sarda chiliensis*	SCOMBRIDAE	Least Concern	Decreasing	(13–14)

[1]IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2 http://www.iucnredlist.org Downloaded on 2 December 2011.
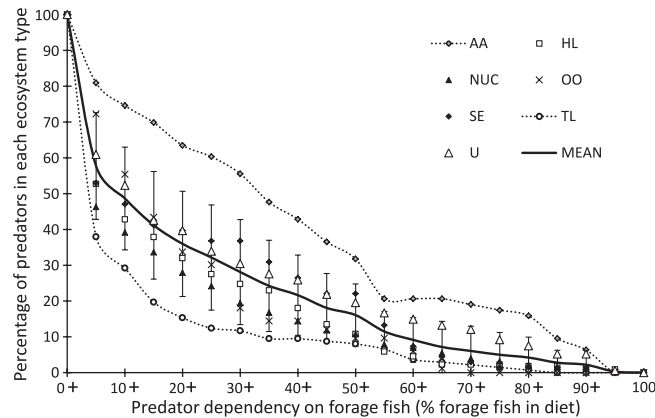
Figure 2 Percentage of forage fish predators in analysed ecosystems ($n = 72$) and their dependence on forage fish (% forage fish in diet). Solid line represents the Mean ± SD for all predators in this analysis. Ecosystem types: AA, Antarctic; OO, open ocean; U, upwelling current; HL, Arctic high latitude; SE, semi-enclosed; NUC, non-upwelling coastal; TL, tropical lagoon.

proportion of forage fish predators in their models for any level of forage fish dependence compared to other ecosystem model types (Fig. 2). Upwelling ecosystems had the second highest percentage of predators with 90% forage fish dependence levels. Tropical lagoon ecosystem types had the lowest proportion of predators for a given forage fish dependence level (Fig. 2).

Support service contribution to ecosystem predator production

The total predator production (tonne km^{-2} $year^{-1}$) supported by forage fish varied greatly among the 72 models in this analysis (Fig. 3). Supported predator production was the largest for two upwelling ecosystem models, the northern California Current model and central Chile model, and one non-upwelling coastal ecosystem (Falkland Islands model). Forage fish contributed 52 and 17 tonne km^{-2} $year^{-1}$ to predator production in northern California Current and central Chile models respectively, and the contribution in the Falkland Islands model was 18.9 tonne km^{-2} $year^{-1}$. When the contribution of krill to the production of other forage fish (e.g. krill, sardines, anchovies) was removed in the northern California Current and Falkland Islands models, the support service to predators dropped to 32 and 3.3 tonne km^{-2} $year^{-1}$ respectively.

Across ecosystem types, the greatest support service contribution of forage fish to predator production was seen in upwelling and Antarctic eco-

systems (Fig. 4a). The support service contribution to predator production in both these ecosystem types exceeded 9 tonne km^{-2} $year^{-1}$, and were more than three times greater than values seen for Arctic ecosystems and non-upwelling coastal ecosystems and more than an order of magnitude greater than open-ocean, tropical lagoon and semi-enclosed ecosystem types (Fig. 4a). In terms of latitude groupings (with upwelling ecosystems excluded), we found the greatest support service contributions to predator production in high latitude regions (3.79 tonne km^{-2} $year^{-1}$ ± 1.23 SE), followed by temperate latitudes (1.81 tonne km^{-2} $year^{-1}$ ± 0.59 SE) and finally tropical-subtropical latitudes (1.18 tonne km^{-2} $year^{-1}$ ± 0.17 SE; Fig. 4b).

Importance of forage fish to commercial fisheries

Forage fish catch varied greatly among models examined, both in tonnage and ex-vessel price value. In some models, we found no forage fish catch reported (e.g. Central Atlantic Ocean), while others had extremely large forage fish catches (e.g. Sechura Bay, Peru). The highest forage fish catches were found in the Humboldt Current models where the Peruvian anchoveta fishery operates. Of the three Humboldt Current models, the Sechura Bay (Peru) model had an extraordinarily high level of forage fish catch (81 tonne km^{-2} $year^{-1}$) valued at $35 497 (USD km^{-2} $year^{-1}$), whereas in the northern Humboldt Current models for El Niño and La Niña periods, forage fish catches

Figure 3 Support service of forage fish to ecosystem predator production across all Ecopath models in this analysis (*n* = 72).

were 20 tonne km^{-2} year^{-1} ($934 USD km^{-2} year^{-1}) and 39 tonne km^{-2} year^{-1} ($2020 USD km^{-2} year^{-1}), respectively.

