CENTER for BIOLOGICAL DIVERSITY Because life is good.

Via electronic and certified mail

September 7, 2021

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Re: 60-Day Notice of Intent to Sue: Violations of the Endangered Species Act Related to the California/Oregon/Washington Sablefish Pot Fishery

Dear Secretary Raimondo, Director Marzin, and Regional Administrator Thom:

On behalf of the Center for Biological Diversity (the "Center"), this letter serves as a sixty-day notice of intent to sue the National Marine Fisheries Service ("NMFS") over violations of sections 7 and 9 of the Endangered Species Act ("ESA"), 16 U.S.C. §§ 1531-1544, for actions and inactions related to the management and authorization of the California/Oregon/Washington sablefish pot fishery ("Fishery").

First, NMFS's continued authorization of the Fishery without a valid permit to take ESA-listed humpback whales violates the ESA's prohibition on take of endangered animals. To authorize the lawful take of ESA-listed marine mammals, the ESA requires a Marine Mammal Protection Act ("MMPA") authorization, which for this Fishery expired September 4, 2016.[1] Accordingly, the continuing take of humpback whales during the Fishery's operation is unlawful.

Second, NMFS failed to use the best available science in its 2020 biological opinion on the Continuing Operation of the Pacific Coast Groundfish Fishery ("Biological Opinion").[2] It

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[1] 16 U.S.C. § 1536(b)(4); *Taking of Threatened or Endangered Marine Mammals Incidental to Commercial Fishing Operations; Issuance of Permit, Notice*, 80 Fed. Reg. 22709 (Apr. 23, 2015) (amending the permit issued on September 4, 2013).

[2] Endangered Species Act Biological Opinion, Continuing Operation of the Pacific Coast Groundfish Fishery (Reinitiation of consultation #NWR-2012-876) – Humpback whale (*Megaptera novaeangliae*),

failed to consider: (1) NMFS's determination that the Central America population is a demographically independent population and that the stock assessment is outdated, (2) scientific papers assessing the Fishery's entanglement risk for humpback whales, and (3) estimates of humpback mortality from ship strikes that are several times higher than those in the Biological Opinion. NMFS's reliance on this legally flawed Biological Opinion to authorize the Fishery violates the agency's duty to ensure its actions are not likely to jeopardize the continued existence of ESA-listed humpback whales or destroy or adversely modify their critical habitat.[3]

Third, NMFS must reinitiate consultation in light of new information since publication of the Biological Opinion that reveals effects of the Fishery on humpback whales and their critical habitat to an extent NMFS has not previously considered.[4] This new information includes: (1) at least three scientific papers that present new information relevant to assessing the effects of the Fishery on humpback whales, and (2) the final humpback whale critical habitat rule that added specific examples to the descriptions of the prey feature for each humpback whale distinct population segment, plus new information showing that humpback whales' prey abundance is severely compromised. NMFS's ongoing failure to reinitiate and complete consultation violates section 7 of the ESA.

To remedy these legal deficiencies, we request that NMFS propose an emergency regulation to remain in place until NMFS has published a new biological opinion that includes an incidental take statement for humpback whales. The emergency rule would close the Fishery in humpback whale critical habitat unless ropeless or popup fishing gear is used.

Ropeless fishing gear is a solution to the entanglement problem afflicting the Fishery. This gear, also known as "on-demand" or "pop-up buoy" gear, eliminates or reduces the risk of entanglement by removing the unattended vertical line running through the water column. It is the only way to prevent entanglements while allowing fishing to continue without ESA authorizations. We urge NMFS to consider seriously its implementation as soon as possible.

I. Legal Background

Congress enacted the ESA, in part, to provide a "means whereby the ecosystems upon which endangered species and threatened species depend may be conserved . . . [and] a program for the conservation of such endangered species and threatened species."[5]

Section 2(c) of the ESA establishes that it is "the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species and shall utilize their authorities in furtherance of the purposes of this Act."[6] The ESA defines "conservation" to mean "the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to

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NMFS Consultation Number WCRO-2018-01378; *see* 16 U.S.C. § 1536(a)(2); 50 C.F.R. § 402.14(d), (g).

[3] 16 U.S.C. § 1536(a)(2).

[4] *Id.*; 50 C.F.R. § 402.16.

[5] 16 U.S.C. § 1531(b).

[6] *Id*. § 1531(c)(1).

this Act are no longer necessary."[7] Similarly, section 7(a)(1) of the ESA directs that NMFS and other federal agencies shall use their programs and authorities to conserve endangered and threatened species.[8]

To fulfill the purposes of the ESA, section 9 of the ESA prohibits any "person" from "taking" any endangered species, including endangered humpback whales.[9] This take prohibition also applies to threatened humpback whales.[10] The term "take" means "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct."[11] Incidental take is defined as take that is incidental to, and not for the purpose of, the carrying out of an otherwise lawful activity.[12]

Additionally, section 7(a)(2) of the ESA requires federal agencies to "insure that any action authorized, funded, or carried out by such agency . . . is not likely to jeopardize the continued existence of any endangered species or threatened species or result in the destruction or adverse modification of [their federally designated critical] habitat."[13] To comply with this mandate, section 7(a)(2) requires federal agencies to consult with the departments of Commerce or Interior whenever their actions "may affect" a listed species and utilize the "best scientific and commercial data available" in doing so.[14]

Where, as here, NMFS is both the action agency and the consulting agency, NMFS must undertake intra-agency consultation. At the completion of consultation, the consulting branch of NMFS issues a biological opinion that determines whether the action is likely to jeopardize the continued existence of the species. If NMFS concludes that the action will not cause jeopardy, but may result in the take of endangered species, NMFS will issue an incidental take statement ("ITS") that specifies "the impact, i.e., the amount or extent, of . . . incidental taking" that may occur.[15] An ITS must include "reasonable and prudent measures . . . necessary . . . to minimize such impact,[16] and must specify the permissible level of taking, "thus . . . serv[ing] as a check on the agency's original decision that the incidental take of listed species resulting from the proposed action will not [jeopardize the continued existence of the species]."[17] Additionally, when the endangered species to be taken are marine mammals, the ITS must also "specif[y] those measures that are necessary to comply with section 1371(a)(5) of this title [the MMPA's section 101(a)(5)] with regard to such taking."[18] The take of a listed species in compliance with the terms of a valid ITS is not prohibited under section 9 of the ESA.[19]

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[7] *Id.* § 1532(3).
[8] *Id.* § 1536(a)(1).
[9] *Id.* § 1538.
[10] 50 C.F.R. § 223.213.
[11] 16 U.S.C. § 1532(19).
[12] *Id.* § 1539(a)(1)(B).
[13] *Id.* § 1536(a)(2); 50 C.F.R. § 402.14(a).
[14] 16 U.S.C. § 1536(a)(2).
[15] 50 C.F.R. § 402.14(h)(4).
[16] 16 U.S.C. § 1536(b)(4).
[17] *Id.*; *Center for Biological Diversity v. Salazar*, 695 F.3d 893, 911 (9th Cir. 2012).
[18] 16 U.S.C. § 1536(b)(4)(C)(iii).
[19] *Id.* §§ 1536(b)(4), (o)(2); 50 C.F.R. § 402.14(i)(5).

After the issuance of a final biological opinion and "where discretionary Federal involvement or control over the action has been retained or is authorized by law," the agency must reinitiate formal consultation if, among other things, "the amount or extent of taking specified in the incidental take statement is exceeded;" "new information reveals effects of the action that may affect listed species or critical habitat in a manner or to an extent not previously considered;" or "a new species is listed…that may be affected by the identified action."[20]

The MMPA places a moratorium on the taking of marine mammals, and only after invoking limited exceptions to this moratorium may NMFS allow take incidental to commercial fishing operations.[21] Specifically, MMPA section 101(a)(5)(E) requires that for endangered or threatened marine mammals, NMFS must make a finding that any incidental mortality or serious injury from commercial fisheries will have a negligible impact on such species or stock. Therefore, NMFS may only authorize incidental take of endangered marine mammals when it has authorized take under both the MMPA and the ESA.

II. NMFS Is Causing Ongoing Humpback Whale-Fishery Interactions in Violation of ESA Section 9

Since 2014's drastic increase in reported West Coast whale entanglements, fishery entanglements of humpback whales have remained a serious conservation problem. In 2020, NMFS confirmed 17 entangled whales off the West Coast.[22] This is fewer confirmed reports than in any year since 2013 yet is still far too high and represents an underestimate of whales entangled. The actual entanglements are likely far higher because most confirmed reports come from opportunistic sightings of entangled whales. Decreases in monitoring effort (e.g., whale watching) during the pandemic may have led to decreases in confirmed reports.

The Fishery entangles humpback whales in sablefish pot gear, which is set in approximately two-mile-long strings of 30 to 50 pots and fished generally from April to October. NMFS records since 1982 include five confirmed humpback whale entanglements involving sablefish pot gear.[23] One of the entanglements was reported in August 2006. More recent entanglements occurred in October 2014, two in 2016 in April and May, and one in July 2017.[24] In the 2014 report and one of the entanglements in 2016, the gear was originally set in Oregon, while the set location for the other entanglements are unknown. More details about the four most recent confirmed entanglements are below.[25]

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[20] 50 C.F.R. § 402.16.

[21] 16 U.S.C. § 1371(a) ("There shall be a moratorium on the taking and importation of marine mammals . . . during which time no permit may be issued for the taking of any marine mammal . . . except in the following cases").

[22] NOAA Fisheries, 2020 West Coast Whale Entanglement Summary, (2021). https://media.fisheries.noaa.gov/2021-03/2020_West_Coast_Whale_Entanglement_Summary.pdf?null.

[23] Saez, L., D. Lawson, and M. DeAngelis. "Large whale entanglements off the U.S. West Coast, from 1982-2017." NOAA Tech. Memo. NMFS-OPR-63A, 50 p. (2021) https://www.fisheries.noaa.gov/resource/document/large-whale-entanglements-us-west-coast-1982-2017.

[24] *Id.*

[25] The captures of two humpback whales by vessels using trawl gear in 2020 are described in the biological opinion and will not be repeated here because to our knowledge NMFS has not released additional information about the entanglements.

A. Directly Observed Humpback Whale-Fishery Interactions

One humpback interaction was observed in 2014.[26] In October 2014, an observer aboard a limited entry sablefish pot vessel fishing off the Washington/Oregon border saw a deceased adult humpback whale brought next to the vessel while recovering a string of approximately 35 pots with weighted line between traps. The whale had apparently been caught in a portion of the ground line between the pots and drowned.

This event prompted a deckhand on the vessel to report a similar encounter on another limited entry sablefish vessel two months prior. At that time, the whale was entangled in the buoy line. The crew was able to pull the whale's tail near the rail of the vessel and cut the line with knives in hand to free it and the whale was able to swim away.

Two reports of entanglements in 2016 were attributed to the sablefish pot fishery.[27] In April 2016 a fisherman and fishery observer disentangled a humpback from sablefish gear off Humboldt, California. It was unclear whether the whale was fully disentangled. In May 2016, a juvenile humpback was disentangled off Oregon. It had been entangled with ¾" line with sablefish pot gear, three poly balls and a high flyer. The entire gear set included a total of 37 traps set at intervals at 220 fathoms and 80-pound anchors at each end. The whale swam away from the disentanglement efforts with about three feet of line on its tail.

The 2017 humpback whale entanglement involved a mooring line set during the operation of sablefish pot fishing, and the whale subsequently became entangled with multiple sets of coonstripe shrimp traps as well.[28] While additional corroborating information is provided in NMFS's annual report on marine mammal serious injury and mortality,[29] the Biological Opinion mentions this interaction only briefly.[30]

B. Estimated Humpback Whale-Fishery Interactions

Pot and trap fisheries in general represent the majority of documented fishery interactions with humpbacks along the U.S. West Coast, yet the number of observed humpback whales caught in the Fishery is relatively low, so NMFS has estimated the bycatch in the Fishery's pots

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[26] J. Carretta, et al. 2016. Sources of human-related injury and mortality for U.S. Pacific West Coast Marine Mammal Stock Assessments, 2010-2014. NOAA-TM-NMFS-SWFSC-554, at 92, https://docs.lib.noaa.gov/noaa_documents/NMFS/SWFSC/TM_NMFS_SWFSC/NOAA-TM-NMFS-SWFSC-554.pdf.

[27] NMFS. 2016. West Coast Entanglement Summary: Overview of Entanglement Data. March 2017. http://www.westcoast fisheries.noaa.gov/mediacenter/WCR%202016%20Whale%20Entanglements_3-26-17_Final.pdf.

[28] Saez et al. 2021.

[29] Carretta, J.V., et al. "Sources of Human-related Injury and Mortality for U.S. Pacific West Coast Marine Mammal Stock Assessments," 2015-2019. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-643 (2021).

[30] Biological Opinion at 45 ("In addition, during this period (2011-2017), there have also been three other humpback whale entanglements reported to NMFS through opportunistic observations from ocean users that have been identified as involving sablefish pot gear; one in 2006, 2016, and 2017.").

(Table 1). NMFS has estimated that more than one humpback whale has been caught every year since 2003.[31]

Table 1. Bycatch estimates of humpback whale observed bycatch in the Limited Entry (LE) and Open Access (OA) pot fishery.[32]

Year	Mean (LE)	Lower 95% CI	Upper 95% CI	Mean (OA)	Lower 95% CI	Upper 95% CI	Total
2002	**0.35**	0.00	1.38	**N/A**	N/A	N/A	**0.35**
2003	**0.41**	0.00	1.43	**9.00**	0.10	30.34	**9.41**
2004	**0.74**	0.00	2.95	**2.99**	0.09	8.91	**3.73**
2005	**0.16**	0.00	0.65	**5.12**	0.10	17.30	**5.28**
2006	**0.26**	0.00	0.98	**7.63**	0.10	25.85	**7.89**
2007	**0.43**	0.00	1.82	**5.12**	0.10	17.10	**5.55**
2008	**0.11**	0.00	0.48	**3.98**	0.19	13.70	**4.09**
2009	**0.65**	0.00	2.42	**5.73**	0.00	18.45	**6.38**
2010	**0.38**	0.00	1.37	**4.92**	0.09	16.24	**5.30**
2011	**0.20**	0.00	0.82	**2.27**	0.00	7.50	**2.47**
2012	**0.29**	0.00	1.04	**2.14**	0.00	7.14	**2.43**
2013	**0.55**	0.00	2.32	**1.42**	0.00	4.75	**1.97**
2014	**1.26**	1.00	2.04	**1.90**	0.00	6.26	**3.16**
2015	**0.07**	0.00	0.31	**2.23**	0.00	7.39	**2.30**
2016	**0.07**	0.00	0.26	**3.19**	1.00	8.41	**3.26**
2017	**0.25**	0.00	1.04	**1.73**	0.00	5.12	**1.98**
2018	**0.06**	0.00	0.26	**1.72**	0.00	5.41	**1.78**
2019	**0.17**	0.00	0.65	**1.43**	0.00	4.73	**1.60**

These ongoing interactions violate section 9 of the ESA because the Biological Opinion fails to include an ITS for humpback whales "because the incidental take of humpback whales has not been authorized under section 101(a)(5)(E) of the Marine Mammal Protection Act (MMPA) (see 16 U.S.C. 1536(b)(4)(C))."[33] The Biological Opinion further states that "NMFS is actively pursuing an authorization under section 101(a)(5)(E) and anticipates a proposed authorization may be available in late 2020 or early 2021."[34] To our knowledge NMFS has not received such authorization or provided an update on when a proposed authorization will be available.

As the agency that authorizes and manages the Fishery,[35] NMFS is liable for any take of ESA-listed species that results from operation of the Fishery. By continuing to permit, authorize,

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[31] Hanson, M.B., et al. "Estimated Humpback Whale Bycatch in the U.S. West Coast Groundfish Fisheries, 2002-2019." Pacific Fishery Management Council Agenda Item G.4.a, NMFS Report 4, Appendices 1 and 2, June 2021.

[32] *Id.*

[33] Biological Opinion at 63.

[34] *Id.*

[35] 50 C.F.R. § 660.25.

and manage the Fishery, NMFS's actions and inactions have caused, and will continue to cause, the unpermitted take of endangered humpback whales in the Central America distinct population segment ("DPS") and threatened humpback whales in the Mexico DPS in violation of section 9 of the ESA.[36]

III. The Biological Opinion Does Not Include the Best Available Science and NMFS's Reliance on the Biological Opinion Violates Its ESA Section 7 Duties.

The Biological Opinion fails to consider the best scientific data available with respect to estimating the abundance of the Central America DPS and Mexico DPS of humpback whales, the entanglement risk of the Fishery, and the estimates of humpback whale mortality from ships strikes.

A. There Is No Data To Support NMFS's Assumption That ESA-Listed Humpback DPSs Have Increased Six Percent Annually For Fifteen Years.

First, the Biological Opinion does not adequately consider that NMFS has recognized that the Central America population is a demographically independent population ("DIP") under the MMPA and that the stock assessment's stock designation for humpback whales should be considered for revision.[37] In 2019 NMFS released guidance on "Reviewing and Designating Stocks" that reiterated "that a stock generally comprises a single DIP," though in relatively few cases this may be impractical.[38] In 2019 NMFS also published a handbook for delineating marine mammals DIPs, which stated that

> the endangered Central American distinct population segment (DPS) . . . contains a single migratory herd and also comprises a single DIP. A known threat is entanglement in California. Thus, the boundary for this DIP would run from Central America, through its migratory corridor in Mexico and to California and Oregon.[39]

This paragraph clearly states that the Central America population is not only a DPS under the ESA but also a DIP under the MMPA.

