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When does fishing forage species affect their predators?

Ray Hilborn[a,*], Ricardo O. Amoroso[a], Eugenia Bogazzi[a], Olaf P. Jensen[b], Ana M. Parma[c], Cody Szuwalski[d], Carl J. Walters[e]

[a] School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195 USA
[b] Department of Marine & Coastal Sciences, Rutgers University, 71 Dudley Rd., New Brunswick, NJ 08901 USA
[c] Centro para el Estudio de Sistemas Marinos, Centro Nacional Patagónico-CONICET, Blvd. Brown 2915, U 9120 ACF Puerto Madryn, Chubut, Argentina
[d] Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, CA 93101 USA
[e] Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC V6T1Z4 Canada

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ABSTRACT

This paper explores the impact of fishing low trophic level “forage” species on higher trophic level marine predators including other fish, birds and marine mammals. We show that existing analyses using trophic models have generally ignored a number of important factors including (1) the high level of natural variability of forage fish, (2) the weak relationship between forage fish spawning stock size and recruitment and the role of environmental productivity regimes, (3) the size distribution of forage fish, their predators and subsequent size selective predation (4) the changes in spatial distribution of the forage fish as it influences the reproductive success of predators. We show that taking account of these factors generally tends to make the impact of fishing forage fish on their predators less than estimated from trophic models. We also explore the empirical relationship between forage fish abundance and predator abundance for a range of U.S. fisheries and show that there is little evidence for a strong connection between forage fish abundance and the rate of change in the abundance of their predators. We suggest that any evaluation of harvest policies for forage fish needs to include these issues, and that models tailored for individual species and ecosystems are needed to guide fisheries management policy.

1. Introduction

There has been considerable interest in recent years on the impact of fishing low trophic level fishes, commonly called “forage fish”, on the higher trophic level fishes, marine birds and marine mammals (Cury et al., 2011; Pikitch et al., 2012; Smith et al., 2011). For our purposes we consider forage fish to be the major small pelagic fishes and squid, but the juveniles of many species are also an important part of the diet of many predators. There is good evidence and theory to suggest that (1) fishing reduces the abundance of targeted fish stocks, and (2) reproductive success of predators is affected by the local density of their prey. The logic seems clear, lower fishing pressure results in more forage fish in the ocean, and thus better reproductive success and higher abundance of the higher trophic level predators. Pikitch et al. and Smith et al. used ecosystem models to quantitatively evaluate the impact of fishing forage fish on their predators, and both papers suggested that forage fish should be harvested at rates lower than would provide long term maximum yield of the forage fish.

Although it would therefore seem obvious that fishing forage fish would have a negative effect on the abundance of their predators, the empirical relationships between forage fish abundance and predator abundance, or population rates of change, have not been examined in a systematic way. There is evidence in the literature (Cury et al., 2011) showing changes in reproductive success in relation to local food abundance, but the assumed link between the changes in total population size of predators and the total forage fish abundance has not been evaluated against historical trends in abundance. Another way to explore the impact of fishing forage fish is to examine the population trends in a dependent predator. Given that most forage fish in the U.S. have been harvested more heavily in the past than they are at present, if predator populations increased under past fishing pressure on forage species, then fishing at those levels did not preclude the ability of the predators to increase. For many reasons, the predators of most concern should be those others that have been decreasing in abundance over recent decades.

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* Corresponding author.
E-mail addresses: hilbornr@gmail.com (R. Hilborn), ricardoamoroso@yahoo.com (R.O. Amoroso), ebogazzi@gmail.com (E. Bogazzi), olaf.p.jensen@gmail.com (O.P. Jensen), parma@cenpat-conicet.gob.ar (A.M. Parma), c.s.szuwalski@gmail.com (C. Szuwalski), c.walters@oceans.ubc.ca (C.J. Walters).

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Most forage fish are well documented to undergo substantial fluctuations in abundance unrelated to fishing (Schwartzlose et al., 1999), a feature that is ignored in the ecosystem models used to evaluate ecological impacts of fishing which were mentioned above. This was recognized as a deficiency by the authors of the Pikitch et al. paper. "Major fluctuations in forage fish abundance have been observed and recorded for centuries. Forage fish can respond dramatically to shifts in oceanic conditions and may exhibit strong decadal-scale variability. Forage fish may be capable of responding quickly to favorable environmental conditions, but their populations cannot be expected to maintain a steady state and can plummet when conditions become unfavorable" (Pikitch et al., 2012, page 84).

Such fluctuations can range over three orders of magnitude. Vert-pre et al. (2013) showed that for about 50% of fish stocks, there were major changes in the productivity of the stocks unrelated to fish stock size. Given great natural variability in abundance of forage fish, a key question is how much does fishing impact abundance relative to the natural fluctuations?

The commonly accepted assumption that higher spawning stock sizes lead (in expectation) to higher recruitment (Myers and Barrowman, 1996; Myers et al., 1994) is implicit in EwE models that do not break taxonomic groups into size or age groups, and explicit in ATLANTIS models and EwE models that do break a group into stages. The assumption that increasing spawning stock size will lead to higher recruitment has been challenged first by Gilbert (1997) then by Szuwalski et al. (2014) who showed that most stocks do not exhibit a stock recruit relationship and of those that do, a large fraction of them have shifts in average recruitment over time. Myers et al. (1999) estimated that forage fish show clear relationships between spawning stock abundance and recruitment, but low spawning stock and low recruitment can be explained equally well by low recruitment generating low spawning stock (Szuwalski et al., 2014). If abundance of forage fish and their recruitment are primarily environmentally driven, then the impact of fishing on the food supply of higher trophic level predators is mainly through depletion of prey cohorts by fishing, not by reduced recruitment.

In addition to the assumption of a direct link between spawning stock and recruitment, the EwE models used to evaluate the impacts of fishing forage fish have a direct link between forage fish abundance, predator consumption and predator abundance implicit in the dynamics. However, few of these models have considered the life histories of the forage fish and their predators in enough detail to capture several key issues in the interaction between fishing on forage fish and impacts on dependent predators. None of the 11 EwE models used by Pikitch et al. considered the size or age structure of the forage fish (Essington and Plaganyi, 2013) and in five cases the modeling was not conducted at the species level, but instead grouped up to eight forage species, amongst which many may exhibit negative covariation in abundance. Indeed, two of the authors of the Pikitch et al. study subsequently questioned the use of "recycled" ecosystem models (i.e., those developed for other purposes) to understand the impacts of forage fish abundance on their predators; "We find that the depth and breadth with which predator species are represented are commonly insufficient for evaluating sensitivities of predator populations to forage fish depletion" (Essington and Plaganyi, 2013). All of the models used by Pikitch et al. were such recycled models.

A key factor determining reproductive success of many birds and marine mammals is the local density of prey within their foraging range of the breeding sites (Thaxter et al., 2012). So in addition to the variability induced by natural fluctuations in total abundance of the forage fish, the spatial availability can also vary, and two breeding colonies feeding on the same stock may see strikingly different food availability. Local density can either amplify natural variability in food supply, or the predators may be able to concentrate on high density locations even at low prey abundance, thus buffering them from the fluctuations in total abundance. Despite the importance of local forage abundance for central place foragers, there is little evidence relating abundance of forage species to the abundance of mobile predators. Jensen et al. (2012) cited several of the studies showing the importance of local abundance to central place foragers but also reviewed the empirical literature relating marine predatory fish abundance to abundance of their prey and found few clear links apart from a decline in cod productivity following the collapse of both herring and capelin in the Barents Sea (Hamre, 1994; Hjermann et al., 2004).