Forage fish contributed important support to other commercial fisheries in all models that contained such fisheries. Of the ecosystems we examined, forage fish were most important as prey, in terms of tonnage, to commercial fisheries in central Chile (3.82 tonne km^{-2} year^{-1}), Prince William Sound (pre-oil spill model; 3.58 tonne km^{-2} year^{-1}) and the northern California Current (3.13 tonne km^{-2} year^{-1}; Fig. 5). In terms of value, forage fish provided the greatest support service to fisheries in the Prince William Sound

model (pre-oil spill model) at a value of $5942 USD km^{-2} year^{-1}, followed by the Chesapeake Bay at a value of $3095 USD km^{-2} year^{-1}. The high support service values in these ecosystems are due to the large contribution of forage fish to the diets of salmon (*Oncorhynchus* spp., Salmonidae) in Prince William Sound and striped bass (*Morone saxatilis*, Percichthyidae) in Chesapeake Bay, both of which have relatively high ex-vessel price values.

In 13 out of 56 models, 100% of the total forage fish value was derived from support to other fisheries (i.e. there were no forage fish fisheries reported in these 13 ecosystems). In more than half the models (30 out of 56), the value of the fisheries
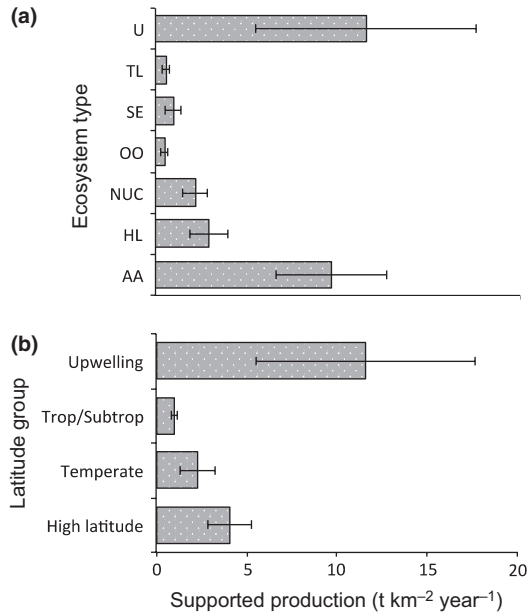
Figure 4 Mean forage fish contribution to (non-commercial) ecosystem predator production by ecosystem type (a) and latitude grouping (b) with standard error plotted. Ecosystem types: U, upwelling current; TL, tropical lagoon; SE, semi-enclosed; OO, open ocean; NUC, non-upwelling coastal; HL, Arctic high latitude; and AA, Antarctic.

supported by forage fish was greater than the value of forage fish catch (Fig. 6).

Comparisons across latitude groups and ecosystem types

The largest forage fish catches were found in the tropical-subtropical latitude group (4.95 tonne km^{-2} $year^{-1}$ ± 2.5 SE) and decreased monotonically as polar regions were approached. In contrast, the level of other commercial catch supported by forage fish was the lowest in the tropical-subtropical latitude group (0.23 tonne km^{-2} $year^{-1}$ ± 0.05 SE) but greater in temperate (0.63 tonne km^{-2} $year^{-1}$ ± 0.2 SE) and high latitude ecosystems (0.35 tonne km^{-2} $year^{-1}$ ± 0.29 SE). We separated upwelling ecosystem models from these latitude groupings, as forage fish catches play a dominant role in these ecosystems. We found that temperate models had the highest forage fish fisheries catch when compared with the remaining two latitude groups (Fig. 7a). Forage fish catch value (excluding upwelling ecosystems) was the greatest in the tropical-subtropical latitude group and diminished poleward (Fig. 7b). The sup-

port service provided by forage fish for other commercial fisheries, in both catch and catch value, increased poleward so that it was equivalent (in catch) or exceeded (in catch value) the forage fish catch or catch value in high latitudes (Fig. 7a,b).

Forage fish catch (tonne km^{-2} $year^{-1}$) was the highest in upwelling ecosystems (Fig. 8a), exceeding that of all other ecosystem types combined by a factor of four. Forage fish catch exceeded the catch of other model groups that preyed on forage fish for all ecosystem types (Fig. 8a). Similarly, forage fish had the highest catch value in upwelling ecosystems at $5660 USD km^{-2} $year^{-1}$ ± $4980 SE (Fig. 8b). Other ecosystem types had substantially lower forage fish catch values, each contributing < $830 USD km^{-2} $year^{-1}$. The value of forage fish catches was the smallest in high latitude Arctic and Antarctic ecosystems ($184 USD km^{-2} $year^{-1}$ and $149 USD km^{-2} $year^{-1}$, respectively). In contrast, the support service value of forage fish was the greatest in the Arctic ecosystems (HL, mean = $706 USD km^{-2} $year^{-1}$) – over 3.5 times greater than the forage fish value for that ecosystem type (Fig. 8b).