Rather than considering this information, the Biological Opinion relied on studies concluding that West Coast humpback whales (including populations not listed under the ESA) have increased over 30+ years to assume that the endangered Central America DPS and threatened Mexico DPS have increased likewise:

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[36] 16 U.S.C. § 1538.

[37] Procedural Directive 02-204-03: Reviewing and Designating Stocks and Issuing Stock Assessment Reports under the Marine Mammal Protection Act (November 2019); *2019 Marine Mammal Stock Assessment Reports, Notice; response to comments*, 85 Fed. Reg. 46589, 46591 (Aug. 3, 2020).

[38] Procedural Directive 02-204-03 (2019) at 2.

[39] Martien, K.K. et al. "The DIP Delineation Handbook: A Guide to Using Multiple Lines of Evidence to Delineate Demographically Independent Populations of Marine Mammals." U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-622 (2019) at 33-34.

> if we assume that the population estimated by Wade (2017) based on information from 2004-2006 (783 animals) has increased by 6 percent annually in the last 15 years, the current abundance estimate of the [Central American DPS] would be 1,876 animals.[40]

This leap of logic assumes that an increase in humpbacks generally, including unlisted humpbacks, means that there has been an increase in a small, endangered humpback whale DPS. Nowhere in the Biological Opinion does NMFS explain how the Central America population can be a DIP and have the same abundance trend as West Coast humpbacks as a whole. Rather, NMFS does "not know whether these increases are applicable to all three DPSs that forage" off the West Coast.[41]

This has potentially significant conservation implications for the endangered Central America DPS, which in 2016 NMFS estimated had 411 individuals.[42] The handbook also listed the abundance of the Central America DIP as 411.[43] If the Central America DPS were considered a stock under the MMPA, the potential biological removal level ("PBR") would be less than one whale.[44] (The Guidance on revising stock assessment reports states that it "should provide DIP-specific information where available, including a DIP-specific PBR if it can be calculated."[45]) Thus the Fishery's mortality and serious injury of humpback whales potentially has severe population-level impacts.

The Biological Opinion's reliance on the abundance trends for the outdated stock designation of California/Oregon/Washington humpback whales is inexplicable. NMFS has stated repeatedly in the *Federal Register* that the California/Oregon/Washington humpback whale stock should be considered for stock designation revisions and that NMFS intends to address these revisions in future SARs.[46] Yet the Biological Opinion cites two sources for an increase in humpback whales, both of which only estimate abundance for the outdated humpback stock.[47]

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[40] Biological Opinion at 28 (replacing Mexico DPS with Central American DPS to correct what seems to be a copy-and-paste mistake); *see also id.* at 61 (estimating there to be "approximately 1,876 whales given a 6 percent increase over the last 15 years, [so] we expect there to be a maximum impact to the DPS of 0.53 percent of abundance").

[41] Biological Opinion at 29.

[42] Endangered and Threatened Species; Identification of 14 Distinct Population Segments of the Humpback Whale (*Megaptera novaeangliae*) and Revision of Species-Wide Listing; Final Rule, 81 Fed. Reg. 62,260, 62307 (Sept. 8, 2016).

[43] *Id.* Figure 5.1.

[44] Letter from Rebecca J. Lent, Ph.D., Executive Director, Marine Mammal Commission, to Chris Yates, National Marine Fisheries Service, West Coast Region, dated Feb. 13, 2017, regarding 82 Fed. Reg. 2,954 (Jan. 10, 2017).

[45] Procedural Directive 02-204-03 (2019) at 8.

[46] *See, e.g.,* 85 Fed. Reg. 46590-91; *2020 Marine Mammal Stock Assessment Reports, Notice; response to comments*, 86 Fed. Reg. 38991, 39001 (July 23, 2021).

[47] Biological Opinion at 60 (citing Carretta et al. (2020) and Calambokidis and Barlow (2020)).

B. NMFS Ignored Its Own Studies Of Fishery Entanglement Risk.

Second, NMFS has published scientific papers assessing the Fishery's entanglement risk for humpback whales that it did not consider in the Biological Opinion. The first paper, Saez et al. (2013), performed an entanglement risk assessment for eleven fisheries, including Washington/Oregon/California sablefish pot.[48] Sablefish pots and sablefish longline tied for the third-highest entanglement risk for humpback whales.[49] The model identified areas of elevated risk for where and when large whales are more likely to encounter fixed commercial gear and possibly become entangled.[50] The Biological Opinion unlawfully failed to consider this scientific data about the impact of the Fishery on humpback whales.

Similarly, Feist et al. (2015) overlaid the predicted densities of humpback whales with data for commercial fishing effort of the fixed-gear (pots), at-sea hake mid-water trawl, and bottom trawl fleets of the West Coast groundfish fishery. [51] The authors, all NMFS scientists, characterized the study as an important first step "in generating formal risk assessments for quantification of the impacts of various fishing fleets on populations of cetacean species that occur in the California Current."[52] The paper found that for "the observed fixed fleet, peak areas of overlap with the humpback whale (*R*s>17) occurred north of Cape Mendocino, California, off the central Oregon coast, and off Astoria Canyon, Oregon." This information is helpful in describing the areas and gears in the Fishery that have highest entanglement risk. Yet this paper too was ignored by NMFS in the Biological Opinion.

C. Ship Strike Mortality For Humpback Whales Is Higher Than Observed Mortality and Exceeds Relevant Biological Thresholds For Anthropogenic Death.

Third, NMFS did not properly consider the high level of humpback mortality from ship strikes in the Biological Opinion. Specifically, published science shows that (1) whale mortality from ship strikes is many times greater than observed mortality; and (2) this mortality is negatively impacting whale recovery. [53] Rockwood *et al*. (2017) concluded that "mortality estimates" for humpback whales, in addition to other endangered whales, are "far higher than current estimates."[54] Even the study's most conservative model estimated mortality to be 7.8 times higher than NMFS's recommended serious injury and mortality limit (i.e. potential biological removal level) for humpback whales.[55] A 2019 follow-up study concluded that even the 2017 study estimates were an underestimate, particularly in relation to humpback whale

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[48] Saez, Lauren, et al. "Understanding the co-occurrence of large whales and commercial fixed gear fisheries off the west coast of the United States." NOAA Tech Memo, NOAA-TM-NMFS-SWR-044 (2013).

[49] *Id*. at 74, Table 7.

[50] *See id.* at 98.

[51] Feist, Blake Edward. "Potential overlap between cetaceans and commercial groundfish fleets that operate in the California Current Large Marine Ecosystem," NOAA Professional Paper NMFS 17 (2015).

[52] *Id.*at 1.

[53] Rockwood RC, Calambokidis J, Jahncke J. "High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protection." PLoS ONE 12(8): e0183052 (2017).

[54] *Id.*

[55] *Id.*

mortality during winter months.[56] Because ship strikes of humpback whales cause serious injury and mortality that exceeds PBR, the Biological Opinion's failure to consider could materially affect the outcome of the jeopardy analysis and thus makes the consultation unlawful.

In short, the Biological Opinion is legally flawed and does not ensure against the likelihood of jeopardy of ESA-listed humpback whales from operation of the Fishery or ensure the Fishery will not destroy or adversely modify their designated critical habitat. By relying on the Biological Opinion to support the continued permitting, authorization, and management of the Fishery, NMFS is failing to ensure its actions will avoid the likelihood of jeopardy to ESA-listed humpback whales and is failing to ensure its actions will not destroy or adversely modify their critical habitat. Thus, NMFS has violated, and continues to violate, section 7(a)(2) of the ESA.[57]

IV. NMFS Must Reinitiate Consultation Based on Information Revealing New Fishery Effects On Humpback Whales and Critical Habitat.

A. Entanglement Risk Assessments Show the Increasing Likelihood of Fishery Interactions with Humpback Whales.

While vertical lines in the water are always a threat for whales, research published since the Biological Opinion showed that changing environmental conditions and whale migrations have increased the time in which humpback whales are at risk of entanglement off the Gulf of the Farallones.[58] Based on these models, climate change is likely to continue to exacerbate the risk of whale entanglement on the West Coast.[59] It is therefore important for NMFS to reinitiate consultation to assess accurately future entanglement risk and include terms and conditions to mitigate the risk.

Harmful algal blooms, for example, can delay the start of the Dungeness crab season, as occurred in spring 2016. During the closures fishing effort shifted from the Dungeness crab fleet to other fisheries, including sablefish pots.[60] Since 2016, the California Dungeness crab fishery has implemented a risk assessment program that includes delayed starts when entanglement risk is high. Spillover of fishing effort to the sablefish pots during these closures could increase the risk of entanglements in sablefish pots.

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[56] C. Rockwood and Jahncke, J. "Management recommendations to reduce deadly whale strikes off California." Report for the National Oceanic Atmospheric Administration, the United States Coast Guard, and the Maritime Industry (2019).

[57] 16 U.S.C. § 1536(a)(2).

[58] Ingman, Kaytlin, et al. "Modeling changes in baleen whale seasonal abundance, timing of migration, and environmental variables to explain the sudden rise in entanglements in California." *Plos one* 16.4 (2021): e0248557.

[59] *Id.*

[60] Fisher, Mary C., et al. "Climate shock effects and mediation in fisheries." *Proceedings of the National Academy of Sciences* 118.2 (2021), https://repository.library.noaa.gov/view/noaa/30641/noaa_30641_DS1.pdf.

NMFS scientists studying the uptick in humpback whale entanglements beginning in 2014 concluded it was due primarily to large whales moving closer in proximity to long-standing fisheries footprints. [61] The study used data showing the contemporaneous overlap between fishing activity and entanglement sightings.[62] For the pot-and trap-based sablefish fishery most of the overlap in high humpback whale density regions occurred off California.[63] These studies provide valuable information about the potential Fishery interactions with humpback whales and how to minimize humpback whale take that the Biological Opinion must consider.

B. <u>The Final Rule For Humpback Critical Habitat Underscores the Importance of Dwindling Prey Items.</u>

Since publication of the Biological Opinion, NMFS has published the final humpback whale critical habitat rule that added specific examples to the descriptions of the prey feature for each DPS.[64] These are:

> [For the Central America] DPS: Prey species, primarily euphausiids (Thysanoessa, Euphausia, Nyctiphanes, and Nematoscelis) and small pelagic schooling fishes, such as Pacific sardine (Sardinops sagax), northern anchovy (Engraulis mordax), and Pacific herring (Clupea pallasii), of sufficient quality, abundance, and accessibility within humpback whale feeding areas to support feeding and population growth.
>
> [For the Mexico] DPS: Prey species, primarily euphausiids (*Thysanoessa, Euphausia, Nyctiphanes,* and *Nematoscelis*) and small pelagic schooling fishes, such as Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), juvenile walleye pollock (*Gadus chalcogrammus*), and Pacific sand lance (*Ammodytes personatus*) of sufficient quality, abundance, and accessibility within humpback whale feeding areas to support feeding and population growth.[65]

The prey items necessary for the conservation of each species differ in part because the two DPSs have different but overlapping foraging grounds.

Unfortunately, some of the DPS's shared prey items – Pacific sardine and northern anchovy – have new information about low or declining abundances that suggests that harvest, even if small, may affect humpback whale critical habitat to a degree not considered in the Biological Opinion. For Pacific sardine, for example, NMFS made a projection in the spring of 2021 that biomass would be just 14,011 mt in July 2021, after an order-of-magnitude decline

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[61] Feist, Blake E., et al. "Footprints of fixed-gear fisheries in relation to rising whale entanglements on the US West Coast." *Fisheries Management and Ecology* 28.3: 283-294 (2021).

[62] *Id.*

[63] *Id.*

[64] *Endangered and Threatened Wildlife and Plants: Designating Critical Habitat for the Central America, Mexico, and Western North Pacific Distinct Population Segments of Humpback Whales,* 86 Fed Reg. 21082, 21084.

[65] *Id.*

over 15 years.[66] This is consistent with recent science that shows that marine heatwaves caused both sardine and anchovy biomass to decrease despite science that once predicted that sardine biomass would increase with warmer temperatures resulting from decadal-scale changes.[67] At low abundances, even small harvest could further stress humpback whales that are trying to find large quantities of food.[68]

NMFS must therefore reinitiate consultation on the impacts of the Fishery on ESA-listed humpback whales. NMFS's failure to do so violates the agency's procedural and substantive duties under section 7(a)(2) of the ESA.[69]

V. Conclusion

The ESA violations contained herein warrant a rapid remedy. Specifically, we request an emergency regulation to remain in place until NMFS has published a biological opinion that includes an incidental take statement for humpback whales. The proposed emergency rule would close the Fishery in all humpback whale critical habitat unless ropeless fishing gear is used.

Please contact me with any questions or to discuss this letter.

Sincerely,

/s/ *Catherine W. Kilduff*

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[66] Peter T. Kuriyama et al., "Assessment of the Pacific Sardine Resources in 2020 for U.S. Management in 2020–2021" at xi (May 2020); Peter T. Kuriyama et al., "Catch-only projection of the Pacific sardine resource in 2021 for U.S. management in 2021-2022" (April 2021), https://www.pcouncil.org/documents/2021/03/e-4-attachment-1-catch-only-projection-estimate.pdf/

[67] Cheung, William WL, and Thomas L. Frölicher. "Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific." *Scientific reports* 10.1: 1-10 (2020) ("warm regimes tend to favor sardine's recruitment and abundance while cool regimes favor anchovy. Thus, under decade-scale mean ocean warming, sardine was projected to increase in biomass while the opposite was projected for anchovy in the California Current. In contrast, poleward range expansion of sardine and anchovy was projected to result in long-term increase in their abundance in the Gulf of Alaska. However, the projected short-term rapid warming under MHWs pushed environmental temperature beyond those preferred by both sardine and anchovy, leading to a drop in their biomasses in both the California Current and Gulf of Alaska.")

[68] *See also Oceana v. Ross,* Case No. Case 5:19-cv-03809, "Order Regarding Motions For Summary Judgment," Dkt. 77 (N.D. Cal., Sept. 2, 2020). ("NMFS was required to consider the substantial evidence in the record indicating that fishing could exacerbate population fluctuations and declines, even if the [anchovy] population fluctuations were largely driven by environmental factors.").

[69] 16 U.S.C. § 1536(a)(2).

MARINE MAMMAL COMMISSION

13 February 2017

Mr. Chris Yates
National Marine Fisheries Service
West Coast Region
501 W. Ocean Blvd., Suite 4200
Long Beach, CA 90802

Dear Mr. Yates:

The Marine Mammal Commission (the Commission), in consultation with its Committee of Scientific Advisors on Marine Mammals, has reviewed and offers the following comments on the National Marine Fisheries Service's (NMFS) 10 January 2017 *Federal Register* notice (82 Fed. Reg. 2954) proposing a draft negligible impact determination (NID) for the California (CA) thresher shark/swordfish drift gillnet fishery (<14 inch mesh) and the Washington (WA)/Oregon (OR)/CA sablefish pot fishery.

Background

NMFS is proposing to issue permits pursuant to section 101(a)(5)(E) of the Marine Mammal Protection Act (MMPA) to allow the unintentional mortality or serious injury (M/SI) of two marine mammal species listed under the Endangered Species Act (ESA), the humpback whale (CA/OR/WA stock) and sperm whale (CA/OR/WA stock). As required under the MMPA, NMFS notes that recovery plans have been completed for these two species, and take reduction plans and monitoring programs have been implemented for managing takes of both species incidental to the CA thresher shark/swordfish drift gillnet fishery (<14 inch mesh) and the WA/OR/CA sablefish pot fishery. Both species, however, are also taken by other regional fisheries (e.g., sperm whales by the open access fixed gear hook and line fishery and humpback whales by the Dungeness crab pot fishery) at comparable or greater levels.

In 1999, NMFS adopted criteria for making NIDs when considering the effects of commercial fishing on endangered and threatened marine mammal populations. For the two fisheries included in the proposed incidental take authorization, the notice states that NMFS has reached a preliminary conclusion that the issuance of permits is warranted for both of the marine mammal species based on Criterion 3[1].

Humpback Whales

The proposed NID for this species is based on there being a single CA/OR/WA stock of humpback whales. This is the stock that is recognized in the most recent final stock assessment report (June 2014). However, as recognized in the 2016 draft stock assessment report, NMFS

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[1] See http://www.fisheries.noaa.gov/pr/species/documents/draft_nid_2017.pdf (pp. vi-vii) for an explanation of the five criteria for NID.

recently revised its listing of humpback whales under ESA based on the recognition of several distinct population segments (DPSs), which do not correspond with current stock delineations under the MMPA. As noted in the 2016 draft stock assessment report, NMFS is evaluating the stock structure of humpback whales under the MMPA, but has yet to propose any changes.

Based on the information contained in the revised listing of humpback whales under the ESA (81 Fed. Reg. 62260), both the Endangered Central America DPS and the Threatened Mexico DPS occur off of the U.S. West Coast and, presumably are subject to entanglement in the CA thresher shark/swordfish drift gillnet fishery, the WA/OR/CA sablefish pot fishery and other fisheries known to take humpback whales off the West Coast. We are particularly concerned about the potential for humpback whales from the Central America DPS to be killed or seriously injured in these fisheries. As noted in the listing rule, this DPS has an estimated 411 individuals and trend information is lacking. If the Central America DPS were considered a stock under the MMPA, the PBR level would be less than one whale. As such, it would not meet any of the negligible impact criteria established by NMFS under section 101(a)(5)(E) of the MMPA. Even if PBR were significantly greater than one, the requirements under Criterion 3 would not be satisfied, inasmuch as data are lacking to conclude that the population is stable or increasing.