This brings us to another important factor in the life history of forage fish and their predators that is neglected in almost all of the EwE models. Some marine predators consume forage fish at sizes and ages before the fishery harvests them. This is most true for predatory fish and marine birds, where mouth gape sizes limit the maximum size of prey that can be eaten, and probably least true for marine mammals. As an example, Nelson et al. (2006) showed that the mean size of Atlantic menhaden (*Brevoortia tyrannus*) eaten by striped bass (*Morone saxatilis*) in Massachusetts was 8.4 cm but the mean size taken by the fishery was 28 cm. In the extreme, if the recruitment of forage fish is not affected by fishing, and the predators consume sizes smaller than taken by the fishery, then the fishery would have no impact on the food available to the predator. In other words, the fishery harvests only those individuals that have survived and grown large enough to escape most of their predators.

To summarize, the impact of fishing forage fish on dependent predators will depend on (1) the alternative prey available to the predators, (2) the impact of fishing on the recruitment of the forage fish, (3) natural variability in recruitment, (4) the relationship between abundance of the forage fish and what is actually available to the predators, (5) the overlap between sizes/ages eaten by the predators and those taken by the fishery, and (6) other factors that may limit the predator population abundance.

In this paper we explore these issues for a range of U.S. forage fish and their predators. First, we examine the relationship between forage fish abundance and predator population growth rates, then we evaluate the recruitment pattern for each forage species and evaluate the evidence regarding the relative importance of fishing and environmental influences on the recruitment. Thirdly, we compare the size/ages taken by predators to those taken by the fishery. We then model the changes in forage fish abundance as a function of different assumptions regarding the dependence of recruitment on fish stock size and environmental variability to generate scenarios of forage fish abundance as a function of fishing pressure. Finally we examine how much the abundance of forage fish in the target size range is affected by fishing.

2. Materials and methods

Eleven species of forage fish in the U.S. were selected for analysis, and for each of these species we conducted a literature review to identify: (1) what predators eat those species, (2) the importance of the forage fish species in the diet of the predator, and (3) the size range of each forage species found in the diet of the predator. The selected forage species were the Pacific sardine (*Sardinops sagax*), Northern anchovy (*Engraulis mordax*), Market squid (*Doryteuthis opalescens*), Pacific hake (*Merluccius productus*), Pacific chub mackerel (*Scomber japonicus*), Atlantic herring (*Clupea harengus*), Atlantic menhaden, Atlantic mackerel (*Scomber scombrus*), Shortfin squid (*Illex illecebrosus*), Longfin inshore squid (*Doryteuthis pealeii*) and Gulf menhaden (*Brevoortia patronus*).

2.1. Literature search

A systematic review of the literature was conducted by querying the Academic Search and Google's online search engine for articles on prey and predators occurring in the California Current, U.S. East Coast and the Gulf of Mexico. Queries included topical keywords for diet and abundance for identified predators in the geographic range.

2.1.1. Diet

We recorded data from 127 relevant citations in peer-reviewed journal publications, books, technical reports, theses and from online databases (e.g. www.fishecology.org in September and October 2015). Data included individual occurrences of a predator eating a prey. Each record includes information on the citation, study location, date (year and season of observations), sampling methods (e.g. stomach content, visual observation), predator (life-history stage, size/age/sex, sample size) and prey (amount consumed and size eaten, usually estimated through otoliths or beak measurements).

The importance of a prey species in the diet of a predator was defined as the mean proportion of a forage fish consumed by a specific predator reported in a specific unit for measuring consumption. When more than one unit of consumption was available, the following order of preference was set: prey proportions by mass were preferred, followed by numbers, energetic contribution and finally frequency of occurrence.

2.1.2. Abundance of predators

The predators for which the importance of a single prey species was equal to or greater than 0.2 were selected as "dependent predators". We identified 86 different populations of dependent predators of which 52 are commercially important fish species or stocks, 33 are top predators (seabirds and marine mammals) and one is an invertebrate.

Abundance data for the dependent predators were obtained from several sources. For marine mammals, data were obtained primarily from the NMFS Marine Mammal Stock Assessments (Caretta et al., 2006; Waring et al., 2015). For commercially important fish species, data were obtained primarily from the RAM Legacy Stock Assessment Database (Ricard et al., 2012). Other sources of abundance data for seabirds and other species include agencies and government websites, peer-reviewed journal publications, books, technical reports and theses. Information on abundance trends were found for 50 of the 86 dependent predators species identified in this study.

An index of abundance was calculated using available data such as total and spawning stock biomass, density, estimated number of individuals, counts, pup production, nesting pairs, standardized catch per unit effort, breeding pairs and number of nests. The sources for these data are shown in supplemental Table S1.

Graphical data were extracted with DataThief III (Tummers, 2006) when original data in tabular form could not be found.

We compared the population per capita rates of change of the predators to the abundance of forage fish. For exploited species, we used the surplus production, should be there instead of; defined as the change in abundance from one year to the next, plus the catch. The relationship between forage fish abundance and predator rate of change was assessed using a linear model and the significance of the slope was tested using an F test.

2.2. Recruitment analysis

We analyzed the estimated forage fish abundance and subsequent recruitment to assess if recruitment was better explained by environmental variability or fish abundance. The spawner-recruit data were obtained from the RAM Legacy Stock Assessment Database (www.ramlegacy.org) for the forage fish of concern. Four models were fit to the data and compared using AIC: a traditional Beverton-Holt stock-recruitment model, a hockey-stick model, a model that assumes that recruitment is random and independent of stock size and a regime-shift model. In the latter, the presence of regimes was identified by estimating breakpoints in the recruitment time series where the statistical properties (mean and/or variance) change. Different segmentation algorithms exist to search over the entire parameter space for the number and location of breakpoints that maximize the likelihood of the data subject to a penalty to prevent overfitting. We used the PELT algorithm (Pruned Exact Linear Time) proposed by Killick et al. (2012) implemented in the "change point" library (Killick and Eckley, 2014) for the statistical software R (R Core Team, 2014). Differences in both the mean and the variance among segments were allowed and model selection was based on AIC while constraining the minimum segment length to either 5 or 10 years. The PELT method was preferred over the simpler sequential t-test method of Rodionov and Overland (2005) used by Vert-pre et al. (2013) because the later does not search over all possible combinations of breakpoint locations.

Stock-recruitment models (other than regime shift) were fitted using the software AD Model Builder (Fournier et al., 2012). For each model we computed the likelihood and the AIC assuming lognormal errors. The number of parameters in the regime-shift model was computed as the number of breakpoints plus the number of means and variances estimated. We excluded from the analysis the squid as well as the Northern anchovy, because the time series of abundance data available for these stocks were discontinuous.