Global estimate of forage fish value to fisheries

The estimated total ex-vessel price value of forage fish to global commercial fisheries was $16.9 billion ($USD). This estimate combines global forage fish fishery value of $5.6 billion (33%, USD) with a support service value to other fisheries of $11.3 billion (67%, USD). This value represents nearly 20% ($16.9b/$85b) of the ex-vessel catch values of all world fisheries, estimated at between $80 and 85 billion USD $year^{-1}$ (Sumaila *et al.* 2007; FAO 2010). Importantly, we found that the value of commercial fisheries supported by forage fish (e.g. cod, striped bass, salmon) was twice the value of forage fish fisheries at a global scale.

Discussion

We recognize that using Ecopath models, like any mathematical representation of an ecosystem, has certain limitations. However, our approach was built around the idea that, within the constraints of the model assumptions, averaging across many models will at least reduce the effects of stochastic uncertainty. Ecopath models provide only a single spatial and temporal representation of an ecosystem and they contain numerous assumptions
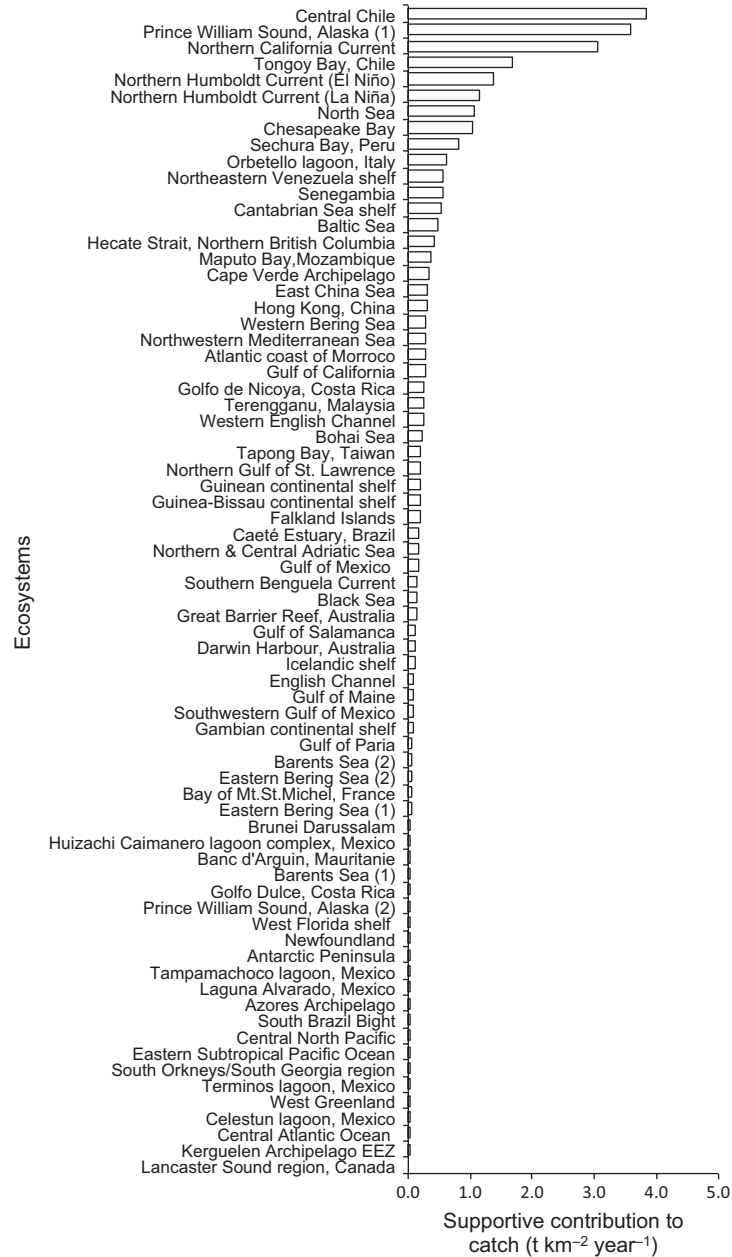
Figure 5 Support service contributions of forage fish to other fisheries catch across all Ecopath models (*n* = 72).