While we recognize that a DPS under the ESA is not necessarily equivalent to a stock under the MMPA, the two classifications have some similarities. A stock is defined under section 3(11) of the MMPA as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature." To warrant designation as a DPS under the ESA, that population segment must also exhibit discreteness and "interbreed when mature." Thus, until NMFS has completed its assessment as to how the newly recognized DPSs under the ESA comport with stock delineations under the MMPA, the Commission recommends that NMFS take a precautionary approach and treat those DPSs identified under the ESA listing process as putative stocks under the MMPA. The Commission further recommends that, in its analyses under section 101(a)(5)(E) for humpback whales, NMFS consider both the Central America and Mexico DPSs as stocks under the MMPA, unless and until it has completed its assessment of stock structure for whales along the West Coast and concluded that some other structure should be used. The Commission also notes that in other cases of overlapping stocks (e.g., bottlenose dolphins off the coast of North Carolina) for which takes cannot be ascribed to any particular stock, the entire take within the overlap area is applied to each stock within the range separately. As such, the current estimate of takes from the Central America DPS, and perhaps the Mexico DPS, would exceed PBR and not meet the NID criteria.

Finally, we note that in 2015 there was a significant increase in humpback whale mortality and serious injury (M/SI) off the U.S. west coast. For example, Carretta et al.[2] indicate that there were 35 humpback whale M/SI in 2015 alone, including at least 26 attributable to fishery interactions. To ensure that recent trends towards increasing fishery-related M/SI involving humpback whales in the region are recognized, the Commission recommends that NMFS use the average annual M/SI of humpbacks over the most recent five-year period for which data are available, including data for 2015, in its evaluation.

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[2] Carretta, JV, MM Muto, J Greenman, K Wilkinson, D Lawson, J Viezbicke, and J Jannot. 2017. Sources of Human-Related Mortality for the U.S. Pacific West Coast Marine Mammal Stock Assessments, 2011-2015. PSRG-217-07. National Marine Fisheries Service, Southwest Fisheries Science Center

Negligible Impact Determinations

Although we believe that additional analyses are necessary to justify making a NID that includes humpback whales, the Commission recommends that NMFS issue the proposed NID for sperm whales for the two fisheries, subject to the following comments and recommendations—

1) NMFS issued a proposed rule (81 Fed. Reg. 70660) in October 2016 that would implement hard caps in the CA/OR large mesh drift gillnet fishery. This rulemaking would alter the management of marine mammal bycatch in this fishery and potentially impact the NIDs made in this notice. The Commission recommends that NMFS consider any potential impacts of these regulatory changes prior to issuing the final permits.
2) As the Commission has recommended in the past, the NID criteria need to be updated given new scientific information and overall policy changes. The Commission understands that NMFS is planning to update these criteria, and would welcome an opportunity to assist NMFS in this effort.

Thank you for the opportunity to comment on the proposed NIDs and incidental take permits. Please contact me if you have any questions regarding our recommendations.

Sincerely,

Rebecca J. Lent

Rebecca J. Lent, Ph.D.
Executive Director

PLOS ONE

RESEARCH ARTICLE

Modeling changes in baleen whale seasonal abundance, timing of migration, and environmental variables to explain the sudden rise in entanglements in California

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Abstract

We document changes in the number of sightings and timing of humpback (*Megaptera novaeangliae*), blue (*Balaenoptera musculus*), and gray (*Eschrichtius robustus*) whale migratory phases in the vicinity of the Farallon Islands, California. We hypothesized that changes in the timing of migration off central California were driven by local oceanography, regional upwelling, and basin-scale climate conditions. Using 24 years of daily whale counts collected from Southeast Farallon Island, we developed negative binomial regression models to evaluate trends in local whale sightings over time. We then used linear models to assess trends in the timing of migration, and to identify potential environmental drivers. These drivers included local, regional and basin-scale patterns; the latter included the El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the North Pacific Gyre Oscillation, which influence, wind-driven upwelling, and overall productivity in the California Current System. We then created a forecast model to predict the timing of migration. Humpback whale sightings significantly increased over the study period, but blue and gray whale counts did not, though there was variability across the time series. Date of breeding migration (departure) for all species showed little to no change, whereas date of migration towards feeding areas (arrival) occurred earlier for humpback and blue whales. Timing was significantly influenced by a mix of local oceanography, regional, and basin-scale climate variables. Earlier arrival time without concomitant earlier departure time results in longer periods when blue and humpback whales are at risk of entanglement in the Gulf of the Farallones. We maintain that these changes have increased whale exposure to pot and trap fishery gear off the central California coast during the spring, elevating the risk of entanglements. Humpback entanglement rates were significantly associated with increased counts and early arrival in central California. Actions to decrease the temporal overlap between

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Data Availability Statement: All whale counts and sightings data files are available from the ACCESS Oceans database (URLs) http://www.accessoceans.org/wp-content/uploads/2019/06/Ingman_et_al_sighting_dataset.csv, http://www.accessoceans.org/wp-content/uploads/2019/06/Ingman_et_al_timing_dataset.csv).

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Competing interests: The authors have declared that no competing interests exist.

whales and pot/trap fishing gear, particularly when whales arrive earlier in warm water years, would likely decrease the risk of entanglements.

Introduction

The California Current System (CCS) is one of four highly productive wind-driven upwelling systems [1, 2] and an important destination for migrating marine megafauna [3–5]. Wind-driven upwelling brings cold, saline, nutrient-rich water to the surface in the spring and summer, enhancing both primary and secondary production, as well as attracting foraging top predators [1, 2, 4]. Variability in ocean conditions in the northeastern Pacific Ocean is mainly driven by the El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) [6–8]. These basin-scale climate patterns alter atmospheric circulation, wind patterns, and overall coastal upwelling strength, which in turn affects sea surface temperature (SST), sea surface salinity (SSS), nutrients, and productivity on annual to decadal timescales [7, 9–11]. Mid-trophic level species are highly susceptible to changes in water mass properties and productivity [5, 12]. Copepod (Family: Calanoidea) abundance and species composition in central California change in response to climate [13]. Krill (Family: Euphausiidae) abundance can decrease up to 30% in response to reduced upwelling and productivity [14]. Forage fish species, such as juvenile rockfish (Family: Scorpaenidae) and northern anchovy (*Engraulis mordax)*, also decline in abundance or shift distributions during poor upwelling years [12]. Changes in the prey field generally have negative consequences for higher trophic levels, including baleen whales [15].

Three baleen whale species migrate through central California: humpback (*Megaptera novaeangliae*), blue (*Balaenoptera musculus*), and gray (*Eschrichtius robustus)* whales. Blue whales come to the area to feed on krill and humpbacks come to feed on both krill and forage fish during the upwelling season in the summer and fall [15, 16]. These two species winter in their breeding grounds in the tropics [15, 16]. Though gray whales also winter in their breeding grounds at lower latitudes, central California is not a primary feeding ground [17]. They are commonly spotted on either their northward non-breeding migration for a few months in early spring, or on their southward breeding migration beginning in the fall [17].

Range shifts and expansions in cetacean species in the CCS, including the three species mentioned previously, have been documented [18–20]. For example, gray whales altered the timing of migration to decrease thermal stress during warm, unproductive periods, such as El Niño years [21, 22]. Blue whales changed migration routes, tracking their prey as krill abundance patterns changed with PDO phases [23]. Humpback whales modified the timing of their migration [21], followed prey patches [3], and switched prey when krill was less available in response to El Niño, warm-phase PDO, and the unproductive NPGO phase [24]. Identifying and understanding spatial and temporal patterns of behavior in these species contributes to the prediction and mitigation of emerging threats [25].

Baleen whales were commercially harvested and nearly globally eradicated by the early- to mid-20th century [26]. Whales have been protected from harvest in the USA since 1972, and internationally by the International Whaling Commission since 1986, initiating the slow recovery of these populations [26].

However, indirect mortality remains a threat and a major anthropogenic threat facing baleen whales nowadays is entanglement in fishing gear [27]. Commercial fisheries are an important part of California's economy. One of the most lucrative is the California Dungeness crab pot and line fishery [28], averaging about $75 million annually between the 2010/11 and 2017/18 seasons [29]. Recently, the rate of confirmed whale entanglements along the western

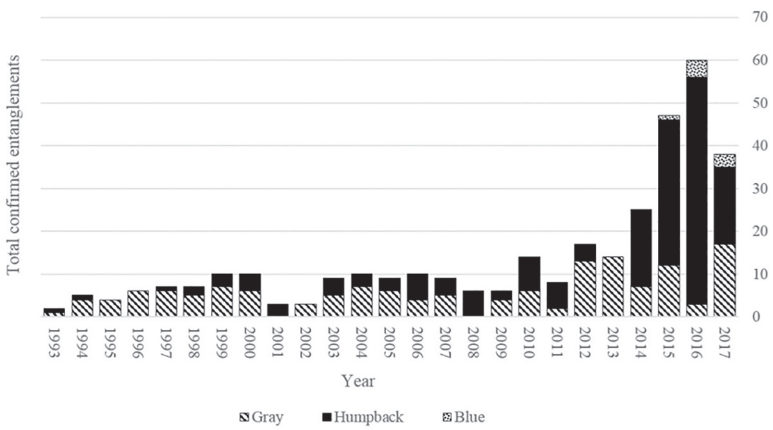

Fig 1. Total number of confirmed humpback (solid black), blue (dotted pattern) and gray whale (diagonal stripes) entanglements in fishing gear from 1993 to 2017 off the coast of California [32, Lauren Saez, pers. comm.].

https://doi.org/10.1371/journal.pone.0248557.g001

coast of the United States increased dramatically from 8–10 per year in 1993–2010, to a record 60 in 2016 [30] (Fig 1). Though total entanglements dropped in 2018 (46 confirmed) and 2019 (26 confirmed), they are still higher than the pre-2014 average of about 10 entanglements per year [29]. The highest percentage of these entanglements were reported in the central California region [31]. Although mitigation strategies (i.e., education, gear alteration, and increased efforts by a disentanglement team) and concrete management actions have been in place since 2013 [29], entanglements continue to be a threat to local whale populations [31].

Predictive models that implement near real-time local oceanographic conditions can help mitigate baleen whale and fishery interactions [32, 33]. They can provide insights into baleen whale migration and distribution patterns that influence the risk of entanglements in central California [34, 35]. Generalized Linear Modeling (GLM), relating baleen species sightings data (counts) to climate, oceanography and other environmental variables, can be a useful tool with which to develop statistical predictive models. GLMs have been used in marine mammal research to predict and relate timing to environmental variability at a variety of timescales [32, 34, 35].

For this study, we used a 24-year time series of humpback, blue, and gray daily whale counts from Southeast Farallon Island (SEFI) to identify changes in local whale sightings, timing of local migration, and entanglement risk. A field station on SEFI, off the coast of San Francisco, operated by Point Blue Conservation Science in cooperation with the U.S. Fish and Wildlife Service, began systematically tracking sightings of blue, humpback, and gray whales in 1993 (Fig 2) [4]. Our goal was to explore possible reasons for the significant increase in entanglements in the study area. To determine this, we looked at how the number of overall sightings and the timing of whale arrival and departures have changed over time. For effective management, predicting the concentration of whales in a fishing area would be useful towards mitigating the overall risk of entanglements. We asked if there were any local, regional, or basin-scale environmental predictors of changes in arrival and departure time. We postulated that if the timing of migration could be accurately predicted, then these predictions can be applied to inform management actions to decrease entanglements in pot and trap fishing gear.

Materials and methods

Study area

SEFI (37’42”N, 123’01”W) is located 48 km off the coast of San Francisco in north central California. SEFI is the southernmost island of the seven rocky outcrops that make up the Farallon

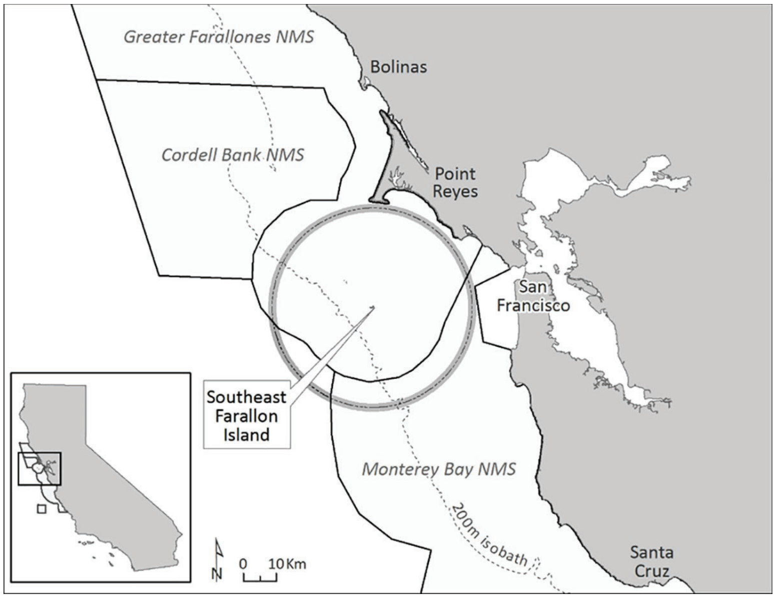

Fig 2. Map of the study area located off the coast of central California showing the location of Southeast Farallon Island and the 30km sight range. The Greater Farallones, Cordell Bank, and Monterey Bay National Marine Sanctuaries (NMS), which border the central California coast are outlined. The 200m isobath is depicted by the dashed line.

https://doi.org/10.1371/journal.pone.0248557.g002

Islands National Wildlife Refuge, also within the Greater Farallones National Marine Sanctuary (Fig 2). Due to the nature of the data collected (see below), we recorded observations within 30km, the limit within which whales could be accurately identified to the species level (Fig 2).

Species data collection

As part of an ongoing cetacean population study, systematic visual surveys were conducted daily from 1993 to the present by trained scientists from Point Blue Conservation Science [4]. All observations were recorded to the species level using 10X and 25X binoculars. Only positive observations at the species level were recorded and daily totals were conservatively estimated when large numbers were present [4]. We only included humpback, blue, and gray whale observations in this study because they accounted for about 99% of total baleen whale counts and were consistently observed throughout the time-series.

Additionally, standardized cetacean observation procedures were added in 2013 to implement new technology for data entry (Spotter Pro and Whale Alert Apps, 1515 N. Swinton Ave, Delray Beach, FL, 33444). Spotter Pro and Whale Alert are applications designed by Conserve. IO to report whale sightings along the west coast of the United States in real time to the National Oceanic and Atmospheric Administration (NOAA). This process is designed to inform NOAA, the U.S. Coast Guard, and commercial shipping vessels when large aggregations of whales are seen in the vicinity of shipping lanes (J. Jahncke, pers. comm.). Trained observers were employed to systematically count and record all observed cetaceans for an hour each day from the lighthouse on SEFI at an elevation of 90m [4], except during the gray whale winter migration when both morning and evening surveys were performed. For gray whales, the average of the morning and evening counts was used for the daily count. Observation days (subsequently referred to as "effort") occurred when visibility was greater than 11.2 km, with no low-hanging fog, Beaufort wind scale was less than or equal to 4, and swells were less than 3 m.

Opportunistic, daily whale observations on SEFI were initiated in 1987. However, consistent systematic protocol only began in 1993; therefore, our analyses begin with that year. The database of daily whale counts from 1993 to 2012 only included values when animals were detected (counts ≥ 1), hence, it was unclear if the lack of data on a given day represented zero detections (count = 0) or no-effort due to weather conditions. Days with no effort represented false zeros [36]; to exclude these days, in the absence of daily-effort information prior to 2013, we used data from 2013 to 2016, collected via the Spotter Pro App on SEFI, to determine associations between effort and weather. Then we used the resulting statistical associations to identify days before 2013 that were likely no-effort days. Weather data were collected *in-situ* by the biologist on the island and included percent cloud cover, visibility (miles), barometric pressure (millibars), air temperature (Celsius), daily precipitation (inches), wind direction (in degrees), wind speed (knots), swell height (feet), and swell direction. First, we performed a Classification and Regression Tree (CART) analysis to split the weather data into effort and no-effort predictors. For example, days with high swells were classified as having a low chance of effort, while high visibility days were classified as having an increased chance of effort. CART results were then input into a predictive model, resulting in the likelihood of effort estimated from 0–1 for each day. We used Optimal Cutoff analysis to determine the value in which predicted effort could be optimally classified as a 0 (no-effort) or 1 (effort) [37]. Days that had zero recorded counts and a predicted effort of zero were removed from the dataset, leaving only days where effort was likely to have been recorded. Daily counts were then summed over seven day periods, and these weekly counts were used in the analyses (see below). The use of weekly counts reduced residual variance. Distance sampling [38] would be a valuable approach in this situation, but distance measurements were not recorded before 2013.

Two ecological anomalies were observed in the blue whale dataset. In all years except 2014, blue whales were absent during the winter months. More specifically, the number of blue whales observed in January-February was near zero (0.01 per week; less than 0.1% of all sightings). For that reason, we exclude winter months from all subsequent analyses of blue whale counts. However, we note that in 2014 sighting in January and February increase by several orders of magnitude compared to all other years, averaging 26.4 per week; much greater values than in the subsequent spring, summer, and fall (average 4.0 per week). Because of the near-total absence of blue whales in the winter of the other 23 years, we present analyses of the spring, summer, and fall for blue whales.

In 2006, blue whales abandoned the area and only two were recorded in the entire year (cf. average of 141 per year in all other years). Therefore, neither arrival nor departure could be assessed. This year was considered an ecological anomaly and was removed from both the sightings and timing models.