2.3. Impacts of fisheries on prey abundance

We gathered biological and fisheries information on six species of forage fish and implemented a simulation model to quantify the reduction in food availability to predators from fishing given the size selectivity of both the fishery and the predators. An age structured model was used to simulate the effects of different fishing mortalities on fish abundance. The numbers of individuals of age a at time t were modeled as:

$$N_{a+1,t+1} = N_{a,t}\exp^{(-M+Fv_a)} \tag{1}$$

where M is the natural mortality, F the fishing mortality and v_a is an age specific selectivity. Two different scenarios of recruitment were simulated:

$$\begin{cases} N_{1,t} = R_t & \textit{Scenario 1} \\ N_{1,t} = \dfrac{aSE_{t-1}}{1+bS} & \textit{Scenario 2} \end{cases} \tag{2}$$

In Scenario 1, we assumed that recruitment was independent of the spawning biomass, while in Scenario 2 we used the standard Beverton-Holt stock-recruitment equation. Spawning stock biomass was calculated as:

$$S_t = \sum_a w_a m_a N_a \tag{3}$$

where w_a is the average weight of an individual of age a and m_a is the proportion of sexually mature individuals of age a. Weight at age was calculated as a power function of the average length

$$w_a = \alpha L_a{}^{\beta} \tag{4}$$

Length at age was modeled using the standard Von Bertalanffy growth equation.

$$L_a = L_\infty(1 - e^{(-k(a-t_0))}) \tag{5}$$

Table 1
Stock specific parameters used in the simulations. L∞ is asymptotic length, K is the Von-Bertalanffy growth rate, t0 = scale parameter of growth curve, M = instantaneous natural mortality rate, α = length to weight scale parameter, β = length to weight power.

Stock Parameters	Atlantic Herring	Atlantic Menhaden	Gulf Menhaden	Pacific Chub Mackerel	Pacific Hake	Pacific Sardine
L∞ (cm)	32	36.5	26.25	39.2	52	23.7
K	0.36	0.363	0.39	0.39	0.32	0.318
t0 (years)	−1.17	−1.3	−0.99	−2	0	−2.01
M	0.52	0.45	1.1	0.5	0.213	0.4
α ($\times 10^{-6}$)	8.21	4.07	7.41	2.7	5	7.52
B	3	3.2	3.19	3.4	3	3.2332
Maturity at age	1 = 0; 2 = 0.01; 3 = 0.21; 4 = 0.81; 5 = 0.98; 6+ = 1	<2 = 0; 2 = 0.12; 3 = 0.85; 4+ = 1	<2=0; 2 + = 1	0 = 0; 1 = 0.48; 2 = 0.63; 3 = 0.76; 4 = 0.85; 5–6 = 0.91; 7+ = 1	1 = 0; 2 = 0.01; 3 = 0.21; 4 = 0.82; 5 = 0.98; 6+ = 1	1 = 0; 2 = 0.99; 2+ = 1
Selectivity at age	1 = 0; 2 = 0.18; 3 = 0.54; 4 = 0.7; 5+ = 1	<2=0; 2 = 0.1; 3–4 = 1; 5 = 0.19; 6 + =0	1 = 0.05; 2 = 1; 3–4 = 0.35; 5 + =0	0 = 0.5; 1 + = 1	1 = 0.07; 2 = 0.18; 3 = 0.37; 4 = 0.62; 5 = 0.81; 6 = 0.92; 7 = 0.97; 8+ = 1	1 = 0.18; 2 = 0.37; 3 = 0.62; 4 = 0.81; 5 = 0.92; 6 + = 1

A global food depletion estimate can be calculated by comparing the equilibrium biomass for a given *F* with the equilibrium biomass in the unfished state. However, as predators may select prey by size, we are interested in assessing the food depletion for different prey's length intervals. We generated a length composition of the population by assuming that the size of individuals within an age class is normally distributed with mean L_a and standard deviation σ_a. For simulation purposes we assumed a constant coefficient of variation in size-at-age of 20%. We calculated the numbers of individuals (Eq. (6)) and the biomass (Eq. (7)) in the size interval $l_1 - l_2$ as:

$$N_{l_1-l_2} = \sum_a N_{a,l_1-l_2} \tag{6}$$

$$B_{l_1-l_2} = \sum_a w_a N_{a,l_1-l_2} \tag{7}$$

For each fish stock we ran the model for 5000 years under different fishing mortalities and randomly sampled 500 iterations to assess the reduction in the food available to predators. Under Scenario 1, the model was forced using the historical recruitment estimated in stock assessments in order to account for natural variability (we sequentially repeated the recruitment time series to achieve 5000 observations). To perform the simulation under the assumption of a stock recruitment relationship (Scenario 2) we used the spawner-recruit curve best fit to the stock assessment data. To account for natural variability, we calculated the log residuals and used them as multiplicative errors. Similar to Scenario 1, we sequentially repeated the observed errors to achieve 5000 observations.

Our simulations are a simplification of the stock dynamics, since key parameters such as selectivity, growth and natural mortality can be time, size or density dependent. For each fish stock we gathered mortality, growth, maturity, vulnerability to fishing and weight-at-length parameters from stock assessment documents. We ran the simulations for only one fishery for a given stock; when more than one fishery targeted that stock, we used the vulnerability to the fishery that accounted for the largest fraction of the catch.

We calculated the biomass depletion for four size ranges, (small, small-medium, medium-large and large fish) set at the quartiles of the length frequency distribution in the unfished state. We explored the impacts of fishing under $F = 0$, $0.5\,F_{\mathrm{MSY}}$, and F_{MSY}. When possible, the value of F_{MSY} was calculated using the stock-recruitment, maturity and growth parameters used in the simulations. For stocks where the stock-recruitment relationship was a flat line, the calculation of F_{MSY} was unreliable, and instead we used the value estimated as part of the stock assessment which was often a proxy. For each *F*, we computed the median biomass compared to median biomass in the unfished state. Parameters used in the simulations are summarized in Table 1.

3. Results

3.1. Diet data compilation

The literature review yielded 1041 predator-prey pairs that contained information on predators' diet (size eaten and/or proportion of the prey in the diet). For a given predator and prey species, the database can contain several records, since we included an individual entry for the same pair of species if data were obtained in different locations and/or different years or when the data were recorded for different sexes or stages in the life cycle. These records corresponded to 119 species of predators and 11 species of prey, and included multiple years of data for the same species in one location as well as data for one species from different regions. The number of individual predator species identified for each forage fish ranged from five for the Gulf menhaden to 46 for the Northern anchovy.

We identified 203 prey-predator pairs where the mean proportion of a prey item in the diet in a given location was larger than 0.2 (Table S1).

3.2. Empirical relationships between predator and prey trends

Trends in abundance of both predator and prey covering overlapping periods were available for 50 predator-prey pairs out of the 203 pairs where the proportion of a specific forage fish in the diet was larger than 0.2. When multiple abundance time series were available we selected the longest one that did not present gaps in the data. Trends in abundance of most dependent predators were either growing, stable, or fluctuating between periods of high and low abundance (Figs. 1 and S1). Six cases showed a clear decreasing trend in the predator's abundance index over time: Atlantic cod (*Gadus morhua*) in Georges Bank, sablefish (*Anoplopoma fimbria*) on the Pacific coast, mako shark (*Isurus oxyrinchus*), silky shark (*Carcharhinus falciformis*) and spiny dogfish (*Squalus acanthias*) in the N.W. Atlantic, and yellowtail rockfish (*Sebastes flavidus*) on the Pacific coast. No obvious relationship between the prey and predator abundance was apparent in the majority of the cases (Fig. 1 insets).