whose consequences are often impossible to assess and could be important. This means, at the very least, that they do not capture changes in ecosystem dynamics and fisheries effort over space and time. Models are constructed based on data availability and the author's understanding of the ecosystem and research objectives, allowing for a gradient in model complexity and quality. The models contain simplified diet information of predators included in the models, which needs to be

considered when interpreting or using the results of this study. For example, some Ecopath models lacked predators that are known to prey on forage fish, and in other cases, investigators pooled individual predator species together into a single trophic group. Nearly 30% (21 out of 72) of the models in our study did not have any seabird model groups, while 33% (24 out of 72) did not have a marine mammal group. Our estimates for predator production therefore are likely conserva-
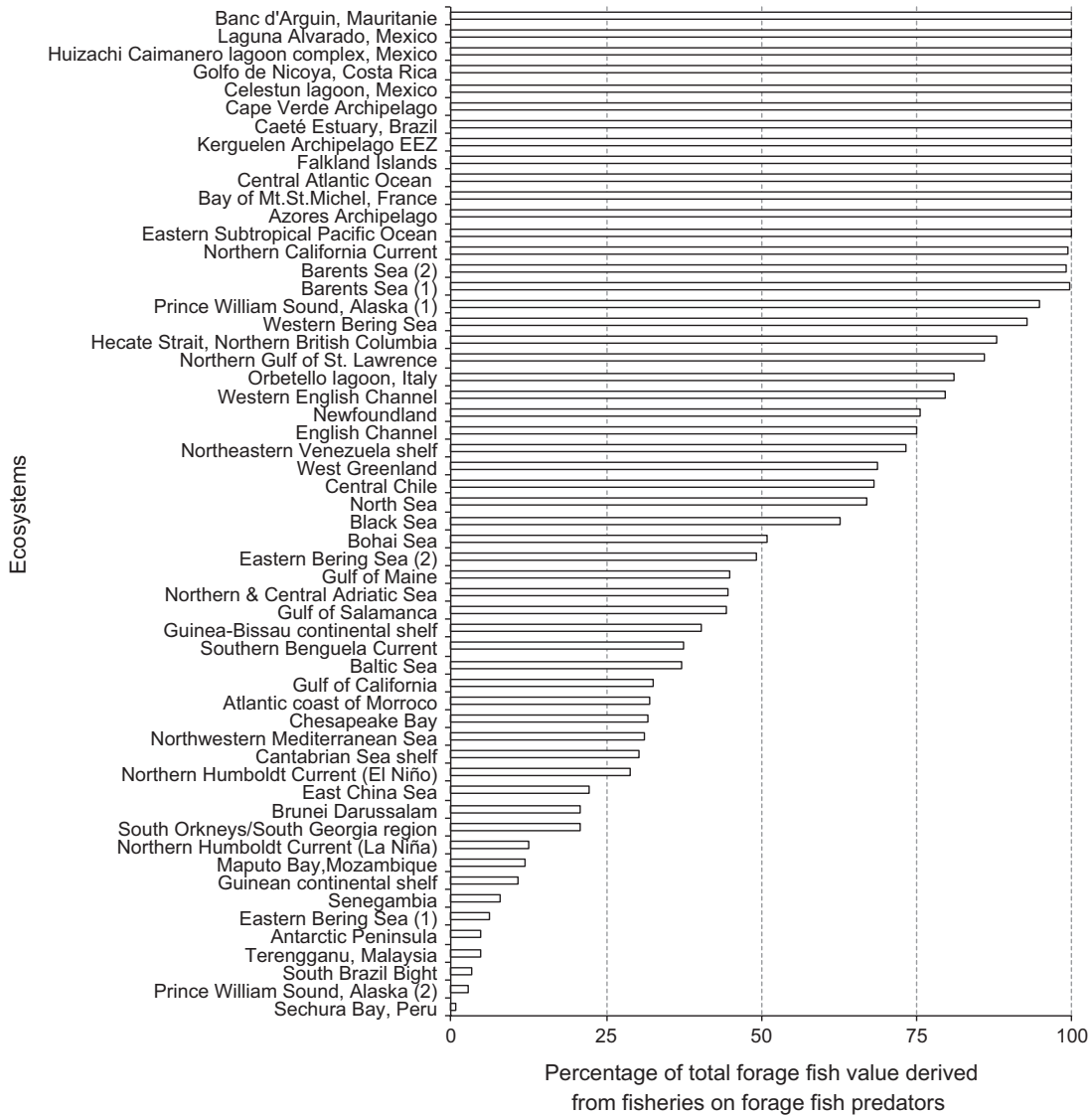
Figure 6 Percentage of total forage fish values (forage fish fisheries value + support service value to other fisheries) across Ecopath models (*n* = 56) derived from forage fish support service to other commercial fisheries. Ecosystems with 100% support service to other commercial fisheries do not have active forage fish fisheries in their respective ecosystem model.