Average blue and humpback whale counts during the course of the year followed a unimodal distribution curve with a peak in the summer, so analysis was performed for all years starting on January 1st. Gray whale counts within the year followed a bimodal distribution with peaks in January and March, corresponding to southward and northward migration respectively. We analyzed these two peaks separately. To avoid splitting the first migration phase between calendar years, we used an adjusted year where day 1 is June 1st, and analyzed these data separately. We refer to the January peak as the gray south-bound breeding migration peak (gray-south), and the March peak as the gray north-bound feeding migration peak (gray-north).

Environmental variable processing

Local variables. In situ daily SST and sea surface salinity (SSS) values were collected by scientists on SEFI. Front Intensity Index (FII) values were calculated at 5, 10, 15, and 20 km

Table 1. Oceanographic and climate data used as environmental covariates.

Variable (Unit)	Mean ± SD	Min-Max values	Description	Data Source
Local oceanography				
SST (˚C)	12.49 ± 1.44	8.77–18.24	Avg. sea surface temperature	https://scripps.ucsd.edu/programs/shorestations/shore-stations-data/data-farallon/
SSS (PSU)	33.40 ± 0.56	26.81–34.27	Avg. sea surface salinity	https://scripps.ucsd.edu/programs/shorestations/shore-stations-data/data-farallon/
FII (˚C/km)	0.0331 ± 0.0144	0.0084–0.0990	Avg. front intensity index	http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html
Regional				
UI (m^3/s/100m)	108.62 ± 104.16	-283–409.5	Avg. monthly Upwelling Index	http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html
STB (day anomaly from day 90)	85.05 ± 20.57	50–122	Avg. spring transition date	http://www.ndbc.noaa.gov/station_history.php?station = 46013
Basin scale climate				
SOI (standardized index)	-0.20 ± 1.85	-6.7–5.2	Avg. monthly Southern Oscillation Index values	http://www.cgd.ucar.edu/cas/catalog/climind/soi.html
PDO (standardized index)	0.133 ± 1.14	-2.33–2.79	Avg. monthly Pacific Decadal Oscillation values	http://jisao.washington.edu/pdo/PDO.latest
NPGO (standardized index)	0.245 ± 1.25	-2.99–2.96	Avg. monthly North Pacific Gyre Oscillation values	http://eros.eas.gatech.edu/npgo/

https://doi.org/10.1371/journal.pone.0248557.t001

radii from SEFI by obtaining the maximum absolute value of the remotely sensed SST gradient within each radius. FII values were derived from the Operational Sea Surface Temperature and Ice Analysis (OSTIA) [39] (Table 1).

Regional variables. The upwelling index (UI) was downloaded from the Pacific Fisheries Environmental Laboratory website and averaged for the coastal region from Big Sur (36˚N 122˚W) to Point Arena (39˚N 125˚W), as SEFI lies between these two locations (Table 1). The spring transition anomaly (STB) was determined based on wind strength and direction data from the NOAA buoy 46013 in Bodega Bay, after estimating Ekman transport and the relative cumulative upwelling for each year (Table 1).

Basin-scale climate variables. SOI is a measure of the difference in pressure between Darwin and Tahiti used to identify El Niño and La Niña events [40], PDO is a measure of SST anomalies in the Pacific Ocean north of 20˚ [10], and NPGO is a measure of sea surface height and associated with fluctuations in SSS and nutrients in the Northern Pacific [7] (Table 1). The response of whales to shifts in climate patterns exhibits a delay because whale residency near SEFI was associated with prey availability [41]. PDO, for example, alters upwelling favorable wind strength which drives the concentration of nutrients and overall productivity [42]. Krill takes advantage of these productive areas [5]. This process takes time to make its way up the food chain. We calculated lags of 1, 2, and 3 months to account for such potential delays [43, 44].

Sightings

Whales observed near SEFI migrate and forage in small groups. Therefore, the count data were skewed towards low daily numbers and a large number of days with zero counts. We used negative binomial regression to determine how whale sightings changed through time. All statistical analyses were carried out with Stata 16.1 (Stata Corp., 2019). Negative binomial regression modeling is recommended when count variables have a high variance, i.e., are over-dispersed [36, 44, 45]. We modeled weekly whale counts as a function of year to determine overall trends through time, incorporated month (as a quantitative variable) to account for seasonality within the year, and tested for any interactions between year and month. These covariates were tested for linear, quadratic, and cubic relationships with the count data. The log number of on-effort days per week (see *Species Data Collection* for more details) was used as an offset to control for differences in effort days among weeks.

Timing

Average annual arrival, peak, and departure times were calculated for each species by identifying the day on which the 10th, 50th, and 90th percentiles of annual sightings were recorded. Residency, which refers to the number of days that whales were near SEFI, was determined by subtracting the arrival day of each year from the departure day. For the gray-south dataset, weeks 1–18 (June-Sept.) were not analyzed. There were on average 10 to 15 gray whales seen per week during the summer near SEFI; however, the same whales were likely counted repeatedly (J. Jahncke, pers. comm.). This small resident population present in the summer is not applicable to the migrating portion of the population, which is observed in the late fall, winter, and spring.

Environmental variables were averaged annually and seasonally (Dec-Feb; Mar-May; Jun-Aug; Sep-Nov). We calculated annual and seasonal environmental values for gray whales based on the adjusted gray whale year (see above). Arrival, peak, and departure times were used in linear models as the dependent variable and the environmental variables (including linear, quadratic, and cubic terms) were tested as the independent variables. Significant covariates with the appropriate transformation (quadratic or cubic if either was significant) were then added to a preliminary linear regression multivariable model, and backwards stepwise elimination was used to sequentially drop non-significant variables until all variables remaining in the model were significant ($P<0.05$; [46]). The transformation of the highest order (cubic, quadratic, linear) was used if significant, in which case all lower order terms for that variable were retained. We then used the variance inflation factor (VIF) to verify that predictor variables were not collinear ($VIF<10$, [47]). The significant retained variables in the final multivariable models were used to estimate timing for each species. We used Akaike Information Criterion to confirm that a more parsimonious model was not preferred to our final models. To depict the relationship of each timing variable to the respective environmental variables in the final models of arrival or departure, we used the margins command in Stata, which provides predicted values and 95% CI, which holding all other variables in the statistical model at their mean value.

We created a set of forecast models, as an exercise to test how much power our model had in predicting the timing of arrival, peak, and departure variables. The forecast model included only significant environmental variables that occurred before the whale migration period in that particular year, reducing the number of variables and the performance of these models. In addition, we performed a year-removal validation by running the full model for each year, one year at a time, with that year's observation removed. Predicted values for each year were compared to the actual observed values and model results were compared to the predictive ability of the original full model.

Entanglements

Species-specific entanglement records were obtained from 1993 to 2016 and grouped by month. These data were collected and managed by National Marine Fisheries Service West Coast Region. We used a set of regression models to determine relationships between observed monthly entanglements and monthly whale count data and timing of migration.

We fit linear models to identify associations between monthly entanglements (dependent variable), monthly whale counts, and timing related variables (i.e., arrival and departure) by year for humpback whales, which were the only species to show a significant change in entanglements over time (see *Results*). The linear regression was chosen for this model because the distribution of residuals analyzing entanglements per year were consistent with a normal distribution, rather than following a negative binomial distribution, as was the case for weekly whale sightings (as described above).

First, we modeled monthly entanglements as a function of year to determine trends through time. Then, we created a combined sightings and timing model to see how arrival, departure, and the whale count per month influenced the number of entanglements in each month. Preferred transformations for each covariate were input into a preliminary multivariable linear regression model, and backwards stepwise elimination was used to reduce the model until all remaining variables were significant. VIF was again used to test collinearity between variables (i.e., VIF<10).

To compare the relative contribution of each predictor variable in accounting for variation in linear models, we compared the square of the t statistic, since the variance in the dependent variable due to a predictor in a linear model is proportional to the square of the t statistic [48].

Results

Changes in local sightings

Humpback, blue, and gray whale (both south and north) sightings by week showed non-linear trends with year (Negative Binomial Regression, humpback n = 1,217, blue n = 851, gray-south n = 320, gray-north n = 453). The modeled number of humpback whale sightings per week increased in a quadratic fashion, with little change from 1993 to about 2004 (about 2 per week), then accelerating, reaching six in 2016 ($P<0.001$ for the overall model, Fig 3A). Predicted blue whale sightings displayed a cubic trend, increasing between 1993 and 1998, from two to five, but then decreasing gradually until 2011 ($P<0.001$ for the overall model, Fig 3B).

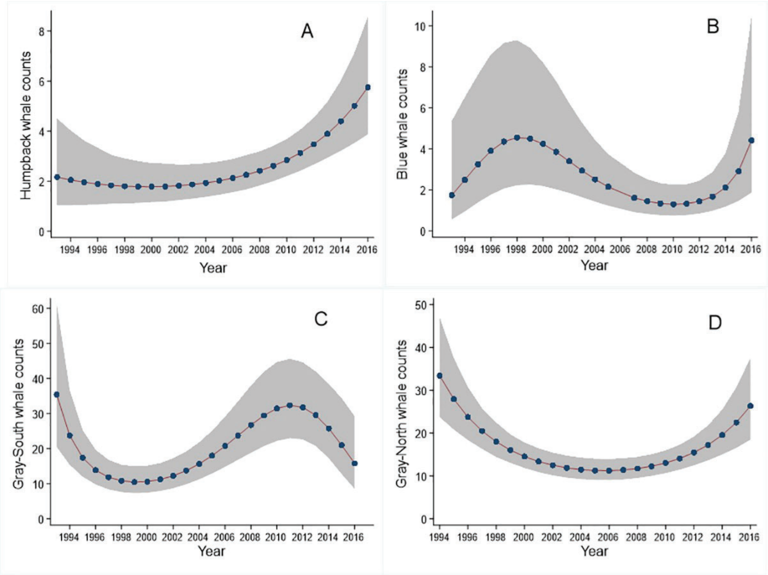

Fig 3. Interannual trends in average weekly predicted counts of (A) humpback, (B) blue, (C) south-bound gray, and (D) north-bound gray whales. The 95% confidence intervals are shown in gray shading.

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Between 2012 and 2016, sightings increased sharply from two to five. Gray-south and gray-north sightings per week showed similar sightings at the beginning of the time series with about 35 predicted sightings in 1993 ($P<0.01$ Fig 3C, $P<0.001$ Fig 3D). Both decreased to about 10 sightings but at different points, in the early 2000s for gray-south and in the late 2000s for gray-north. Gray-south sightings increased through the late 2000's until about 2012 (30 sightings), but then dropped again to 15 sightings in 2016, thus displaying a cubic trend (Fig 3C). Gray-north sightings, instead, displayed a quadratic trend, starting to increase steadily from 2009, reaching about 30 sightings in 2016 (Fig 3D).

Timing of local migration

We found significant changes in timing of arrival for humpback and blue whales, as well as the timing of peak sightings and departure for humpbacks and gray-north. Here, we summarize patterns with regard to arrival and departure. Additional information about changes in peak times can be found in the (S1 Table in S1 File). All three species showed significant linear or quadratic trends for arrival and/or departure, but there were no significant cubic trends (Table 2, Fig 4). Humpback and blue whale timing of arrivals displayed linear trends over the time series and occurred, on average, 120 and 100 days earlier, respectively, comparing 2016 with 1993. Humpback whale timing of departure and gray whale departure dates during the feeding migration showed significant quadratic trends with year, representing a delay in the mid-2000's, which was then reversed (Table 2). We found no significant association with year, for blue whale departure timing, gray-north arrival, or any of the gray-south migration metrics (Table 2, Fig 4).

The timing of migration for all species was influenced largely by basin-scale environmental variables, and less by local and regional variables, as described below (Summary of Linear Regression model statistics (Table 3): humpback $n = 24$, arrival and departure, $P<0.001$ for overall model; blue $n = 23$, arrival $P<0.001$, departure $P>0.1$, gray-south $n = 24$, arrival and departure $P>0.1$; gray-north $n = 23$, arrival $P>0.3$, departure $P<0.001$).

Local drivers. FII was not a significant driver in any of the models and SSS was only significant in the gray-north departure model (Table 3, Fig 5J). SST was a significant variable in blue arrival, indicating early arrival when the annual temperature was warmer (Fig 5F). Gray whales departing to feed left the area earlier when SST was warmer in the summer; this variable was the most important for gray-north departure ($P < 0.001$, Fig 5I).

Regional drivers. UI as a regional average was significant in humpback departure and blue whale arrival (Table 3, Fig 5C and 5G). However, in neither species-specific model was it the most significant driver. STB was not significant in any model (Table 3).

Table 2. Changes in timing for humpback, blue, and gray whale arrival and departure times.

Species	Number of Years	Trend	P-Value
Humpback Arrival	24	L(-)	P<0.001
Humpback Departure	24	Q(-)	P<0.05
Blue Arrival	23	L(-)	P<0.01
Blue Departure	23	NA	Not Significant
Gray-south Arrival	24	NA	Not Significant
Gray-south Departure	24	NA	Not Significant
Gray-north Arrival	23	NA	Not Significant
Gray-north Departure	23	Q(-)	P<0.05

Trends are depicted as linear (L), quadratic (Q), or cubic (C). The coefficients for the highest order term in the model are depicted as positive (+) or negative (-).

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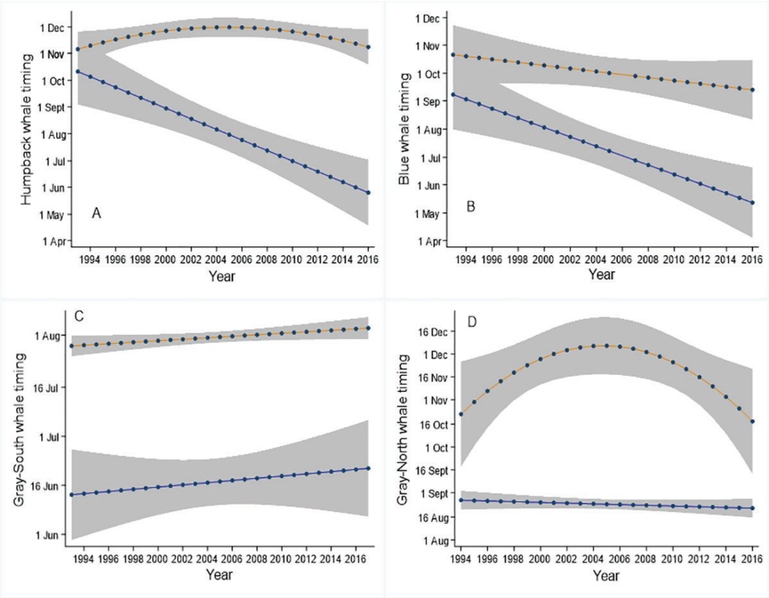

Fig 4. Interannual trends in the timing of day of arrival and departure. Shown are the arrival (blue) and departure (orange) trends for humpback (A), blue (B), gray-south (C), and gray-north (D). Blue whale departure, gray-north arrival, and gray-south arrival and departure, trends were significant ($P>0.05$); in this case we depict the linear trend. The other four trends shown were significant. The 95% confidence intervals are depicted in gray shading.

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Basin-scale drivers. Among the basin-scale variables, SOI was the most commonly selected variable, achieving significance in all models except for gray whales on their feeding migration. High SOI values were associated with early arrival in both humpback and blue whales (Fig 5A and 5H). SOI in the previous winter was the most significant variable for blue whale arrival ($P < 0.001$) and humpback departure ($P < 0.01$). Annual PDO was the most significant variable explaining humpback arrival ($P < 0.001$), but NPGO also was significant in

Table 3. Results from the multivariable timing model for humpback, blue, and gray whales.

Variable	Humpback arrival	Humpback departure	Blue arrival	Gray-north departure
SST			Q(-)*	
SST summer				L(-)***
SSS previous winter				Q(-)**
UI summer		L(-)*		
UI fall			C(+)*	
SOI previous spring	L(-)**			
SOI previous winter		C(-)**	C(-)***	
PDO	Q(-)***			
NPGO summer		Q(-)*		
Adjusted R^2	0.6615	0.6808	0.7699	0.7011
P-value	0.0005	0.0001	0.0001	<<0.00001

Models of blue departure, gray-north arrival, and both gray-south metrics were not significant ($P>0.05$), and so are not shown.

Relationships are depicted as linear (L), quadratic (Q), or cubic (C). The coefficients for the multivariable model were depicted as positive (+) or negative (-). The most dominant variables (see text) are shown in gray shading. The level of significance is depicted by *** $P\leq0.001$

** $P\leq0.01$

* $P\leq0.05$.