Although a positive relationship between prey and predator abundance can be interpreted as evidence of trophic dependence, a better way to assess the role of prey abundance in the population dynamics of the predator is to analyze the predator population rate of change or surplus production against the abundance of the

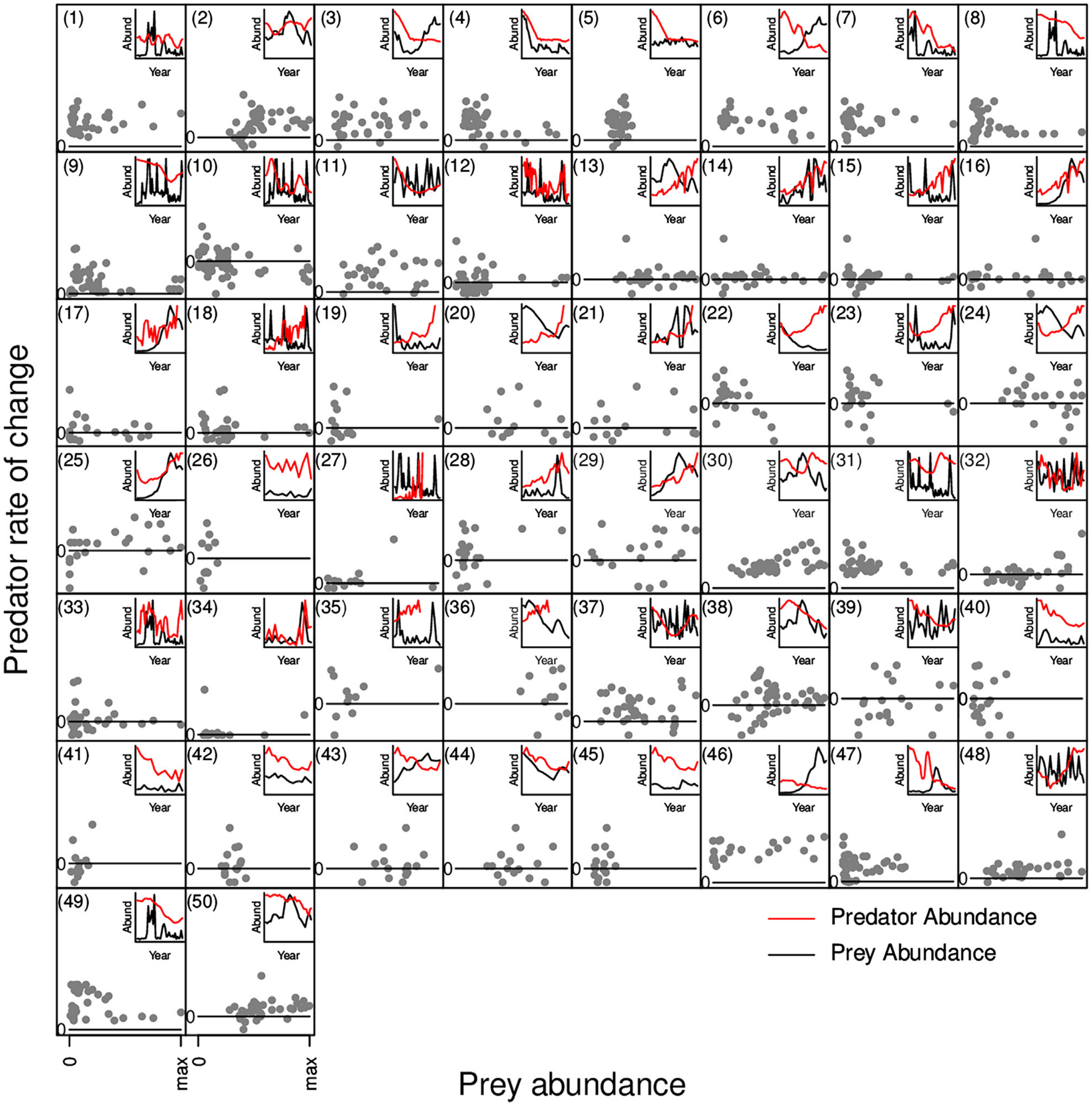

Fig. 1. Relationship between the annual surplus production of the predators and prey abundance. Each panel shows a pair of temporally overlapping predator rate of change and prey abundance data (grey dots). The subplot in each panel shows the relative trend in the abundance index for the prey (black line) and the predator (red line). (1) albacore tuna and shortfin squid; (2) arrowtooth flounder and Pacific hake; (3) Atlantic bluefin tuna and Atlantic herring; (4) Atlantic bluefin tuna and Atlantic mackerel; (5) Atlantic bluefin tuna and Atlantic menhaden; (6) Atlantic cod and Atlantic herring; (7) Atlantic cod and shortfin squid; (8) bigeye tuna and shortfin squid; (9) black rockfish and Northern anchovy; (10) bluefin tuna and Northern anchovy; (11) bluefish and longfin inshore squid; (12) Brandt's cormorant and Northern anchovy; (13) California sea lion and Pacific hake; (14) California sea lion and market squid; (15) California sea lion and Northern anchovy; (16) California sea lion and Pacific sardine; (17) California brown pelican and Pacific sardine (18) California brown pelican and Northern anchovy; (19) common murre and Northern anchovy; (20) common murre and Pacific hake; (21) common murre and market squid; (22) thresher shark and Pacific chub mackerel; (23) thresher shark and Northern anchovy; (24) thresher shark and Pacific hake; (25) thresher shark and Pacific sardine; (26) dolphinfish and shortfin squid; (27) elegant tern (chicks) and Northern anchovy; (28) humpback whale and Northern anchovy; (29) humpback whale and Pacific sardine; (30) North Pacific albacore and Pacific hake; (31) North Pacific albacore and Northern anchovy; (32) offshore hake (mid Atlantic bight) and longfin inshore squid; (33) offshore hake (mid Atlantic bight) and shortfin squid; (34) Pacific bonito and Northern anchovy; (35) Pacific harbor seal and Northern anchovy; (36) Pacific harbor seal and Pacific hake; (37) Gulf of Maine pollock and longfin inshore squid; (38) sablefish and Pacific hake; (39) shortfin mako shark and longfin inshore squid; (40) shortfin mako shark and shortfin squid; (41) silky shark and shortfin squid; (42) spiny dogfish and Atlantic menhaden; (43) spiny dogfish and Atlantic herring; (44) spiny dogfish and Pacific hake; (45) spiny dogfish and Atlantic mackerel; (46) striped marlin and Pacific sardine; (47) striped marlin and Pacific chub mackerel; (48) summer flounder and longfin inshore squid; (49) swordfish and shortfin squid; (50) yellowtail rockfish and Pacific hake.

prey. The data set showed almost no evidence of a strong positive relationship between the predator surplus production and the prey abundance (Fig. 1). While in half of the cases the slope estimates were positive, in only four cases did we find a statistically significant positive relationships between predator and prey abundance (Fig. S2) (with no correction for multiple comparisons): arrowtooth flounder (*Atheresthes stomias*) and Pacific hake (Figure 1.2), yellowtail rockfish and Pacific hake (Figure 1.50), North Pacific

Table 2
Summary table for the regime shift (shifts), random, Beverton-Holt and hockey-stick stock recruitment (SR) models. We recognize that this violates the independence assumption of the AIC, but believe it is indicative of relative strength of evidence for competing hypotheses. N is number of years in the time series and Corr is the coefficient of auto-correlation of the logarithm of recruitment. N shifts = number of estimated breakpoints.