tive, as we were not able to capture the importance of forage fish to these predators not included in the models. Likewise, aggregating predator species into model groups results in an averaged diet dependence on forage fish for the model group, which may mask high diet dependence for one or more individual species in that group. Averaging diet dependence for a single species over a large geographic area may also mask high diet dependencies that occur on smaller spatial or temporal scales. Validating every model to determine how
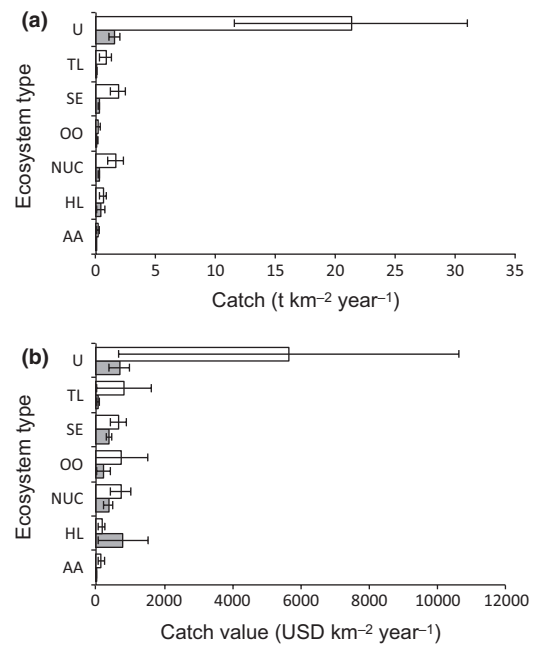
well it represents its respective ecosystem and biological components was beyond the scope of this analysis, but Ecopath pedigree index information for a subset of models shows that the majority used in this analysis are of acceptable quality (Table 1). Using published models provided us with a large number of models covering the widest range of ecosystems and latitudes possible.

Here we used information on catches, catch values and food web connections to estimate the global contribution of forage fish to fisheries and
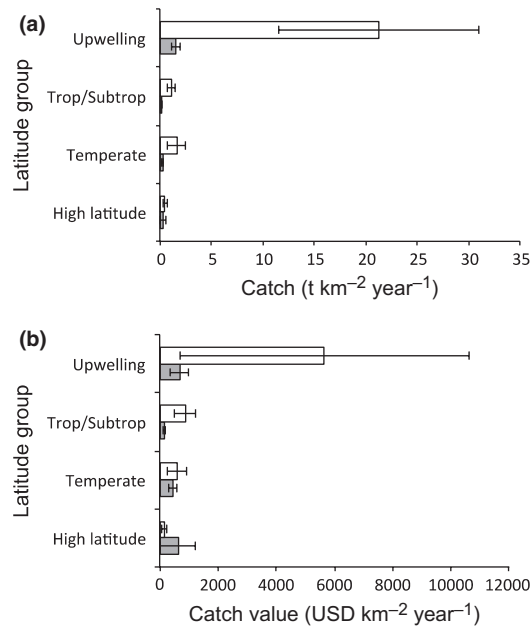
Figure 7 Mean catch (a) and mean catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars), by latitude group. Bars indicate standard error. Upwelling ecosystem models were separated out to more clearly demonstrate latitudinal patterns.

Figure 8 Mean catch (a) and catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars). Bars indicate standard error. Ecosystem types: U, upwelling current; TL, tropical lagoon; SE, semi-enclosed; OO, Open ocean; NUC, non-upwelling coastal; HL, Arctic high latitude; and AA, Antarctic.

ecosystems. While we find that the importance of forage fish varies geographically, it is clear that these species are of critical importance to many predators, including humans. We consider our approach as a reliable and relatively quick way of assessing the importance of forage fish in marine ecosystems and fisheries around the world. Ecopath models in this analysis covered 33% of the total EEZs and HSAs and covered 47% of the IFA (Table S2, Appendix S2), which is where 97% of the global forage fisheries catch value is derived (Sumaila *et al.* 2007). We acknowledge that geographic coverage is limited in the Indian Ocean. Although EEZ and HSA areas in the Indian Ocean account for 20% of the total EEZ and HSA area, they represent <15% of the total fisheries catch value (excluding non-cephalopod or non-krill invertebrates) and <12% of the total forage fish catch value. Furthermore, Indian Ocean EEZ and HSA areas accounted for <10% of the total global supportive value of forage fish. More robust fisheries information from this data-poor region (De Young 2006) would benefit future analyses.

At the global scale the supportive value of forage fish to fisheries greatly exceeds their direct commodity value. We note that the estimated total ex-vessel value ($16.9 billion USD annually) is likely an underestimate, because it does not take into account the contribution of forage species to early life history stages of predators that are not yet of commercial catch size (e.g. juvenile cod, juvenile striped bass). We also have not included in our analysis the contributions of species that are considered forage fish only during juvenile life stages (e.g. Alaska pollock). Accounting for these types of forage species would increase our estimates of support to ecosystem predator production and marine fisheries in certain ecosystems. More importantly, the ex-vessel value of commercial fisheries is only one of many other indicators of the economic contributions of forage fish, and thus is clearly an underestimate of total economic worth. We have not accounted for the potential economic value of forage fish to recreational fisheries, to ecotourism [e.g. the whale watching industry is estimated at $2.5 billion 2009 USD

annually (Cisneros-Montemayor *et al.* 2010)], as bait for fisheries, and to the provision of other ecosystem services such as water filtration.