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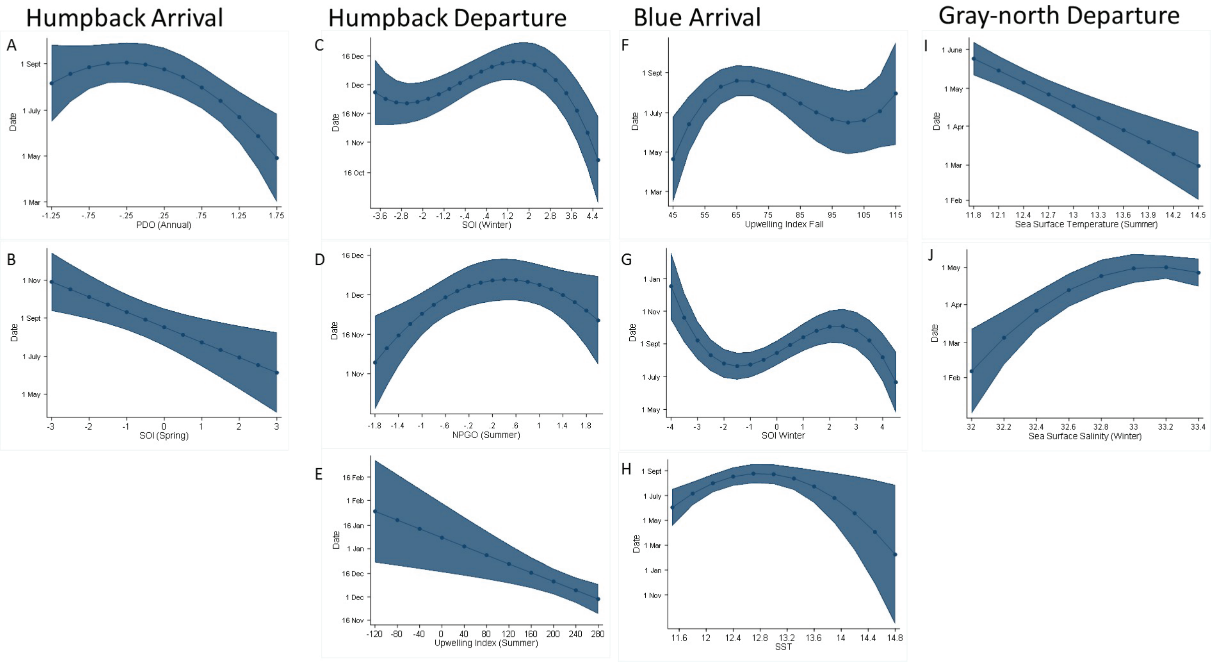

Fig 5. Visual depiction of the environmental multivariable timing models for humpback, blue, and gray whales. For each timing model shown in Table 3, the model predictions for each environmental variable is graphed while controlling for all the other significant variables in the model. Humpback arrival: SOI previous spring (A), NPGO-summer (B); Humpback departure: UI summer (C), SOI previous winter (D) NPGO summer (E); Blue arrival: annual SST (F), UI fall (G), SOI previous-winter (H); Gray-north departure SST summer (I), SSS previous winter (J). Shading indicates 95% CIs.

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the humpback departure model ($P < 0.05$). Humpbacks arrived earlier during years of cool phase PDO (Fig 5A), and departed later when NPGO values were neutral to higher (Fig 5D).

For most environmental variables (local, regional, and basin-scale) seasonal averages were significant and were retained in the statistical models (Table 3). However, for SST and PDO, annual averages were significant and retained when analyzing blue arrival and humpback arrival, respectively (Table 3).

Forecast timing and validation. Timing of migration models for humpback, blue and gray whales were used to forecast arrival and departure times. Considering only the four timing models that were significant (see above), all four forecast models were significant as well (humpback arrival and departure, $P < 0.001$; blue arrival $P < 0.05$; gray-north departure, $P < 0.05$). The forecast models explained 34–60% of the variance in the original, full model (Table 4).

Table 4. Coefficient of determination and model significance comparison between the full, forecast, and year-removal validation models.

	Full Model		Forecast Model		Year Removal Validation		Ratio: Forecast to Full Model
	R^2	P-value	R^2	P-value	R^2	P-value	
Humpback Arrival (n = 24)	0.662	P<0.001	0.458	P<0.001	0.471	P<0.001	0.599
Humpback Departure (n = 24)	0.681	P<0.001	0.681 No variables removed	P<0.001	0.588	P<0.001	1.0
Blue Arrival (n = 23)	0.770	P<0.001	0.263	P<0.050	0.574	P<0.001	0.342
Gray-North Departure (n = 23)	0.701	P<0.001	0.290	P<0.050	0.579	P<0.001	0.414

Only results from statistically significant timing models are shown here.

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Table 5. Results from the multivariable model for confirmed entangled humpback whales.

Variable	
Humpback Counts	L(+)*
Humpback Arrival Day	L(-)*
Model Statistics	
Adjusted R^2	0.1604
P-value	0.0007

Relationships are depicted as linear (L), quadratic (Q), or cubic (C). The coefficients for the multivariable model are depicted as positive (+) or negative (-). The level of significance is depicted by $^{***}P \leq 0.001$, ** $P \leq 0.01$ $^{*}P \leq 0.05$.

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Predictive models were validated by a year removal test, predicting timing for each year based on a model fit without that year's data. The year-removal models showed good ability to predict that year's value (R^2 varied from 0.471 to 0.588; $P < 0.001$ for all four models; Table 4). Proportionately, the R^2 of the year-removal model was between 62 and 85% of the R^2 of the full-data model.

Entanglement risk

Humpback whales were the only species that demonstrated a significant change in the total number of entanglements over the time series. There were substantially more entanglements of this species than either of the other two. Therefore, humpback whale entanglement models are the only species reported here.

We found that both the total number of whales and the timing of arrival significantly influenced the number of entanglements (Linear Regression; n = 75, $P<0.05$ for each variable; $P < 0.001$ for the multivariable model, Table 5). The total number of whales had a greater influence on total number of entanglements than the timing of arrival, as indicated by the square of the t statistic for humpback sightings ($t^2 = 10.24$) compared to that of humpback arrival ($t^2 = 5.02$). Thus the number of whales observed per month account for 104% more of the variance in entanglements than do humpback arrival dates.

Discussion

We found that humpback whale model-predicted sightings increased from 1993 to 2016, blue whale sightings fluctuated between two to five average sightings per week, and both species showed a significant change in arrival time to central California (Figs 3 and 4). Gray whales displayed significant trends in sightings for both north-bound and south-bound migration (Fig 3). Gray whales did not have a significant change or timing of arrival, although there was a significant change in the timing of the departure of northbound gray whales (Fig 4). In the northwestern Pacific Ocean, humpback and gray whales have continued to recover from whaling in the last few decades [31, 49]. In addition, blue whale population estimates have been reported to have increased significantly from 2014 [31, 50]. Although our findings displayed variability, predicted blue whale counts were similar at the beginning and end of the time series (Fig 3B) though they do indicate an increase in the most recent years. Our data were limited in spatial extent and should be used to describe local population trends only. Interannual variation in both the number of whales and timing of migration has been reported in baleen whales previous to this study [3, 22, 51], but no trend has previously been documented in this area.

Our findings are unique because they reveal a significant trend towards earlier arrival over three decades in this important feeding area (Fig 4). We found that humpback whales arrived on average 120 days earlier, while blue whales arrived in central California 100 days earlier in 2016 than they did in 1993. Similar changes in the timing of migration have been observed in southern California [51]. Short term, interannual changes in whale species composition and arrival have been previously documented in response to changes in the environment [3]. Baleen whales have been reported to respond to changes in prey availability [3, 18, 52]. These lower trophic levels are highly susceptible to changes in the environment. Thus, this study has connected changes in the physical environment to altered migration patterns.

Throughout our study period, there has been variation in local, regional, and basin-scale environmental conditions. Each species had a unique environmental driver that contributed the majority of the variation in the timing of migration (Table 3). The most common environmental drivers were local SST, regional Upwelling Index (UI), and basin scale climate indexes: Southern Oscillation Index (SOI), Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO). The main environmental drivers for each species occurred on different spatial scales. Humpback arrival and departure were mostly driven by basin-scale variables, gray-north departure by local oceanography, and blue arrival by a combination of variables from local to basin-scale (Table 3). The importance of these variables to whale behavior mirrors findings in previous studies of the CCS [3, 20, 22]. Climate patterns that were associated with increased SST and generally unproductive conditions (Fig 5), showed a strong correlation with changes in timing of all three species.

The most dominant predictor of humpback arrival was annual PDO, with SOI also contributing to the model. Early arrival occurred during warm, non-productive years, indicated by PDO values (Fig 5A) following a productive year as indicated by SOI in the previous year (Fig 5B, Table 3). The humpback departure model was significant and varied by less than 30 days over the study period (Fig 4A). Variation was most strongly driven by summer variables (NPGO and upwelling), with previous year conditions (SOI-winter) contributing as well. Both positive NPGO and cool phase PDO are often strong indicators of overall ocean productivity [6, 7]. In short, the most significant drivers of humpback timing were climate indices that reflected low productivity. Observed differences in humpback sightings from SEFI may be explained by prey switching, which led to changes in feeding locations, such as onshore or offshore habitat use, during the study period [53]. The associations we found in the species-specific models demonstrate how climate patterns affect this system, prey availability, and humpback whale residency.

We found the most significant driver of blue whale arrival time was lagged by nearly a year but local variables (fall upwelling and annual SST) also contributed to the model (Table 3). Early blue whale arrival occurred during warm, non-productive years, as indicated by high annual SST (Fig 5H) and low seasonal upwelling (Fig 5F) following a winter with low productivity (Fig 5G). This significant lag in the driver of early arrival is likely due to the importance of krill biomass in an area [51] and may also be attributed to blue whale memory [54]. Unproductive environmental conditions, such as characterized by strong El Niño years (negative SOI) or increased SST, reduce productivity and contribute to changes in blue whale migration patterns [50, 55].

Gray-north departure was earlier when summer SST was warm, following a winter with increased freshwater input possibly due to increased rain or weak upwelling (Fig 5I and 5J).

Baleen whale residency in an area is considered to be strongly influenced by prey availability [3, 24]. Our results support this assumption. The drivers of whale departure day were local variables such as SST and Upwelling Index (UI), which are associated with prey biomass [56]. The warmest period of SST in our study was from 2014–2016 due to a combination of a strong marine heat wave (also referred to as "the blob"), an anomalous warm patch of water that circulated the northeastern Pacific, and a very strong El Niño event in 2015 [57, 58]. Large whales are highly mobile, and able to travel to optimal conditions where food is most abundant [20]. While the CCS was less productive than normal during this time period, productivity in central California was greater than in southern California [57]. Conditions in southern California, such as low UI and warm SST, likely reduced prey biomass. Possibly, some whales continued to more favorable feeding grounds in central California rather than stay in unproductive feeding grounds in southern California [57]. As both humpback and blue whale populations are recovering [49], increased sightings near SEFI in recent years may indicate higher concentrations of whales in the central California feeding ground (Fig 3).

Entanglements

The environmental variables that drive earlier arrival must be considered with respect to effective management, as whales will be exposed to increasing anthropogenic risk and competition with humans over time [54, 59]. SEFI is located near the heavily urbanized San Francisco Bay. Therefore, it is critical to understand patterns of whale sightings and timing within the context of associated anthropogenic threats. Pot and trap fishing gear was the most common type of gear identified in all entanglements, and the California Dungeness crab fishery was responsible for the majority of those [30, 31]. This fishery historically was open from mid-November to the end of June [28] (Fig 6). In our time series, we found that, on average, humpbacks arrived in early August and departed in mid-November. These arrival and departure times occurred when the crab fishery was closed. Under typical past conditions and migration timing, there was thus little overlap between whales and the pots, which resulted in a relatively low number of humpback entanglements (Fig 6).

Monthly humpback entanglements increased as counts of humpbacks increased. In addition, monthly entanglements increased in years with earlier arrival. While our models showed entanglements in humpbacks associated more with increased sightings, we also saw a strong connection between timing of arrival and entanglements. When whales arrive to the area early, the number of sightings also increased. Our results showed that increased sightings as a result of early arrival increased the concentration of whales in the area which appears to lead to more entanglements. Since 1993, the first humpbacks were observed before the closure of

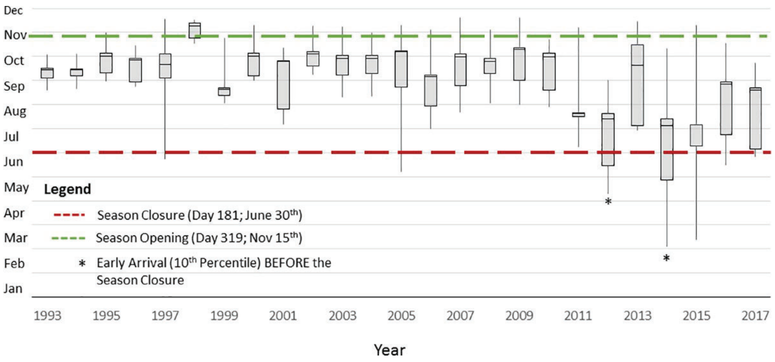

Fig 6. Residency time of humpback whales within 30 km of the Southeast Farallon Islands. The bottom of the box plot corresponds to the arrival time (date of 10th percentile for the year's sightings). The top of the box plot corresponds to the departure time (date of 90th percentile of the year's sightings). The whiskers are the earliest arrival date (bottom) and the last departure date (top). The red line corresponds to the typical closure of the previous year fishing season on June 30th (Day 181) and the green line is the typical opening of the new fishing season on November 15th (Day 319). Years marked with a * correspond to years where there was early arrival.

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the fishery during the El Niño of 1997/98, the ocean anomaly of 2005, and since 2012. The exception to that pattern was observed in 2013, when humpback whales arrived after the closure of the fishery. There were no recorded humpback entanglements in that year, providing support of a causal relationship.

It is important to note that in 1997 and 2005 there were no unusual increases in entanglement rates. However, humpbacks were first observed only 10 days before the fishery closure in 1997 and 35 days before the 2005 closure (Fig 6). More importantly, our arrival metric (10th percentile of sighting) in those two years was not unusually early (Fig 6). Thus, this greatly reduced the chances of the whales interacting with the pots while they were still in the water. In 2014 and 2015, humpbacks were exposed to the lines for about three times as long, so duration of exposure was likely an important factor in the total entanglement number. While gray whale entanglements have been relatively consistent through time, humpback entanglements dramatically increased from an average of less than 10 per year before 2014 to five times that in 2016 (Fig 1). Unusually high humpback entanglements were observed annually since 2014, which corresponds to the earliest arrival times and higher sightings.

SST at SEFI gradually increased from 11.9˚C in July of 1993 to 12.2˚C in July of 2016. These conditions are typically associated with prey switching behavior in humpbacks [24] from krill, which aggregate on the shelf break [53], to forage fish, which migrate north during periods of warmer SST [60]. During the 2015/16 season, a domoic acid outbreak in the Dungeness crab fishery delayed the opening of the season in some areas along the coast of Northern California, so pots were aggregated in a smaller area, closer to shore [56]. Not only were humpbacks observed feeding on forage fish closer together in areas with a high concentration of crab pots [53], but more humpbacks were in the region due to early arrival (Fig 6). All of these factors likely contributed to the dramatic spike in humpback entanglements in 2015–2016.

Only five blue whale entanglements were confirmed in central California through 2016, so statistical analysis was not possible due to the low sample size. All recorded blue whale entanglements have been since 2015. Blue whales feed primarily on krill, which typically aggregate along the shelf-break [56]. Even as blue whales arrived earlier to the area (Fig 4), they would have spent the majority of their time away from the near-shore cluster of crab-pots [53]. However, blue whales still would have had a longer period of overlap with the fishery due to the population arriving early. As these data continue to be collected, future blue whale entanglements will inform us if these few entanglements were isolated incidences, or represent an emerging trend.

We found that gray whales were most commonly seen in the area from December to April, while the crab fishery was open. Gray whales have had consistent interactions with this fishery for the entirety of the time series during these months. This may explain why we found roughly the same number of annual gray whale entanglements through the time series (Fig 1). However, other studies have found that their migrations are changing, similar to the humpback and blue whales we observed [22, 43, 61], so it is important to continue to monitor the entanglement risk that this population faces.

To mitigate the local risk of entanglements, the California Department of Fish and Wildlife closed the Dungeness crab fishery in April in 2019 and 2020. This new earlier closure was intended to limit temporal overlap with whales and result in less entanglements overall. In 2019, there were 26 confirmed entanglements on the west coast [29]. Though less than the 2015 peak, these data are higher than the pre-2013 average.

Predictive models, such as these, can be used to predict arrival and departure dates in advance allowing managers to adjust the length of the fishing season to reduce the temporal overlap with whales. This may decrease entanglement risk. Forecast models were shown to have high predictive value, especially for humpback arrival and departure (Table 4). Based on these results, we can effectively predict humpback arrival and departure in advance.

While we found significant trends in arrival dates (correlated with higher risk), it is difficult to determine whether those will continue. Earlier arrival of humpback and blue whales appears to be a response to a combination of warming oceans and associated changes in prey availability. The waters near the Farallones have warmed; SEFI SST gradually increased through our time series with the highest average monthly temperature recorded in August of 2014 at 17.04˚C. If this ocean warming trend continues as a result of climate change, the unprecedented entanglement rates of whales are likely to continue with negative consequences to whale populations in central California. Long-term, real time monitoring of whale behavior and oceanographic conditions in central California and optimally, across the entirety of the species ranges, is critical for the management and protection of these species.