Species	Area	N	Corr	N shifts	AIC Shifts	AIC BH	AIC Hockey	AIC Random	Winner
Pacific chub mackerel	California Current	79	0.66	6	166	201	206	239	Shift
Atlantic herring	US East Coast	37	0.34	2	76	81	81	85	Shift
Gulf menhaden	Gulf of Mexico	35	0.06	1	20	22	22	20	Random
Atlantic menhaden	US East Coast	51	0.50	3	63	83	91	89	Shift
Pacific hake	California Current	47	−0.29	1	166	168	168	166	Random
Pacific sardine	California Current	27	0.84	2	85	63	62	112	Hockey
Atlantic mackerel	US East Coast	47	0.52	2	143	129	129	155	BH/Hockey

albacore (*Thunnus alalunga*) and Pacific hake (Figure 1.30), and offshore hake (*Merluccius albidus*) (mid Atlantic bight) and longfin inshore squid (*Doryteuthis pealeii*) (Figure 1.32). The percent variance explained in these four cases ranged from 10% to 34%. The 95% confidence bounds on the estimated slope (y and x axes in units of standard deviation) were often wide, with upper bounds exceeding a value of 0.5 in close to half of the cases.

3.3. Recruitment analysis

For the seven species assessed, the stock-recruitment models outperformed the regime shift and the random models in two cases: Pacific sardine and Atlantic herring (Table 2). For the other five species the regime-shift or the random model had lower values of AIC. This result was independent of the minimum segment length specified for the changepoint analysis (shorter segment lengths yielded larger number of breakpoints, but the general result remained the same).

The hockey-stick and the Beverton-Holt models performed similarly when fit to the stock-recruitment data. Only in three cases – Pacific chub mackerel, Atlantic herring and Pacific sardine – was a breakpoint estimated by the hockey-stick model, indicating a decrease in recruitment below a given stock size. The breakpoint was estimated respectively at 17%, 19% and 13% of the maximum value of spawning biomass in the series. For Atlantic mackerel, a linear decrease in recruitment over the entire time series was favored with no identifiable breakpoint. The species for which evidence of decreased recruitment at lower spawning stock size was strongest also showed a highly auto-correlated recruitment (Table 2). By contrast, no evidence of a decrease in recruitment at low stock abundance was observed for the two menhaden stocks and for Pacific hake. Pacific hake and Gulf menhaden both had the lowest AIC for the random model while a regime-shift model was favored for Atlantic menhaden. Pacific chub mackerel and Atlantic herring also had the lowest AIC for the regime-shift model.

Pacific chub mackerel, Atlantic mackerel and Pacific sardine do show significantly lower recruitment at lower spawning stock size. However, each of those species shows highly auto-correlated recruitments that are consistent with environmentally driven regime changes and the apparent spawner recruit relationship may in fact simply be that periods of low recruitment lead to periods of low spawning stock size.

3.4. Simulated impacts of fisheries on prey abundance

For the six examples considered, the simulations conducted assuming recruitment is independent of spawning stock (Scenario 1) suggest that the abundance of small and small-medium size fish is unaffected by fishing (Fig. 2) and even in the absence of fishing the abundance of all sizes fluctuates greatly. Typically, the small sizes tend not to be caught in the corresponding fisheries (Fig. 3). In contrast, the abundance of large fish can be substantially reduced when F is set at F_{MSY}. When a stock-recruitment relationship is assumed (Scenario 2), in most cases a reduction in fish abundance was observed for all size ranges, the magnitude of which increased with fishing pressure.

Additionally, variability was reduced as fishing pressure increased. The two exceptions were Pacific hake and Gulf menhaden (Fig. 2). For these two species, the fit of the Beverton-Holt curve was flat in the range of observed abundances, which is similar to the assumption that recruitment is independent of stock size (Fig. 4). The fishery simulated for Gulf menhaden targeted almost exclusively individuals of age 2 (approximately 15 cm, Fig. 3), while the population was mainly composed of 0+ (small) and 1+ (small-medium) fish. This is most likely the main reason why abundance of fish does not respond to fishing pressure for this stock. In the case of Pacific hake, a substantial fishing impact was observed only for medium-large and large fish, which corresponds to the sizes selected by the fishery.

These results emphasize the relevance of the size composition of the diet when the fishing effects on predators are assessed. Unfortunately, data on the size compositions of diets are scarce. We could only find 74 records of size of forage fish prey (Fig. 3). While some predators selectively eat small fish (usually not selected by the fishery), others prey on a large range of forage fish sizes. The degree of overlap between fisheries and predators is highly variable. For example, most predators foraging on market squid and Pacific hake do not seem to be in direct competition with fisheries. On the other hand, Pacific chub mackerel, Pacific sardine and Atlantic herring fisheries seem to overlap with predator's preferred prey sizes.

4. Discussion

4.1. Trends in predator populations and growth rates of predators vs prey

For the populations studied, we found little evidence that the abundance of individual species of forage fish was positively related to the per capita rate of change in their predator populations. Of the 50 comparisons, we found five that had a significantly positive relationship between prey abundance and predator rate of change The fact that only four of the time series of predator abundance showed a downward trend also provides some evidence that historical fishing practices on forage prey species have not led to major predator decreases.

Given the very large range of abundance fluctuations seen in many of the forage fish populations, it is surprising that a relationship between forage fish abundance and predator rate of change does not emerge. The most obvious explanation would be diet flexibility. If the predators can switch between alternative prey, then the fluctuations in any individual forage species may be well buffered by the predator switching to other forage species. We also explored various time lags between prey abundance and predator rate of change, and did not find higher rates of correlation. We did not look at the abundance of forage species in aggregate in our one species at a time comparison.