Forage fish are integral to marine food webs as prey for a wide variety of higher trophic-level species. For many predators, forage fish constitute a substantial percentage of their diet, possibly making them vulnerable to reductions or fluctuations in forage fish biomass. We found that many extremely dependent predators were species listed on the IUCN Red List as 'Near Threatened', 'Vulnerable' or 'Endangered' (Table 2). These predators were commonly found in upwelling ecosystems, where empirical evidence shows that changes in forage fish abundance – caused by fishing, the environment, or a combination of both – negatively impact predator reproduction (Sunada *et al.* 1981; Becker and Beissinger 2006), breeding (Crawford and Dyer 1995; Cury *et al.* 2011), abundance (Crawford and Jahncke 1999; Jahncke *et al.* 2004), and carrying capacity (Crawford *et al.* 2007). This analysis has identified ecosystems that are likely to have highly to extremely dependent forage fish predators and may assist in ecosystem-based management efforts that consider both commercial fisheries and effects on threatened or endangered species.

We provide the first global estimates of the importance of forage fish as support for predators in marine ecosystems. Quantifying forage fish catch, support service to other commercially targeted predators, and support to all other ecosystem predators allows for identification of potential trade-offs that may occur among uses (Fig. 9). Competition for the use of forage fish biomass among ecological and fisheries interests can result in trade-offs, which can lead to conflicts in the management of forage fish. This is especially important, as forage fish are an increasingly valued commodity (Naylor *et al.* 2009; Tacon and Metian 2009) and provide fundamental ecological support to many other species. Taking a holistic viewpoint of their value is a step towards quantification of the overall contributions forage fish make to marine ecosystems and to the global economy. A challenge that remains for fisheries managers and policy makers is determining acceptable levels of catch that account for the roles forage fish play in the larger marine environment.

The management of trade-offs in marine ecosystems can often be challenging (Okey and Wright 2004; Cheung and Sumaila 2008; Salomon *et al.*
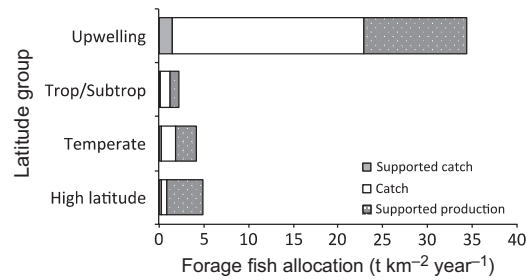
Figure 9 Forage fish allocation across latitude groups in terms of support service to fisheries (grey bars), forage fish catch (white bars) and support service to ecosystem predator production (dotted grey bars).

2011), but accounting for trade-offs is important and can lead to more sustainable levels of exploitation without compromising ecosystem integrity (Okey and Wright 2004). Ultimately, accounting for trade-offs between forage fish fisheries and conservation goals will require knowledge and understanding of the sensitivity to which commercially targeted and non-commercial predator species respond to fisheries induced changes in forage fish abundance. A combination of modelling (Okey and Wright 2004; Cheung and Sumaila 2008; Smith *et al.* 2011) and empirical (Read and Brownstein 2003; Brodziak *et al.* 2004) methods will likely be required to fully understand trade-offs in forage fishery management.

Acknowledgements

References

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K. and Pauly, D. (2008) Forage fish: from ecosystems to markets. *Annual Review of Environment and Resources* **33**, 153–166.

Anthony, J.A., Roby, D.D. and Turco, K.R. (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* **248**, 53–78.

Bakun, A., Babcock, E.A., Lluch-Cota, S.E., Santora, C. and Salvadeo, C.J. (2010) Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. *Reviews in Fish Biology and Fisheries* **20**, 9–29.

Balmford, A., Bruner, A., Cooper, P. *et al.* (2002) Economic reasons for conserving wild nature. *Science* **297**, 950–953.

Barber, R.T. and Chavez, F.P. (1983) Biological consequences of El Niño. *Science* **222**, 1203–1210.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**, 169–193.

Becker, B.H. and Beissinger, S.R. (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* **20**, 470–479.

Beddington, J.R., Agnew, D.J. and Clark, C.W. (2007) Current problems in the management of marine fisheries. *Science* **316**, 1713–1716.

Brodziak, J.K.T., Mace, P.M., Overholtz, W.J. and Rago, P.J. (2004) Ecosystem trade-offs in managing New England fisheries. *Bulletin of Marine Science* **74**, 529–548.