Supporting information

S1 File.
(DOCX)

S1 Fig. Visual depiction of the environmental multivariable timing models for humpback, blue, and gray whales. For each timing model shown in S2 Table in S1 File, the model predictions for each environmental variable is graphed while controlling for all the other significant variables in the model. Humpback Peak: PDO fall (A), SOI spring (B) UI fall (C), annual SST (D) Gray-north peak: annual NPGO previous-year (E) SOI winter (F) Shading indicates 95% CIs.
(TIF)

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References

1. Bakun A. Global Climate Change and Intensification of Coastal Ocean Upwelling. Science (80-) [Internet]. 1990; 247(4939):198–201. Available from: https://doi.org/10.1126/science.247.4939.198 PMID: 17813287
2. Lynn RJ, Simpson JJ. The California Current system: The seasonal variability of its Physical characteristics. J Geophys Res [Internet]. 1987; 92(C12):12947–66. Available from: http://dx.doi.org/10.1029/JC092iC12p12947
3. Benson SR, Croll D a, Marinovic BB, Chavez P, Harvey JT. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. Prog Oceanogr. 2002; 54:279–91.
4. Pyle P, Gilbert L. Occurrence patterns and trends of cetaceans recorded from southeast Farallon Island, California, 1973 to 1994. Northwest Nat [Internet]. 1996; 77(1):1–8. Available from: https://doi.org/10.2307/3536517
5. Dorman JG, Sydeman WJ, García-Reyes M, Zeno RA, Santora JA. Modeling krill aggregations in the central-northern California Current. Mar Ecol Prog Ser [Internet]. 2015; 528:87–99. Available from: http://www.int-res.com/abstracts/meps/v528/p87-99/
6. Chenillat F, Riviére P, Capet X, Di Lorenzo E, Blanke B. North Pacific Gyre Oscillation modulates seasonal timing and ecosystem functioning in the California Current upwelling system. Geophys Res Lett. 2012; 39(1):1–6.
7. Di Lorenzo E, Schneider N, Cobb KM, Franks PJS, Chhak K, Miller AJ, et al. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys Res Lett. 2008; 35(L08607):1–6.
8. Trenberth KE, Hoar TJ. El Niño and climate change. Geophys Res Lett. 1997; 24(23):3057–60.
9. García-Reyes M, Largier J. Observations of increased wind-driven coastal upwelling off Central California. J Geophys Res Ocean. 2010; 115(CO4011):1–8.
10. Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. Bull Am Meteorol Soc. 1997; 78(6):1069–79.
11. Racault M-F, Sathyendranath S, Brewin RJW, Raitsos DE, Jackson T, Platt T. Impact of El Niño Variability on Oceanic Phytoplankton. Front Mar Sci [Internet]. 2017; 4(133):1–15. Available from: http://journal.frontiersin.org/article/10.3389/fmars.2017.00133/full
12. Santora JA, Sydeman WJ, Schroeder ID, Wells BK, Field JC. Mesoscale structure and oceanographic determinants of krill hotspots in the California Current: Implications for trophic transfer and conservation. Prog Oceanogr [Internet]. 2011; 91:397–409. Available from: http://dx.doi.org/10.1016/j.pocean.2011.04.002
13. Fontana RE, Elliott ML, Largier JL, Jahncke J. Temporal variation in copepod abundance and composition in a strong, persistent coastal upwelling zone. Prog Oceanogr [Internet]. 2016; 142:1–16. Available from: http://dx.doi.org/10.1016/j.pocean.2016.01.004
14. Miller AJ, Chai F, Chiba S, Moisan JR, Neilson DJ. Decadal-scale climate and ecosystem interactions in the North Pacific Ocean. J Oceanogr. 2004; 60(3):163–88.
15. Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, et al. From wind to whales: Trophic links in a coastal upwelling system. Mar Ecol Prog Ser. 2005; 289:117–30.
16. Calambokidis J, Steiger GH, Rasmussen K, Urbán-Ramirez J, Jacobsen JK, Baker CS, et al. Migratory destinations of humpback whales that feed off California, Oregon and Washington. Mar Ecol Prog Ser. 2000; 192:295–304.
17. Calambokidis J, Darling JD, Deecke V, Gearin P, Gosho M, Megill W, et al. Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998. J Cetacean Res Manag. 2002; 4(3):267–76.
18. Kerosky SM, Sirovic A, Roche LK, Baumann-pickering S, Wiggins SM, Hildebrand JA. Bryde's whale seasonal range expansion and increasing presence in the Southern California Bight from 2000 to 2010. Deep Res Part I Oceanogr Res Pap. 2012; 65:125–32.
19. Salvadeo CJ, Lluch-Belda D, Gómez-Gallardo A, Urbán-Ramírez J, MacLeod CD. Climate change and a poleward shift in the distribution of the Pacific white-sided dolphin in the northeastern Pacific. Endanger Species Res. 2010; 11:13–9.
20. MacLeod CD. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endanger Species Res. 2009; 7:125–36.
21. Ramp C, Delarue J, Palsbøll PJ, Sears R, Hammond PS. Adapting to a warmer ocean- Seasonal shift of baleen whale movements over three decades. PLoS One [Internet]. 2015; 10(3):e0121374. Available from: https://doi.org/10.1371/journal.pone.0121374 PMID: 25785462

22. Salvadeo CJ, Alejandro GGU, Nájera-Caballero M, Urbán-Ramirez J, Lluch-Belda D. The effect of climate variability on gray whales (Eschrichtius robustus) within their wintering areas. PLoS One [Internet]. 2015; 10(8):e013465. Available from: https://doi.org/10.1371/journal.pone.0134655 PMID: 26309028

23. Busquets-Vass G, Newsome SD, Calambokidis J, Serra-Valente G, Jacobsen JK, Aguíñiga-García S, et al. Estimating blue whale skin isotopic incorporation rates and baleen growth rates: Implications for assessing diet and movement patterns in mysticetes. PLoS One. 2017; 12(5):e0177880. https://doi.org/10.1371/journal.pone.0177880 PMID: 28562625

24. Fleming AH, Clark CT, Calambokidis J, Barlow J. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. Glob Chang Biol. 2016; 22(3):1214–24. https://doi.org/10.1111/gcb.13171 PMID: 26599719

25. Hilty J, Merenlender A. Faunal indicator taxa selection for monitoring ecosystem health. Biol Conserv. 2000; 92:185–97.

26. Tulloch VJD, Richardson AJ, Matear R, Brown C. Future recovery of baleen whales is imperiled by climate change. Glob Chang Biol. 2019; 25:1263–81. https://doi.org/10.1111/gcb.14573 PMID: 30807685

27. Lawson D, Saez L. Updates on whale entanglement reports- comparing years [Internet]. 2016. Available from: http://www.opc.ca.gov/webmaster/ftp/project_pages/whale-entanglement/EntanglementUpdates2014-2016.pdf

28. [CDFW] California Department of Fish and Wildlife. Current California Ocean Recreational Fishing Regulations [Internet]. 2014. Available from: https://www.dfg.ca.gov/marine/mapregs4.asp

29. Ivens-Duran M, Juhasz C. Dungeness Crab, Metacarcinus magister Enhanced Status Report [Internet]. Sacramento, CA; 2019. Available from: nrmsecure.dfg.ca.gov

30. National Marine Fisheries Service. 2016 West Coast Entanglement Summary [Internet]. 2017. Available from: http://www.westcoast.fisheries.noaa.gov/mediacenter/WCR 2016 Whale Entanglements_3-26-17_Final.pdf

31. National Marine Fisheries Service. 2019 West Coast Whale Entanglement Summary. 2020.

32. Becker EA, Foley DG, Forney KA, Barlow J, Redfern J V., Gentemann CL. Forecasting cetacean abundance patterns to enhance management decisions. Endanger Species Res. 2012; 16:97–112.

33. Lewison R, Hobday AJ, Maxwell S, Hazen E, Hartog JR, Dunn DC, et al. Dynamic ocean management: Identifying the critical ingredients of dynamic approaches to ocean resource management. Bioscience [Internet]. 2015; 65:486–98. Available from: http://bioscience.oxfordjournals.org

34. Hazen EL, Palacios DM, Forney KA, Howell EA, Becker E, Hoover AL, et al. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. J Appl Ecol. 2017; 54 (5):1415–28.

35. Silber GK, Lettrich MD, Thomas PO, Baker JD, Baumgartner M, Becker EA, et al. Projecting Marine Mammal Distribution in a Changing Climate. Front Mar Sci [Internet]. 2017; 4(December). Available from: http://journal.frontiersin.org/article/10.3389/fmars.2017.00413/full

36. Dransfield A, Hines E, McGowan J, Holzman B, Nur N, Elliott M, et al. Where the whales are: Using habitat modeling to support changes in shipping regulations within national marine sanctuaries in central California. Endanger Species Res. 2014; 26:39–57.

37. Leeflang MMG, Moons K, Reitsma J, Zwinderman A. Bias in sensitivity and specificity caused by data driven selection of optimal cut-off values: mechanisms, magnitude and solutions. Clin Chem. 2008; 54 (4):729–37. https://doi.org/10.1373/clinchem.2007.096032 PMID: 18258670

38. Buckland ST, Rexstad EA, Marques TA, Oedekoven CS. Distance sampling: methods and applications. 2015.

39. Donlon CJ, Martin M, Stark J, Roberts-Jones J, Fiedler E, Wimmer W. The Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system. Remote Sens Environ. 2012; 116:140–58.

40. Trenberth KE. The Definition of El Niño. Bull Am Meteorol Soc. 2012; 78:12771–7.

41. Santora JA, Sydeman WJ, Schroeder ID, Reiss CS, Wells BK, Field JC, et al. Krill space: A comparative assessment of mesoscale structuring in polar and temperate marine ecosystems. ICES J Mar Sci. 2012; 69:1317–27.

42. Peterson WT, Schwing FB. A new climate regime in northeast pacific ecosystems. Geophys Res Lett. 2003; 30(17):1–4.

43. Rugh DJ, Shelden KEW, Schulman-Janiger A. Timing of the gray whale southbound migration. (Eschrichtius robustus). J Cetacean Res Manag. 2001; 3(1):31–9.

44. Studwell AJ, Hines E, Elliott ML, Howar J, Holzman B, Nur N, et al. Modeling nonresident seabird foraging distributions to inform ocean zoning in Central California. PLoS One. 2017; 12(1):e0169517. https://doi.org/10.1371/journal.pone.0169517 PMID: 28122001

45. Lawless JF. Negative binomial and mixed poisson regression. Can J Stat [Internet]. 1987; 15(3):209–25. Available from: http://doi.wiley.com/10.2307/3314912

46. Yen PPW, Sydeman WJ, Hyrenbach KD. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. J Mar Syst. 2004; 50:79–99.

47. Kutner M, Nachtsheim C, Neter J, Li W. Applied Linear Statistical Models. 5th ed. Irwin, New York: McGraw Hill; 2004.

48. Mood AM, Graybill FA, Boes DC. Introduction to the Theory of Statistics. 3rd ed. Singapore: McGraw-Hill; 1974.

49. Carretta JV, Oleson EM, Baker J, Weller DW, Lang AR, Karin A, et al. U.S. Pacific draft marine mammal stock assessments: 2016. 2016.

50. Monnahan CC, Branch TA, Punt AE. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? Mar Mammal Sci. 2015; 31(1):279–97.

51. Szesciorka AR, Ballance LT, Širovi A, Rice A, Ohman MD, Hildebrand JA, et al. Timing is everything: Drivers of interannual variability in blue whale migration. Nat Sci Reports. 2020; 10:7710. https://doi.org/10.1038/s41598-020-64855-y PMID: 32382054

52. Salvadeo CJ, Flores-Ramirez S, Gomez-Gallardo A, MacLeod C, Lluch-Belda D, Jaume-Schinkel S, et al. Bryde's whale (*Balaenoptera edeni*) in the southwestern Gulf of California: Relationship with ENSO variability and prey availability. Ciencias Mar. 2011; 37(2):215–25.

53. Santora JA, Mantua NJ, Schroeder ID, Field JC, Hazen EL, Bograd SJ, et al. Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. Nat Commun [Internet]. 2020; 11(536):1–12. Available from: https://doi.org/10.1038/s41467-019-14215-w PMID: 31988285

54. Abrahms B, Hazen EL, Aikens EO, Savoca MS, Goldbogen JA, Bograd SJ. Memory and resource tracking drive blue whale migrations. Proc Natl Acad Sci. 2019;1–6. https://doi.org/10.1073/pnas.1819031116 PMID: 30804188

55. Surma S, Pitcher TJ. Predicting the effects of whale population recovery on Northeast Pacific food webs and fisheries: An ecosystem modelling approach. Fish Oceanogr. 2015; 24(3).

56. Santora JA, Field JC, Schroeder ID, Sakuma KM, Wells BK, Sydeman WJ. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. Prog Oceanogr [Internet]. 2012; 106:154–74. Available from: http://dx.doi.org/10.1016/j.pocean.2012.08.005

57. Leising AW, Schroeder I, Bograd S, Abell J, Durazo R, Caxiola-Castro G, et al. State of the California Current 2014–15: Impacts of the warm-water "Blob." Vol. 56, CalCOFI Report. 2015.

58. McClatchie S, Jacox M, Ohman M, Sala L, Goericke R, Kahru M, et al. State of the California Current 2015–16: Comparisons With the 1997–98 El Niño. Vol. 57. 2016.

59. Rockwood RC, Calambokidis J, Jahncke J. High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protection. PLoS One [Internet]. 2017; 12(8):e0183052. Available from: https://doi.org/10.1371/journal.pone.0183052 PMID: 28827838

60. Martínez-Rincón RO, Saldívar-Lucio R, Morales M, Lluch-Cota SE, Lluch-Cota DB, Salvadeo C, et al. Contribution of ocean variability to climate-catch models of Paci fi c sardine. Deep Res Part II [Internet]. 2019; 159:103–11. Available from: https://doi.org/10.1016/j.dsr2.2018.12.001

61. Shelden KEW, Rugh D, Schulman-Janiger A. Gray Whales Born North of Mexico: Indicator of Recovery or Consequence of Regime Shift? Ecol Appl. 2004; 14(6):1789–805.

Climate shock effects and mediation in fisheries

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Climate shocks can reorganize the social–ecological linkages in food-producing communities, leading to a sudden loss of key products in food systems. The extent and persistence of this reorganization are difficult to observe and summarize, but are critical aspects of predicting and rapidly assessing community vulnerability to extreme events. We apply network analysis to evaluate the impact of a climate shock—an unprecedented marine heatwave—on patterns of resource use in California fishing communities, which were severely affected through closures of the Dungeness crab fishery. The climate shock significantly modified flows of users between fishery resources during the closures. These modifications were predicted by pre-shock patterns of resource use and were associated with three strategies used by fishing community member vessels to respond to the closures: temporary exit from the food system, spillover of effort from the Dungeness crab fishery into other fisheries, and spatial shifts in where crab were landed. Regional differences in resource use patterns and vessel-level responses highlighted the Dungeness crab fishery as a seasonal "gilded trap" for northern California fishing communities. We also detected disparities in climate shock response based on vessel size, with larger vessels more likely to display spatial mobility. Our study demonstrates the importance of highly connected and decentralized networks of resource use in reducing the vulnerability of human communities to climate shocks.

social–ecological system | climate shock | adaptive capacity | fisheries | climate change

Climate shocks threaten food systems around the world and are expected to increase in frequency and intensity under climate change (1–5). Distinct from climate change (e.g., long-term warming), climate shocks rapidly outstrip the capacity of a system to cope by inflicting unexpected and highly concentrated damage (6). Vulnerability of communities to climate shocks varies within and across food systems, depending on the severity of the shock and the sensitivity and adaptive capacity of community members (7). Communities that form the harvesting and processing base of food systems—especially agrarian and fishing communities—are often among the most vulnerable to climate shocks (8), as their resource-based economies operate at the interface of environment and society. Marine heatwaves represent one such climate shock of growing importance, as they impact fishing communities by compromising seafood safety, shifting species distributions, and lowering recruitment and survival of fished species (9–12).

Diversifying harvest portfolios is one strategy used by fishers to manage risk (13–16). If marine heatwaves disproportionately affect a subset of species, fishers may respond by shifting participation into less affected fisheries. This response, referred to as "leakage" or "spillover" (17–21), restructures the networks that form as fishers participate in multiple fisheries (19–21). The topology of these fisheries participation networks can reveal the extent to which climate shocks lead to indirect or lasting changes in patterns of resource use within fishing communities and, by drawing on network theory, indicate the sensitivity of these communities to perturbations (18).

The 2014–2016 North Pacific marine heatwave (12, 22) was a climate shock that led to a massive harmful algal bloom (HAB), contaminating Dungeness crab with biotoxins and compelling state managers to coordinate fishery closures along the entire US West Coast (23). In California, where the Dungeness crab fishery represents ~26% of all annual fishery revenue (California Department of Fish and Wildlife; https://wildlife.ca.gov) and supports >25% of all commercial fishing vessels (Pacific Fisheries Information Network; http://pacfin.psmfc.org), the HAB significantly delayed the 2015–16 commercial Dungeness crab fishing season (24). California Dungeness crab landings for the 2015–16 season reached only 52% of the average catch from the previous 5 y, spurring Congress to appropriate >$25 million in federal disaster relief funding (25). Dungeness crab fishers reported shifting participation to alternative fisheries during the 2015–16 season to offset socioeconomic impacts (26, 27); however, to date there has been no quantitative demonstration of spillover from the Dungeness crab fishery, or analysis of how the resulting changes in fisheries participation networks may have varied geographically and persisted after the closures were lifted.

Our study examined the impact of the 2015–16 Dungeness crab fishery closures (hereafter 2016 closures) on patterns of resource use in California fishing communities. We considered seven fishing communities representing a total of 2,516 individual fishing vessels (Table 1). We found significant changes in fisheries participation network topology during the 2016

Significance

Climate shocks are increasingly disruptive to global food systems, with far-reaching consequences for resource-based communities. Yet quantitative assessments of community impacts rarely account for economic connectivity between alternative resources. We show that patterns of resource use influence the sensitivity of US West Coast fishing communities to unprecedented fishery closures in the wake of a recent climate shock. Patterns of participation in commercial fisheries were significantly altered during the fishery closures, but rebounded to preexisting states after closures were lifted, indicating community-level resilience to this particular perturbation. Our study provides evidence that more complex networks of resource use buffer the impact of climate shocks, and reveals strategies that alter emergent patterns of resource use in affected fishing communities.