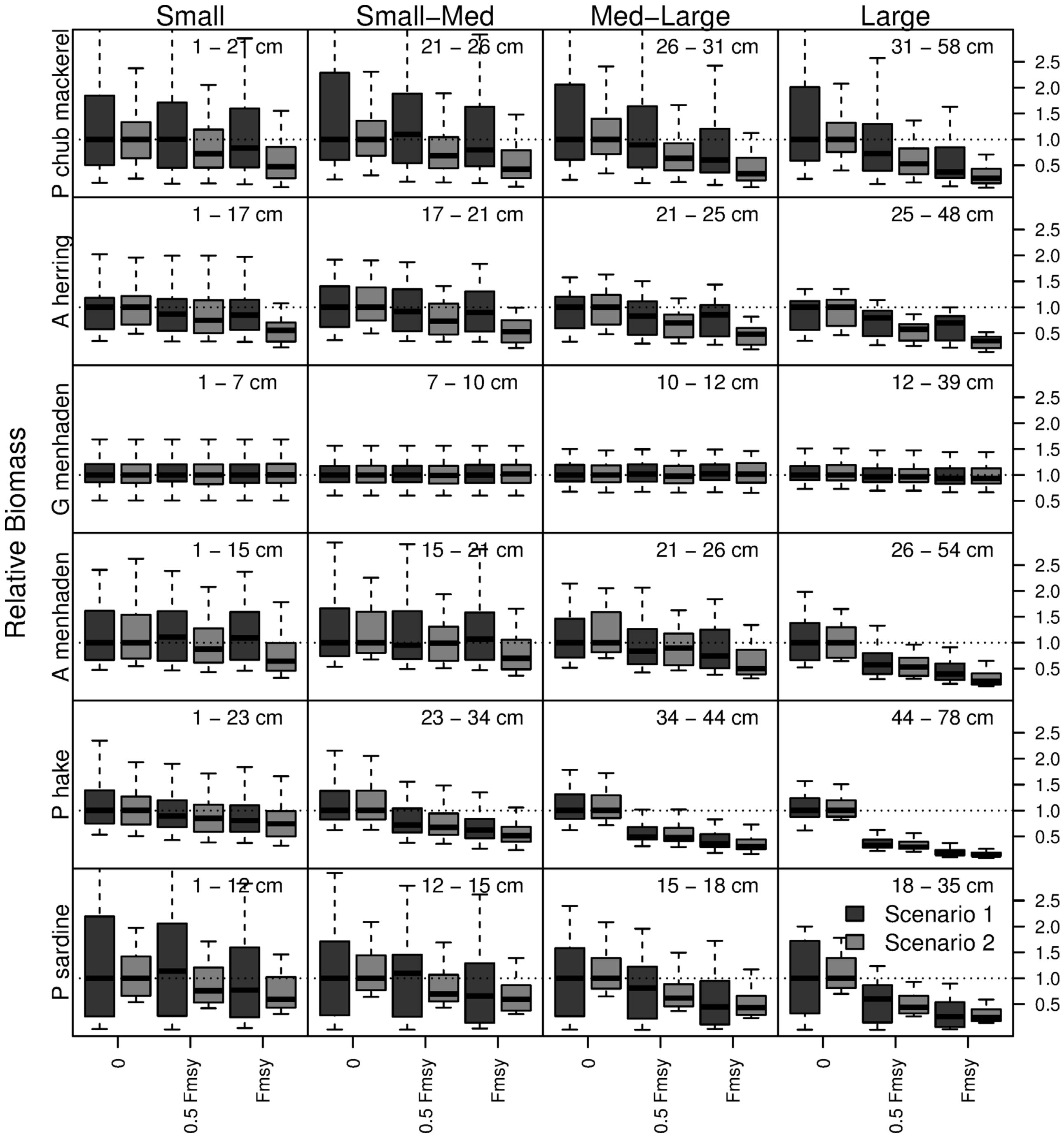

Fig. 2. Change in prey abundance predicted by the simulation model for six forage fish species in different size ranges. Scenario 1: recruitment independent of stock size; Scenario 2: Beverton-Holt stock recruitment relationship.

4.2. Recruitment analysis

If we simply look at the spawner-recruit data for the forage species examined we see little evidence that smaller spawning stocks produce smaller recruitments for both Atlantic and Gulf menhaden, and Pacific hake. Good year classes seem to come from both large and small spawning stock sizes. Pacific chub mackerel, Atlantic mackerel and Pacific sardine do show significantly lower recruitment at lower spawning stock size. However, each of those species shows highly auto-correlated recruitments that are consistent with environmentally driven regime changes and the apparent spawner recruit relationship may in fact simply be that periods of low environmental suitability result in long periods of low recruitment leading to low spawning stock. The relatively short life span of forage fish and several shifts from high to low productivity over the recruitment time series enhances this effect.

We have used statistical tests with changepoint analysis to try to quantify the support for regime changes vs stock-recruitment relationships and for each of these three species (Pacific chub mackerel, Atlantic herring and Atlantic Menhaden) the AIC analysis supports a regime change. This approach is only exploratory and does not provide a reliable basis for choosing a single operating model. Rather, the policy implications of alternative hypotheses should be evaluated within a management-strategy-evaluation framework and understanding the changes in recruitment is essential before evaluating alternative harvest strategies. However, we would argue

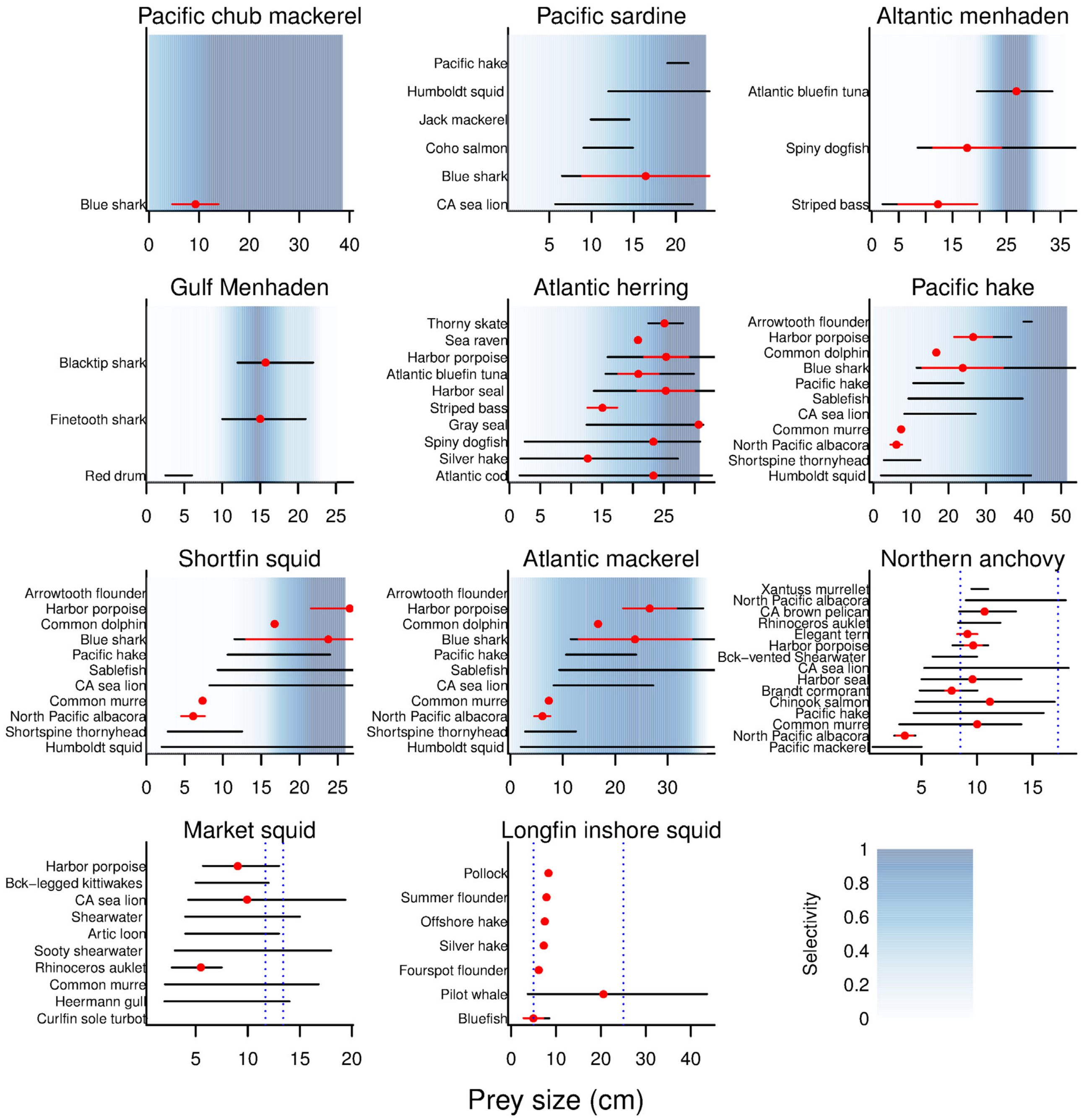

Fig. 3. Prey size consumed by different predators. Black lines indicate the range of sizes eaten. The red dots indicate the mean size of the prey, and the red line the standard deviation. The shading in the background indicates how fishery selectivity changes with fish length. When no estimates of fishery selectivity were found the dotted blue lines indicate the size range of the commercial catch.