Butler, C.M., Rudershausen, P.J. and Buckel, J.A. (2010) Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (*Brevoortia tyrannus*). *Fishery Bulletin* **108**, 56–69.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. and Ñiquen, C.M. (2003) From anchovies to sardines and back: multi-decadal change in the Pacific Ocean. *Science* **299**, 217–221.

Cheung, W.W.L. and Sumaila, U.R. (2008) Trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem. *Ecological Economics* **66**, 193–210.

Christensen, V. and Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109–139.

Christensen, V., Walters, C.J. and Pauly, D. (2005) *Ecopath with Ecosim: A User's Guide*. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p. (available online at http://www.ecopath.org).

Cisneros-Montemayor, A.M., Sumaila, U.R., Kaschner, K. and Pauly, D. (2010) The global potential for whale watching. *Marine Policy* **34**, 1273–1278.

Coll, M., Libralato, S., Tudela, S., Palomera, I. and Pranovi, F. (2008) Ecosystem overfishing in the Ocean. *PLoS One* **3**, 1–10.

Costanza, R., d'Arge, R., de Groot, R. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260.

Crawford, R.J.M. and Dyer, B.M. (1995) Responses by 4 seabird species to a fluctuating availability of cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137**, 329–339.

Crawford, R.J.M. and Jahncke, J. (1999) Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. *South African Journal of Marine Science* **21**, 145–156.

Crawford, R.J.M., Underhill, L.G., Upfold, L. and Dyer, B. M. (2007) An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*). *ICES Journal of Marine Science* **64**, 570–576.

Cury, P., Bakun, A., Crawford, R.J.M. *et al.* (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science* **57**, 603–618.

Cury, P., Shannon, L.J. and Shin, Y.-J. (2003) The functioning of marine ecosystems: a fisheries perspective. In: *Responsible Fisheries in the Marine Ecosystem* (eds M. Sinclair and G. Valdimarsson). CAB International, Wallingford, pp. 103–123.

Cury, P.M., Boyd, I.L., Bonhommeau, S. *et al.* (2011) Global seabird response to forage fish depletion-One-third for the birds. *Science* **334**, 1703–1706.

Daunt, F., Wanless, S., Greenstreet, S.P.R., Jensen, H., Hamer, K.C. and Harris, M.P. (2008) The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 362–381.

De Young, C. (2006) *Review of the State of World Marine Capture Fisheries Management: Indian Ocean*. FAO Fisheries Technical Paper, Food and Agriculture Organization, Rome, p. 458.

FAO (2010) *The State of World Fisheries and Aquaculture 2010*. Food and Agriculture Organization, Rome, p. 197.

Francis, R.C., Hare, S.R., Hollowed, A.B. and Wooster, W.S. (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography* **7**, 1–21.

Fréon, P., Cury, P., Shannon, L. and Roy, C. (2005) Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science* **76**, 385–462.

Fulton, E.A. (2010) Approaches to end-to-end ecosystem models. *Journal of Marine Systems* **81**, 171–183.

Furness, R. (2007) Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* **148**, 247–252.

Gislason, H. (2003) The effects of fishing on non-target species and ecosystem structure and function. In:

Responsible Fisheries in the Marine Ecosystem (eds M. Sinclair and G. Valdimarsson). CAB International, Wallingford, pp. 255–275.

Gurevitch, J. and Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology* **80**, 1142–1149.

Hannesson, R. and Herrick Jr, S.F. (2010) The value of Pacific sardine as forage fish. *Marine Policy* **34**, 935–942.

Hannesson, R., Herrick, S. and Field, J. (2009) Ecological and economic considerations in the conservation and management of the Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 859–868.

Herrick, S.F., Norton, J.G., Hannesson, R., Sumaila, U.R., Ahmed, M. and Pena-Torres, J. (2009) Global production and economics. In: *Climate Change and Small Pelagic Fish* (eds D.M. Checkley, J. Alheit, Y. Oozeki and C. Roy). Cambridge University Press, Cambridge, pp. 256–274.

Hunsicker, M.E., Essington, T.E., Watson, R. and Sumaila, U.R. (2010) The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries* **11**, 421–438.

Jahncke, J., Checkley, D.M. and Hunt, G.L. (2004) Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography* **13**, 208–223.

Kamimura, Y., Kasai, A. and Shoji, J. (2011) Production and prey source of juvenile black rockfish *Sebastes cheni* in a seagrass and macroalgal bed in the Seto Inland Sea, Japan: estimation of the economic value of a nursery. *Aquatic Ecology* **45**, 367–376.

Kelleher, K. (2005) *Discards in the World's Marine Fisheries*. An update. FAO Fisheries Technical Paper. No. 470. Food and Agriculture Organization of the United Nations (FAO), Rome, p. 131.

Logan, J.M., Rodriguez-Marin, E., Goni, N. *et al.* (2011) Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Marine Biology* **158**, 73–85.