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Table 1. Ports of landing and vessel counts for the seven California fishing communities included in this study

Region	Fishing community	Ports of landing	Total annual vessels, 2008–17	Dungeness crab vessel counts (large/small), 2015	Dungeness crab vessel proportions, 2015
North	Crescent City	Crescent City, Other Del Norte County	109 ± 16	68 (40/28)	0.75
	Eureka	Eureka, Fields Landing, Trinidad, Other Humboldt County	150 ± 24	77 (34/43)	0.51
	Fort Bragg	Albion, Point Arena, Fort Bragg, Other Mendocino County	237 ± 96	41 (22/19)	0.12
	Bodega Bay	Bodega Bay, Bolinas, Point Reyes, Tomales Bay, Other Sonoma/Marin County	208 ± 77	105 (56/49)	0.44
	Total		*753 ± 149*	*291 (152/139)*	*0.36*
Central	San Francisco	Alameda, Berkeley, Oakland, Princeton/Half Moon Bay, Richmond, San Francisco Sausalito, Other San Francisco Bay/San Mateo County	388 ± 97	221 (121/100)	0.49
	Monterey Bay	Santa Cruz, Monterey, Moss Landing, Other Santa Cruz/Monterey County	286 ± 83	47 (15/32)	0.14
	Morro Bay	Avila, Morro Bay, Other San Luis Obispo County	187 ± 26	30 (17/13)	0.14
	Total		*567 ± 98*	*298 (153/145)*	*0.30*

The number and proportion of commercial Dungeness crab fishing vessels in the given community is reported for the 2015 crab year. "Total annual vessels" reports the mean annual number of active commercial vessels in the given fishing community, with SD, for crab years 2008 to 2017.

closures, which corresponded with a severe reduction in fishing activity, spillover of fishing effort from the Dungeness crab fishery, and spatial variation in pre-shock network topology. Our analysis captured changing patterns of resource use during a severe climate shock, and demonstrated how this emergent social outcome in fishing communities can be predicted by pre-shock network metrics and related to the adaptive strategies of community member vessels. We discuss the implications of fishery management measures for adaptive decision making and network structure, and provide recommendations for sustainable fishery management during climate shocks.

Evaluating Change in Fisheries Participation Networks

Our analysis used historical landings data and network methodology to quantify the sensitivity of fishing communities to perturbations in the Dungeness crab fishery. We then related expected sensitivity to changes in network topology during and after the 2016 closures, and qualitatively linked those changes to adaptive responses by Dungeness crab vessels. We used a shore-based definition of fishing communities as port groups (18, 28), with vessels landing catch in a given port group as proxies for fishers. We defined fishing community sensitivity as the magnitude of change in fisheries participation network topology caused by a perturbation.

Participation Network Framework. We used two types of participation networks to 1) quantify patterns of resource use in fishing communities, and 2) deconstruct Dungeness crab vessel activity. In both networks, nodes are fisheries, with edges connecting pairs of fisheries based on shared vessel participation. Undirected fisheries participation networks show participation by all vessels in a fishing community, with nondirectional edge weights defined by the number of vessels participating in, and the evenness of revenue generation from, pairs of connected fisheries (18). Directed networks capture spillover from the Dungeness crab fishery during and immediately after the 2016 closures; edges, weighted by the number of vessels, indicate Dungeness crab vessel movement out of fisheries in which they participated during the previous season and into alternative fisheries, to a different fishing community, or out of the California commercial fishing industry for the 2015–16 fishing season.

Drawing on >286,000 landing records, we constructed directed and undirected networks for each Dungeness crab season. We refer to each season using "crab years," from November through October of the following year; the 2016 crab year corresponds to the 2015–16 fishing season (i.e., November 2015 to October 2016). To observe behavioral responses during and immediately after the 2016 closures, we further subdivided each crab year into an early season and a late season, delineated by the dates of the 2016 closures (*SI Appendix*, Table S1). The early season spanned from the typical Dungeness crab fishing season start date (November 15 or December 1) to when the 2016 closures were lifted, and the late season encompassed the remainder of the crab year (Fig. 1 and *SI Appendix*, Table S1). Spatial variation was observed at a regional level, with fishing communities clustered into northern and central regions (Table 1 and *SI Appendix*, Fig. S1).

Quantifying Patterns of Cross-Fishery Participation. We examined three aspects of participation network topology that network theory relates to the ability of individuals and communities to respond to a perturbation (*SI Appendix*, Table S2). The first is overall connectedness, or fisheries connectivity, measured using edge density. In a fisheries context, greater connectivity suggests more flexibility in fishers' participation (18, 29) and thus a greater capacity to adapt to a perturbation without leaving the fishing industry. The second is the degree to which the network is divided into subgroups, quantified by modularity. Modularity is inversely related to sensitivity, because more modular networks tend to limit perturbations to the subgroup in which they occur (18, 30). The third is the degree to which the network is concentrated around a central fishery, represented by network centralization (31). Networks with high centralization display little sensitivity to a perturbation unless the perturbation impacts the central node. Modularity and centralization were calculated using network edge weights (*SI Appendix*, Table S2); we also calculated unweighted modularity and centralization, as well as mean degree for a size-scalable alternative to edge density, and report these results in the *SI Appendix*.

Participation networks are highly dynamic over time in both size and structure (*SI Appendix*, Figs. S2–S4), and can be influenced by a number of social and ecological factors. We used generalized linear models to attribute topological changes during the 2016 crab year to the 2016 Dungeness crab fishery closures, with network metrics as the response variables. Since the Dungeness crab fishery experienced shortened seasons prior to the 2016 crab year (*SI Appendix*, Table S3), we captured the effect of the 2016 closures using a closure duration (D) categorical predictor variable. The 2016 closures represented the highest level of closure duration. We also included network size, crab year, community, and region as predictor variables in our nested models (*SI Appendix*, Tables S4 and S5).

Results

Network-Based Expectations of Community Vulnerability. Prior to the 2016 closures, patterns of fishery participation in California varied substantially between regions (Fig. 1 and *SI Appendix*, Fig. S3). Networks for the northern region fishing communities of Crescent City, Eureka, Fort Bragg, and Bodega Bay were composed of fewer fisheries; more highly centralized around Dungeness crab; had lower size-scaled fisheries connectivity (mean degree); and exhibited less modularity than the central region fishing

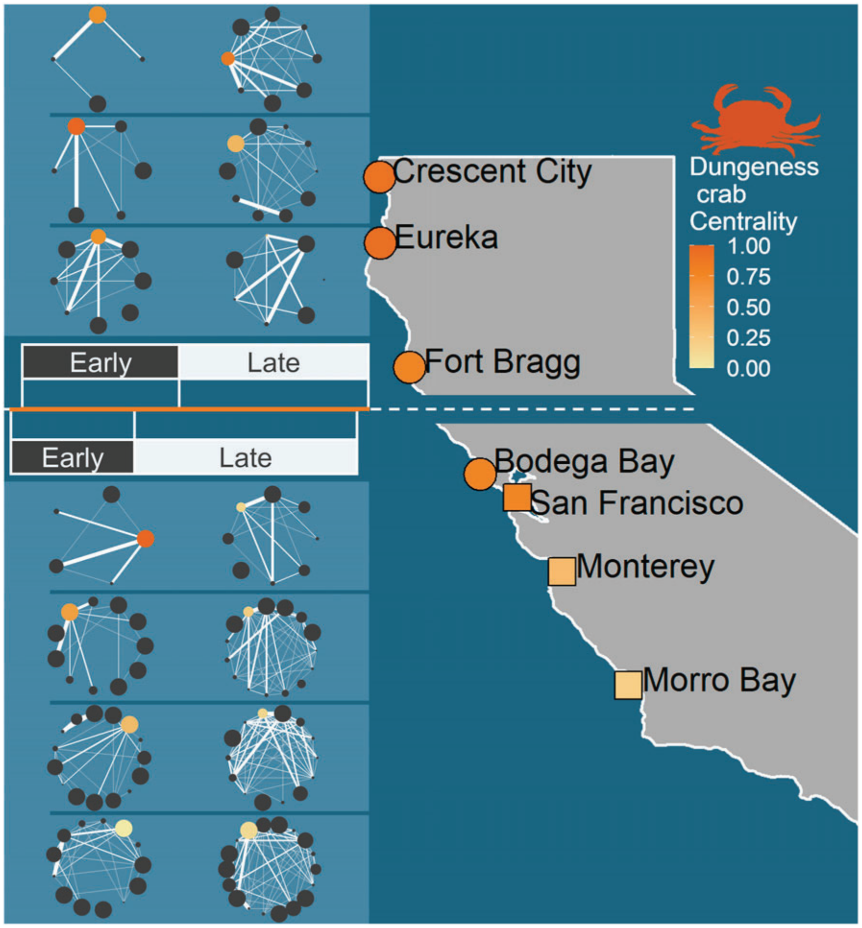

Fig. 1. The seven California fishing communities included in this study and their pre-shock fisheries participation networks. Pre-shock early (*Left*) and late (*Right*) networks represent a 3-y average (crab years 2013 to 2015) of participation prior to the 2016 fishery closures. The Dungeness crab fishery node is shaded orange in each network according to its betweenness centrality, a measure of importance (note that nodes are not consistently positioned across networks). The timeline shows the relative duration of the early and late seasons for fishing communities in the two California management districts (above/below timeline). Point color on the map indicates average Dungeness crab betweenness centrality across the early and late seasons, and point shape indicates whether the fishing community was considered part of the northern region (circle) or the central region (square) for this study.

communities of San Francisco, Monterey, and Morro Bay. These regional differences were particularly pronounced during the early season, when the majority of Dungeness crab landings occur (32, 33). In the late season, northern region networks were more complex and less centralized, lessening most topological differences between regions (*SI Appendix*, Fig. S3). Network theory predicts that fishing communities in the northern region would be more vulnerable to a perturbation in the Dungeness crab fishery due to higher sensitivity (centralization, modularity) and lower adaptive capacity (fisheries connectivity, network size), particularly during the winter months of the early season.

Northern Region Impacts during the Shock. Patterns of fishery participation during the early season were significantly more affected by the 2016 closures in the northern region than in the central region. Networks of fishing communities in the northern region saw significant declines in fisheries connectivity (edge density; −58%) and reduced concentration of participation around a single fishery (centralization; −31%) (Fig. 2*A* and *SI Appendix*, Table S6).

These network changes represent three strategies undertaken by northern region Dungeness crab vessels to cope with, or adapt to, the 2016 closures: vessel dropout, spatial mobility, and spillover into alternative fisheries. The majority of Dungeness crab fishing vessels in the northern region (56.4 ± 16.7%) discontinued all fishing in California during the 2016 closures. Early season vessel dropout was relatively consistent between large (≥40 ft) and small (<40 ft) vessels. Landing catch in a different community, representative of spatial mobility, was mostly undertaken by large vessels, particularly those that spent the previous crab year fishing in Eureka and Crescent City (Fig. 3). Dropout and spatial mobility could have decreased fisheries connectivity if vessels that stopped fishing entirely or moved to a different fishing community would normally have participated in multiple fisheries during the early season.

The observed declines in fisheries connectivity were also tied to vessels that remained active within the same fishing community. Approximately 87% and 84% of active small and large vessels, respectively, concentrated participation in a single alternative fishery and thus did not contribute to fisheries connectivity during the early season of the 2016 crab year. During the early season of the previous crab year, 61% of these vessels spread participation across multiple fisheries (Dungeness crab and others). Spillover resulting from the 2016 closures was concentrated primarily in the sablefish and mixed rockfish/lingcod fisheries (Fig. 3), although northern region Dungeness crab vessels participated in a total of 16 alternative fisheries. Because vessels that normally would have concentrated participation in the Dungeness crab fishery dispersed into different alternatives, network centralization declined.

Central Region Impacts during the Shock. Fisheries connectivity and centralization in the central region increased by 32% and 16%, respectively, during the early season of the 2016 crab year (Fig. 2*A*). These changes were significantly different from the declines that occurred in the northern region during the closures (Fig. 2*A* and *SI Appendix*, Table S6).

Smaller changes in fisheries connectivity and centralization in the central region are consistent with network theory: lower reliance on the Dungeness crab fishery, represented by lower preshock Dungeness crab centrality (Fig. 1), translated to less sensitivity to the loss of access to Dungeness crab. Increases in fisheries connectivity within central region fishing communities coincided with an increase in the diversity of fishery participation by Dungeness crab vessels, particularly in Monterey (n =18 active vessels). While northern region Dungeness crab vessels exhibited more single-fishery participation during the early season of the 2016 crab year compared with the previous year, the proportion of active Dungeness crab vessels participating in two or more fisheries in the central region more than doubled between the 2015 and 2016 early season (from 9% to 20%).

Lower reliance on the Dungeness crab fishery also makes it possible for dynamics external to the Dungeness crab fishery to have an equal or greater effect on patterns of resource use in central region fishing communities. Dungeness crab vessels represented only 14% of all commercial fishing vessels in Monterey and Morro Bay (Table 1), and the majority of central region Dungeness crab vessels stopped fishing entirely during the early season (72.5 ± 0.1%). Therefore, even as concentrated participation in the Dungeness crab fishery was replaced with a number of alternative fisheries, decentralizing participation among Dungeness crab vessels, at a community scale these effects were relatively weak.

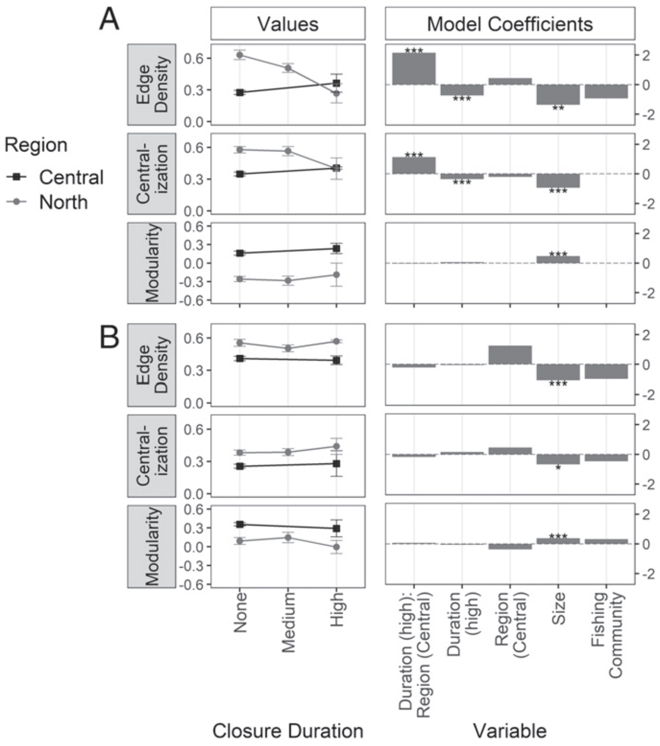

Fig. 2. Mean value and SE at each closure duration level (*Left*) and coefficients from the generalized linear models (*Right*) for each network metric in the early (*A*) and late (*B*) seasons. Coefficients for edge density and centralization are on the logit scale. The *Duration (high) : Region (central)* term describes the change to the coefficient of the *Duration (high)* term when observing central region, compared with northern region, networks. For example, the coefficient for *Duration (high) : Region (central)* in the model for early season edge density (*A*, *Top*), is positive; this indicates that observing a network from the central region compared with the northern region makes the negative association of the 2016 closures with edge density more positive. Significance is indicated above each column. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

California Impacts Immediately after the Shock. We observed minimal, nonsignificant effects of the 2016 closures on late season patterns of fishery participation (Fig. 2). None of the network metrics for either region exhibited significant change during the late season, although increases in centralization in the northern and central regions were significant when not weighted by revenue (unweighted centralization; *SI Appendix*, Table S7). Increased centralization was likely from the concentration of participation in the high-revenue Dungeness crab fishery after the closures were lifted, at a time when fishers would normally have been prioritizing a variety of other fisheries, such as Chinook salmon (*SI Appendix*, Fig. S5).

Discussion

As climate shocks become more frequent and intense under climate change, it is increasingly critical to predict, rapidly assess, and reduce the vulnerability of natural resource-based communities. For fishing communities, vulnerability to resource loss can be closely tied to access to alternative fisheries, an important source of adaptive capacity (13, 15). In this study, we found significant changes in patterns of fishery participation in response to fishery closures, forced by a heatwave-associated HAB. Greater changes in northern California fishing communities corresponded with greater sensitivity (increased specialization or network centralization), less adaptive capacity (lower fisheries connectivity and smaller network size), and heightened exposure (longer duration fishery closures). Patterns of fishery participation mostly returned to their predisturbance state following the opening of the Dungeness crab fishery, indicating community-level resilience to this singular perturbation. This study quantified the impact of a climate shock and subsequent management measures on natural resource use in fishing communities, and revealed the underlying behavior of fishing vessels.