that there is strong evidence that recruitments are largely independent of fishing pressure as has been widely accepted for Pacific sardine (Punt et al., 2016) and suggested for many other species globally (Szuwalski and Hilborn, 2015). It is of course not credible that recruitment is independent of stock size for all stock sizes (no eggs, no recruits). We assert only that the range of spawning stock sizes is often not wide enough within regimes to see any effect. It should be noted that within-regime stock-recruitment analysis is subject to strong time series bias, with over-representation of high recruitments at low stock size and low recruitments at high stock size (Walters, 1985) leading to overestimation of the initial stock-recruitment slope and reduced apparent dependence of recruitment on spawning stock size.

4.3. *Impacts of fisheries on prey abundance*

We found that small size classes are largely unaffected by fishing when the recruitments are simulated at historical levels assuming no impact of spawning stock, and that many, but not all of the predators rely on the smaller sized fish not targeted by fisheries. If we assume a spawner recruit model, then recruitment at F_{MSY} is reduced, so that the abundance of small size classes is also reduced. Given that for most stocks examined, a random recruitment or regime recruitment model was estimated to be best, the evidence for those stocks examined supports little impact of fishing on abundance of smaller size classes of fish. Thus one cannot generalize about the impacts of fishing on food availability to predators

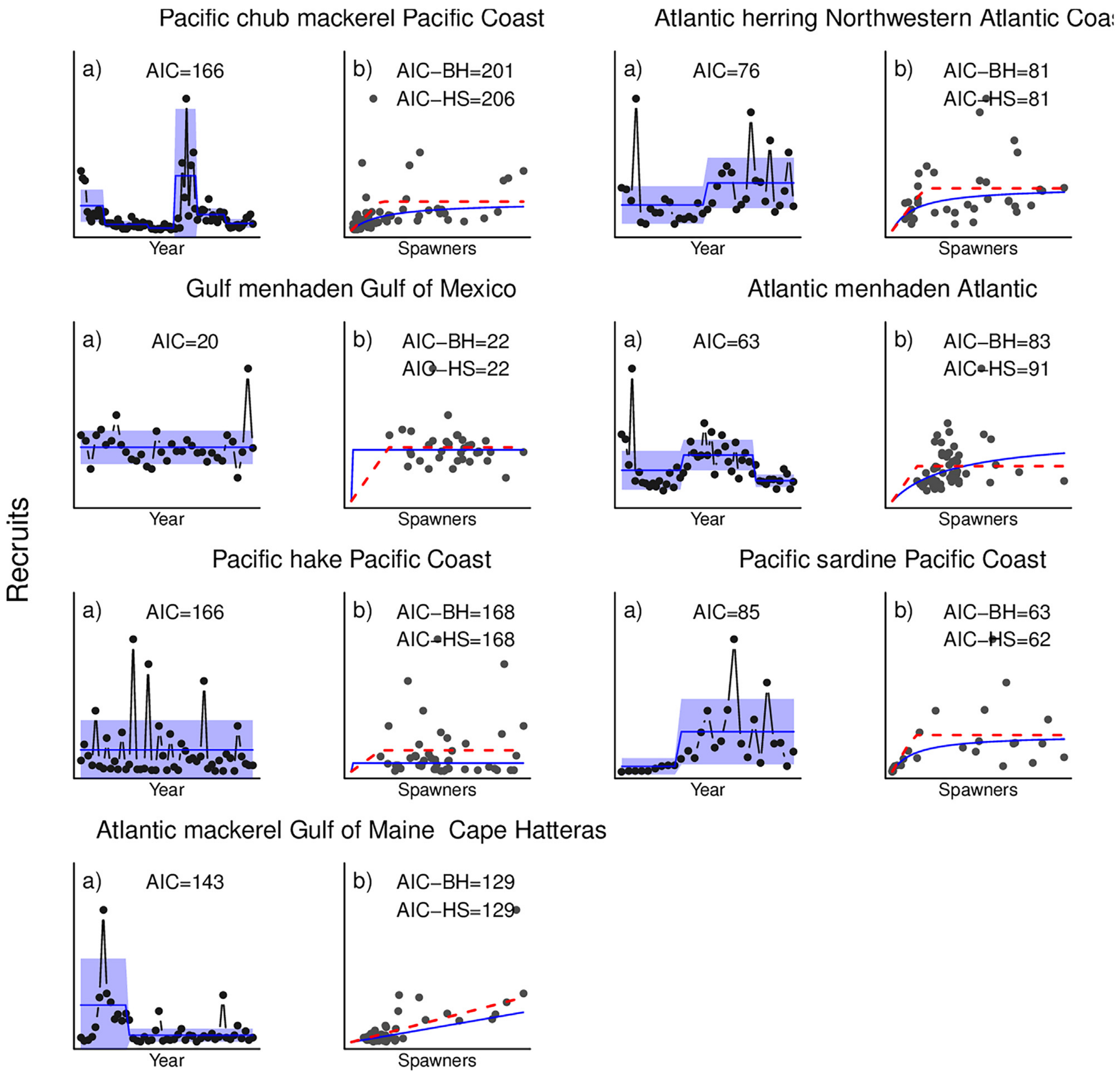

Fig. 4. Alternative models to explain recruitment variability: a regime-shift model, a Beverton-Holt stock-recruitment model and the hockey-stick model. The blue lines indicate the model maximum likelihood estimates. The purple polygons indicate the standard deviation in each regime identified by the changepoint analysis.

and each case must be examined on its own merits with respect to the impact of fishing on recruitment and the size preferences of the predators.

The diet of predators consists not only of the key species we examined here, but many other species, including juveniles of many larger species. Furthermore, the impact of fishing higher trophic level fishes has often caused forage species to be more abundant than they would be in the absence of fishing (Christensen et al., 2014; Kolding et al., 2016; Jennings and Collingridge, 2015).

4.4. *Spatial distribution of forage fish*

A major factor (though one which has been considered only qualitatively in this paper) is the relationship between the distribution of the forage fish, their abundance, and the location of breeding sites for dependent birds and mammals. Large fluctuations in abundance of the forage fish are accompanied by major changes in their distributional range – at high abundance the fish are found over a much larger area than at low abundance (MacCall, 1990). If there tend to be “core” areas where even at low overall abundance the forage fish can be found at high density, and these core areas are close to breeding sites of predators, predators would see far more stability in prey availability than indicated by total population size. On the other hand, if fisheries target prey hotspots or feeding areas close to breeding sites, then the impact of fishing may be larger than expected based on overall prey depletion.