Magnussen, E. (2011) Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. *ICES Journal of Marine Science* **68**, 1909–1917.

McLeod, K.L. and Leslie, H. (2009) *Ecosystem-based Management for the Oceans*. Island Press, Washington, DC, USA, p. 368.

McLeod, K.L., Lubchenco, J., Palumbi, S.R. and Rosenberg, A.A. (2005) Scientific Consensus Statement on Marine Ecosystem-Based Managment. Signed by 217 academic scientists and policy experts with relevant expertise and published by the Communication Partnership for Science and the Sea at http://compassonline.org/?q=EBM (last accessed on 13 November, 2011).

Morissette, L. (2007) *Complexity, cost and quality of ecosystem models and their impact on resilience: a comparitive analysis, with emphasis on marine mammals and the Gulf of St. Lawrence.* PhD thesis, University of British Columbia, Vancouver, BC, 260 pp.

Morissette, L., Hammill, M.O. and Savenkoff, C. (2006) The trophic role of marine mammals in the northern gulf of St. Lawrence. *Marine Mammal Science* **22**, 74–103.

Mullon, C., Mittaine, J.F., Thebaud, O., Peron, G., Merino, G. and Barange, M. (2009) Modeling the global fishmeal and fish oil markets. *Natural Resource Modeling* **22**, 564–609.

Murawski, S.A. (2000) Definitions of overfishing from an ecosystem perspective. *ICES Journal of Marine Science* **57**, 649–658.

Naylor, R.L., Hardy, R.W., Bureau, D.P. *et al.* (2009) Feeding aquaculture in an era of finite resources. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 15103–15110.

Okey, T.A. and Wright, B.A. (2004) Toward ecosystem-based extraction policies for Prince William Sound, Alaska: integrating conflicting objectives and rebuilding pinnipeds. *Bulletin of Marine Science* **74**, 727–747.

Pauly, D., Trites, A.W., Capuli, E. and Christensen, V. (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* **55**, 467–481.

Pikitch, E.K., Santora, C., Babcock, E.A. *et al.* (2004) Ecosystem-based fishery management. *Science* **305**, 346–347.

Polasky, S. and Segerson, K. (2009) Integrating ecology and economics in the study of ecosystem services: some lessons learned. *Annual Review of Resource Economics* **1**, 409–434.

Polovina, J.J. (1984) Model of a coral reef ecosystem: 1. The Ecopath model and its application to French Frigate Shoals. *Coral Reefs* **3**, 1–11.

Polovina, J.J., Howell, E., Kobayashi, D.R. and Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* **49**, 469–483.

Read, A.J. and Brownstein, C.R. (2003) Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine. *Conservation Ecology* **7**, 1–12.

Richerson, K., Levin, P.S. and Mangel, M. (2010) Accounting for indirect effects and non-commensurate values in ecosystem based fishery management (EBFM). *Marine Policy* **34**, 114–119.

Salomon, A.K., Gaichas, S.K., Jensen, O.P. *et al.* (2011) Bridging the divide between fisheries and marine conservation science. *Bulletin of Marine Science* **87**, 251–274.

Smith, A.D.M., Brown, C.J., Bulman, C.M. *et al.* (2011) Impacts of fishing low-trophic level species on marine ecosystems. *Science* **333**, 1147–1150.

Sumaila, U., Marsden, A., Watson, R. and Pauly, D. (2007) A global ex-vessel fish price database: construction and applications. *Journal of Bioeconomics* **9**, 39–51.

Sunada, J.S., Kelly, P.R., Yamashita, I.S. and Gress, F. (1981) The brown pelican as a sampling instrument of age group structure in the northern anchovy population. *California Cooperative Oceanic Fisheries Investigations Reports* **22**, 65–68.

Tacon, A.G.J. and Metian, M. (2009) Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. *Ambio* **38**, 294–302.

Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C. and Racey, P.A. (1996) Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. *Journal of Applied Ecology* **33**, 1572–1584.

Van Pelt, T.I., Piatt, J.F., Lance, B.K. and Roby, D.D. (1997) Proximate composition and energy density of some north pacific forage fishes. *Comparative Biochemistry and Physiology Part A: Physiology* **118**, 1393–1398.

Walter, J.F. and Austin, H.M. (2003) Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay. *Fishery Bulletin* **101**, 414–423.

Watson, R., Kitchingman, A., Gelchu, A. and Pauly, D. (2004) Mapping global fisheries: sharpening our focus. *Fish and Fisheries* **5**, 168–177.

Weise, M.J. and Harvey, J.T. (2008) Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management. *Marine Ecology-Progress Series* **373**, 157–172.

Supporting Information

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

Appendix S1. Full references for Ecopath models used in this analysis in alphabetical order.

Appendix S2. Supplementary Tables (Tables S1 and S2).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.