This spatial dynamic is an important factor in modulating the response of pelican and sea lion abundance to fishing sardines and anchovy on the US West coast. Pelicans are more vulnerable to declines in sardine and anchovy because of a more restricted diet and more limited foraging area compared to sea lions (Punt et al., 2016). Spatial dynamics are especially important to consider when the distribution of forage fish shifts. Robinson et al. (2015) showed that decreases in the penguin population at Robben Island in South Africa were primarily due to changes in the distribution of sardines, not to the total sardine abundance.

Cury et al. (2011) showed a relationship between the abundance of key prey species and reproductive success of birds. However the index of forage fish abundance in half of the data sets they presented was not the total abundance of forage fish, but rather either local abundance measured around the nesting site, or amount of prey brought to the nest. Thus for those data sets, the relationship between total abundance of prey as influenced by fishing and reproductive success would be weaker than the relationship shown in the paper. Perhaps the best example of this is the data presented for three nesting sites for two bird species in Cook Inlet, Alaska (Piatt, 2002). Prey abundance around the nesting site was estimated by hydroacoustic surveys, and two of the sites generally showed good reproductive success associated with high prey abundance while one of the sites showed poor reproductive success and lower prey abundance. However, these results related to the same fish stock, subject to the same fishery, at all three sites.

The EwE models used in the Pikitch et al. and Smith et al. papers did not take the spatial structure of the forage fish populations into account, but instead assumed that total prey abundance, as influenced by fishing, was exactly what would determine the growth and survival of the predators. To evaluate the influence of fishing on the predators reliably, the changes in spatial distribution need to be considered. This is why both the Punt et al. (2016) and Robinson et al. (2015) papers estimate far less influence of fishing on predator populations than the simpler EwE models of Pikitch et al. and Smith et al. though some of the models used in the Smith et al. paper were ATLANTIS models that included some elements of spatial structure. Walters et al. (2016) also showed that the impact of fishing forage fish would depend greatly on how models were structured and that the conclusions of EwE models are very sensitive to model setup.

5. Conclusions

The purpose of this paper is to identify key factors that need to be included when analyzing the impacts of fishing on forage fish. We find several reasons to concur with the conclusion of Essington and Plaganyi (2013) that the models used in previous analysis were frequently inadequate for estimating impact of fishing forage species on their predators.

The most important feature that needs to be considered is the natural variability in forage fish population size. Their abundance is highly variable even in the absence of fishing, and a creditable analysis of the fishing impacts must consider how the extent of fishing-induced depletion compares with that of natural variability. As an example, Punt et al. (2016) estimated that the probability that brown pelicans would drop below 0.5 K with fishing was 5.3%, and without fishing was 4.5%. For marine fishes in general, "stochastic depletion" i.e. populations falling below 0.5 K, can be expected about 5% of the time even in the absence of fishing (Thorson et al., 2014). Models like EwE without stochasticity would suggest zero probability of such declines in the absence of fishing.

There is a need for a much more thorough analysis of the nature of recruitment trends in forage fish. That there are major environmentally-driven regime changes for many species is unarguable, but what exactly changes is unclear. It is unrealistic to assume that there is no relationship between spawning stock abundance and subsequent recruitment, so what is presumably changing with the environment is either the basic carrying capacity for forage fish, the basic productivity (recruits per spawner) or some combination of the two. The actual dynamics may not involve discrete regimes, but rather gradual changes in the spawner recruitment relationship. The harvest strategy that maximizes long-term fishery yield will depend greatly on exactly how the spawner recruit relationship is changing. If it is the carrying capacity that changes, then a constant fishing mortality rate will produce long-term yields that are very close to the theoretical optimum (Walters and Parma, 1996). If, however, it is the underlying productivity that changes, the fishing mortality rate may need to be respectively increased or decreased as productivity changes upwards or downwards.

The size distribution of both predator and prey and the size selectivity in diet need to be included in any analysis. In cases where recruitment is largely independent of spawning stock, and the predators take prey before they are fished, there is no influence of the fishery on availability of prey to predators. We identified numerous examples where this is the case (Fig. 3), but it is not universal. Some predators compete directly with the fishery for the same sizes of prey and such competition must be considered if we are to manage fisheries appropriately for both predators and prey.

We have found several examples of the importance of changes in spatial distribution of prey affecting the predators that suggest any analysis that does not consider such changes will not properly evaluate the impact of fishing forage fish on their predators. These include the South African penguin and sardine interaction and the Cook Inlet example (Piatt, 2002).

Our analysis of the relationship between predator rate of change and abundance of individual prey species suggests little evidence for strong connections. This is likely due to the many factors discussed above that mediate the link between fishing, prey abundance, spatial distribution and size, and predator population dynamics. The fact that few of the predator populations evaluated in this study have been decreasing under existing fishing policies suggests that current harvest strategies do not threaten the predators and there is no pressing need for more conservative management of forage fish. Hannesson (2013) showed that declines of Pacific sardine, Norwegian spring spawning herring, and Peruvian anchoveta had small impacts on their fish predators, although he relied on catches of the predators rather than direct measures of abundance. This is further evidence that general rules proposed by Pikitch et al. (2012) are not appropriate for all species and a case by case analysis is needed.

Pikitch et al. (2012) argued forcefully that their analysis provided general conclusions that should be broadly applied. However, relevant factors are missing from the analysis contained in their work, and this warrants re-examination of the validity and generality of their conclusions. We have illustrated how consideration of several factors which they did not consider would weaken the links between impacts of fishing forage fish on the predator populations.

Smith et al. (2011) were much more reserved in their conclusions, ending primarily with the estimate that fishing mortality rates on forage fish could be well below F_{MSY} with only a 20% decrease in catch of forage fish while having appreciable benefits to their predators. All single species population models show little decrease in yield with fishing mortality rates less than F_{MSY} and this would be true for forage fish as well. The very simple logistic growth model suggests that a fishing morality rate of $0.5\,F_{\mathrm{MSY}}$ would produce 75% of MSY. However, the evidence presented here suggest that reductions in fishing mortality rate would benefit predators less than argued by Pikitch et al. (2012). Most of the issues we raised in this paper apply to most of the models used by Smith et al. (2011).

It must be remembered that small pelagic fish stocks are a highly important part of the human food supply, providing not only calories and protein, but micronutrients, both through direct human consumption and the use of small pelagics as food in aquaculture. Some of the largest potential increases in capture fisheries production would be possible by fishing low trophic levels much harder than currently (Garcia et al., 2012; Kolding et al., 2016). While fishing low trophic levels harder may reduce the abundance of higher level predators, that cost should be weighed against the environmental cost of increasing food production in other ways. As Sharpless and Evans (2013) point out, fish provide food without substantial use of freshwater, fertilizer, antibiotics and soil erosion. Forage fish also have among the lowest carbon footprints of any form of protein production (Pelletier et al., 2011). Thus it is not clear that from a global environmental perspective that reductions in fishing mortality rates on forage fish would necessarily be precautionary.

We have used examples of predators and forage fish only from U.S. fisheries, which are widely recognized to be among the best managed in the world, and also have extensive legal protections for many higher trophic level birds and mammals. While the deficiencies we have identified in the existing models are general, the status and trends of predators and prey may be quite different in other parts of the world.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.01.008.

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