A challenge in predicting community response to anthropogenic and environmental perturbations lies in quantifying community sensitivity and adaptive capacity (7). Network metrics help us do this, serving as indicators of system sensitivity (centralization, modularity) and adaptive capacity (network size, connectivity) in the face of perturbations (18, 34, 35). We can therefore interpret our results through the lens of network theory and the vulnerability framework (7) to provide a forward-looking glimpse into an alternative state under climate change, in which more frequent marine heatwaves and HABs (36, 37) cause the loss of key resources for California fishing communities. On the one hand, minimal spillover and topological changes to fisheries participation networks following the 2016 closures suggest that patterns of fishery participation in California were resilient to this climate shock. However, if Dungeness crab vessel owners and operators were to permanently adopt the alternative fishing strategies observed during the 2016 closures, then our results imply that the northern fishing communities could become more vulnerable to secondary social and ecological perturbations. Even as participation becomes more evenly spread across existing fisheries, the sharp decline of fisheries connectivity (captured here with edge density) predicts a lower capacity for individuals to switch between fisheries. For the central region fishing communities, a more diverse portfolio of early season fishery participation could buffer the impacts of future perturbations if diversification were adopted as a long-term adaptive strategy (as was done by Pacífico Norte fishers; ref. 38); however, it is important to note that the lower reliance on Dungeness crab

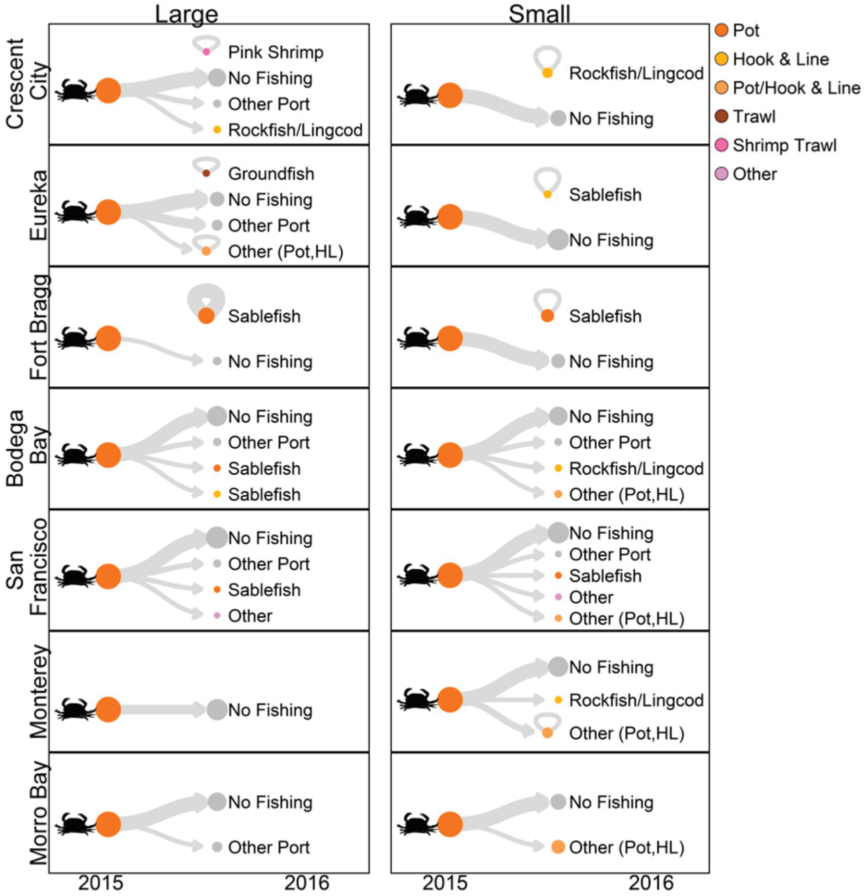

Fig. 3. Changes in early season fishery participation by large (*Left*) and small (*Right*) Dungeness crab vessels from the 2015 to the 2016 crab year. Edges show the flow of vessels out of the 2015 Dungeness crab fishery (left of each network graph, labeled with crab icon) into 2016 alternatives (right of each network graph). Self-loops were included if Dungeness crab vessels participated in a non-Dungeness fishery during both crab years; otherwise, the directed edge represents new early season participation in the 2016 alternative. Edge-weight is proportional to the number of Dungeness crab vessels that undertook the indicated shift in participation. Node size is proportional to the number of Dungeness crab vessels participating in each fishery during the associated crab year (*x*-axis). When multiple fisheries using pot or hook-and-line gear had fewer than three participating vessels, we collapsed the fisheries into a single "Other (Pot, HL)" node; the "Other" node is a similar aggregate but with fisheries using any gear type. We added two nonfishery nodes to indicate whether a vessel stopped fishing altogether during the 2016 Dungeness crab closures ("No Fishing") or stopped fishing at the given fishing community but was recorded landing catch at another California port ("Other Port").

in the central region is also a key factor in maintaining low community vulnerability to secondary perturbations. The ability to reallocate fishing effort conferred by diverse harvest portfolios reduces variation in annual fishing revenue (15) and is critical for individual adaptation not only to climate shocks, but also to fishery management changes (e.g., catch share programs ; refs. 20 and 21). More generally, diversification is a fundamental tenet of resilience theory for social–ecological systems, which emphasize strategies that integrate over variability, shocks, and reorganization to sustain species, economies, and livelihoods (39).

There can be many counterincentives to diversification, however, especially when common species are highly valuable (16) or when there are high barriers to access for certain resources (e.g., permitting structures, capital, knowledge; ref 14). In fisheries, concentration of effort into a single, highly lucrative fishery can result in a "gilded trap" (16, 40). Most notably observed in the Maine American lobster industry, this type of social trap is formed as social drivers increase the value of the resource, even as the resource itself moves closer to an ecological tipping point (16). Our research and community interviews (41) suggest that Dungeness crab might be considered a gilded trap for northern California fishing communities and associated coastal communities. While economically lucrative for fishers and fishing-related industries in the short term, a focus of effort on Dungeness crab increases vulnerability to climate shocks during the winter months when there is little existing activity in other fisheries. The Dungeness crab fishery is presently at risk not only from seafood safety concerns, but also from the bycatch of protected species (42) and the effects of ocean acidification on early life history stages (43). Escape from social traps in resource-based economies requires incentives and policies that address the underlying socioeconomic conditions and behavior reinforcing the trap. This can be a complex undertaking that requires careful investment in institutional capacity at multiple scales (44, 45).

These community patterns summarized in fisheries participation networks emerge from decisions made by individuals, which in turn are influenced by community-scale properties. The vessel activity that we describe highlights how the impacts of climate shocks are likely to be felt unequally within fishing communities, in California and beyond (27, 46). Differences in adaptive capacity during the 2016 closures were related to vessel size, with larger vessels conferring a greater ability to move out of closed areas to fish; we observed a greater proportion of large vessels than small vessels moving between fishing communities, particularly during the longer closures in the northern region. Our findings agree with those of Jardine et al. (27), who used a 3-y baseline of Dungeness crab landings at the same California fishing communities to show that large Dungeness crab vessels were more mobile than small vessels in the 2016 crab year. Fishers with smaller vessels instead relied on alternative fisheries to remain active in-place. This discrepancy arose despite state management measures that seek to restrict mobility during fishery closures, requiring vessels landing Dungeness crab outside a delayed district to wait 30 d before fishing within the delayed district (California Fish and Game Code § 8279.1). Recent amendments (47), motivated in part by vessel movement during the 2016 crab year, may limit the feasibility of spatial redistribution as a strategy to cope with future climate shocks.

Yet, moving to a location where social and ecological conditions are more favorable may be more effective than reliance on strategies to remain active in-place, such as shifting effort to alternative fisheries. Keeping pace with shifting species ranges and abundance under climate change often requires resource users to modify the spatial distribution and intensity of their efforts (48, 49). In addition, the adoption of limited entry and catch share programs may make it increasingly difficult to remain active in-place by accessing alternative fisheries. For example, on the US West Coast, the 2012 Pacific groundfish trawl rationalization and 2002 Pacific sablefish permit stacking programs restricted access to certain groundfish and sablefish fisheries. This led to historically active vessels exiting the affected fisheries (50) and higher costs to new participants (51). A comprehensive comparison of climate adaptation through in-place strategies as opposed to movement must also account for access to diverse employment opportunities beyond fishing (often captured by education and economy size; refs. 52 and 53). Extending participation networks to include nonfisheries job participation (i.e., "livelihood landscapes;" ref. 31) provides this more holistic view of in-place adaptive capacity and may capture co-occurring effects of climate shocks across food systems (5). Livelihood landscapes also focus on individuals or households and so can speak to the heterogeneity in capacity and agency among fishers, something not captured with vessel-level data.

While some individuals move or modify behavior in response to climate shocks, others are unable to access viable alternatives and must simply absorb the impact and rebuild. This "duck-and-cover" strategy is particularly common in fishing and agrarian communities following major storms (54, 55). In the California Dungeness crab fishery, a surprisingly high proportion of large and small Dungeness crab vessels adopted this duck-and-cover strategy and ceased all fishing activity during the 2016 closures. Most vessels waited out the closures in port (26, 41), despite later evidence that alternative fishing activities contributed significantly to fishers' income loss recovery (56). The prevalence of this strategy, and adaptive actions more broadly, may be best understood as the outcome of nested decision making processes at both individual and institutional levels (57). On the US West Coast, HAB monitoring and associated fishery closures are implemented by state and tribal governments; as a result, the structure and effectiveness of early warning systems and communication with stakeholders varies by region (58). California fishers have requested more reliable and clear communication by scientific and regulating institutions during future HAB events to facilitate more effective decision making (41). Communication and prediction are both important for climate shock preparedness and, more generally, in "climate-ready" fisheries management (59).

Another key consideration for developing climate-ready fisheries management is how to facilitate fishing effort spillover in such a way as to increase adaptive capacity and achieve a net decline in vulnerability. Fishers are creative problem solvers with a long history of adapting to challenging conditions (29), but they must also be supported by governance systems. This will require coordination and partnership between governing institutions; in our study system, the Dungeness crab fishery is managed at the state level, but alternatives during the 2016 closures consisted of both state- and federally-managed fisheries. Also needed is careful consideration of unintended outcomes that may arise from improving mobility between fisheries, such as increased or novel interactions with protected species (42) and other ocean use sectors, the potential for overcapitalization of remaining open access fisheries, and incentivization of a "roving bandit" strategy of sequential overharvesting across a participation network (60). When designing governance measures to temporarily facilitate spillover during a climate shock, combining networks of economic and ecological connectivity among fisheries, and considering networks that represent different types of fishery participants, could help to assess direct and indirect social and ecological impacts (19).

Our findings suggest that management approaches that account for connectivity and spillover between fisheries during a climate shock are more likely to anticipate, and potentially mediate, impacts on fishing communities. The impacts of climate shocks are a materialization of underlying risk and vulnerability (61) in fisheries and other components of food systems. Quantifying connectivity between alternative resources can capture these impacts and uncover sources of sensitivity and adaptive capacity in highly dynamic, resource-based communities—a critical step toward achieving sustainability in the face of climate shocks and long-term change.

Materials and Methods

Data. Fisheries landings and vessel registration data for the 2008 to 2017 crab years were retrieved from the Pacific Fisheries Information Network (PacFIN; http://pacfin.psmfc.org) database. Landings data were filtered to include commercial landings from 30 California ports of landing, or seven port groups, where Dungeness crab is an important source of revenue (Fig. 1 and Table 1). Since we expected to find length-based differences in adaptive capacity (27), we used registration data to calculate vessel length in feet (*SI Appendix*) and classified vessels ≥40 feet long as large vessels and those <40 feet long as small vessels (13).

Defining Fisheries and Fishing Communities. We defined fisheries by grouping PacFIN fish tickets based on gear type, species composition of catch, and ex-vessel revenue using a métier analysis (62) modified from Fuller et al. (18). In short, we ran the infoMap community detection algorithm (63) implemented in the R package igraph (64) on data from fish tickets collected during the 2011 and 2012 crab years (chosen because they occurred in the middle of our pre-shock study period). The remaining fish ticket data were matched to the infoMap-processed fish tickets using a *k*-nearest-neighbor (KNN) approach. Fish tickets that failed to be assigned métiers with KNN (i.e., those that recorded unique species/gear combinations) were compiled across crab years and rerun through the infoMap algorithm. Fish tickets are linked to vessels, which formed the foundation of our participation analyses. Thus our definition of a fishing community was a set of vessels that land their catch at a given shore-based port group. We used vessels as proxies for fishers owing to the limitations of available data (18, 50), not because of the notion that a collection of vessels better characterizes a community than a group of people. Although this was an imperfect approximation, it did allow us to track changes in harvesting practices through time, across vessel sizes and geographic regions.

Constructing Networks. Participation networks summarized cross-fishery participation for all vessels in a fishing community. If a single fishing vessel recorded catch in multiple fishing communities within a single crab year, it was considered a member of each fishing community. We used the network framework of Fuller et al. (18), in which the weight of a nondirectional edge between fisheries *i* and *j* represents a measure of fisheries connectivity that is proportional to the number of vessels participating in both fisheries and the evenness with which each vessel generates revenue from fishery *i* v. fishery *j*. We constructed directed networks to observe changes in fishery participation by Dungeness crab vessels in each fishing community. A "Dungeness crab vessel" was defined as any fishing vessel that recorded at least one commercial Dungeness crab landing in California in the 2015 crab year ($n = 477$ unique vessels).

Generalized Linear Models. We evaluated a series of nested models (*SI Appendix*, Table S4) and chose the most informative model using an F-test. Participation network size varies through time and across fishing communities, and certain network metrics, such as edge density and centralization, are known to be dependent on network size. To distinguish between a meaningful signal of change and variability related to network size, we conservatively included network size (N) as a predictor variable based on results from a Spearman rank correlation test (65) between each metric and the number of nodes in the network (*SI Appendix*, Table S5). Standardized residuals and Q-Q plots were used to assess normality, linearity, and homoscedasticity assumptions, and the model was tested for sensitivity to outliers detected with Cook's distance.

Data Availability. Confidential vessel-level landings and registration data may be acquired by direct request from the California Department of Fish and Wildlife, subject to a nondisclosure agreement. Aggregated, nonconfidential data to construct network graphs, network metrics data used as input for the generalized linear models, and R code are available on GitHub (DOI: 10.5281/zenodo.4177949).

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1. E. M. Fischer, C. Schär, Consistent geographical patterns of changes in high-impact European heatwaves. *Nat. Geosci.* **3**, 398–403 (2010).
2. M. A. Bender *et al*., Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* **327**, 454–458 (2010).
3. S. Banholzer, J. Kossin, S. Donner, "The impact of climate change on natural disasters" in *Reducing Disaster: Early Warnings Systems for Climate Change*, A. Singh, S. Zommers, Eds. (Springer, 2014), pp. 21–49.
4. P. Stott, How climate change affects extreme weather events. *Science* **352**, 1517–1518 (2016).
5. R. S. Cottrell *et al*., Food production shocks across land and sea. *Nat. Sustain.* **2**, 130–137 (2019).
6. A. de la Fuente, "Climate shocks and their impacts on assets" in *Human Development Report 2007/2008*, K. Watkins, Ed. (United Nations Development Programme, 2007), p. 23.
7. W. N. Adger, Vulnerability. *Glob. Environ. Change* **16**, 268–281 (2006).
8. J. Porter *et al*., "Food security and production systems" in *Climate Change 2014: Impacts, Adaptation and Vulnerability Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, C. B. Field, *et al*., Eds. (Cambridge University Press, 2014), pp. 485–533.
9. T. L. Frölicher, C. Laufkötter, Emerging risks from marine heat waves. *Nat. Commun.* **9**, 650 (2018).
10. A. Basilio, S. Searcy, A. R. Thompson, Effects of the blob on settlement of spotted sand bass, Paralabrax maculatofasciatus, to Mission Bay, San Diego, CA. *PLoS One* **12**, e0188449 (2017).
11. D. A. Smale *et al*., Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang.* **9**, 306–312 (2019).
12. N. A. Bond, M. F. Cronin, H. Freeland, N. Mantua, Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.* **42**, 3414–3420 (2015).
13. S. Kasperski, D. S. Holland, Income diversification and risk for fishermen. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 2076–2081 (2013).
14. S. C. Anderson *et al*., Benefits and risks of diversification for individual fishers. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 10797–10802 (2017).
15. T. J. Cline, D. E. Schindler, R. Hilborn, Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nat. Commun.* **8**, 14042 (2017).
16. R. S. Steneck *et al*., Creation of a gilded trap by the high economic value of the Maine lobster fishery. *Conserv. Biol.* **25**, 904–912 (2011).
17. S. Cunningham, L. S. Bennaer, M. D. Smith, Spillovers in regional fisheries management: Do catch shares cause leakage? *Land Econ.* **92**, 344–362 (2016).
18. E. C. Fuller, J. F. Samhouri, J. S. Stoll, S. A. Levin, J. R. Watson, Characterizing fisheries connectivity in marine social-ecological systems. *ICES J. Mar. Sci.* **74**, 2087–2096 (2017).
19. J. Yletyinen, J. Hentati-Sundberg, T. Blenckner, Ö. Bodin, Fishing strategy diversification and fishers' ecological dependency. *Ecol. Soc.* **23**, 28 (2018).
20. E. T. Addicott *et al*., Identifying the potential for cross-fishery spillovers: A network analysis of Alaskan permitting patterns. *Can. J. Fish. Aquat. Sci.* **76**, 56–68 (2018).
21. K. Kroetz, M. N. Reimer, J. N. Sanchirico, D. K. Lew, J. Huetteman, Defining the economic scope for ecosystem-based fishery management. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 4188–4193 (2019).
22. E. Di Lorenzo, N. Mantua, Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat. Clim. Chang.* **6**, 1042–1047 (2016).
23. R. M. McCabe *et al*., An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophys. Res. Lett.* **43**, 10366–10376 (2016).
24. S. K. Moore *et al*., An index of fisheries closures due to harmful algal blooms and a framework for identifying vulnerable fishing communities on the US West Coast. *Mar. Policy* **110**, 103543 (2019).
25. D. S. Holland, J. Leonard, Is a delay a disaster? Economic impacts of the delay of the California Dungeness crab fishery due to a harmful algal bloom. *Harmful Algae* **98**, 101904 (2020).
26. K. M. Moore *et al*., Harmful algal blooms: Identifying effective adaptive actions used in fishery-dependent communities in response to a protracted event. *Front. Mar. Sci.* **6**, 803 (2020).
27. S. L. Jardine, M. C. Fisher, D. Perry, S. K. Moore, J. F. Samhouri, Inequality in the economic impacts from climate shocks to fisheries: The case of harmful algal blooms. *Ecol. Econ.* **176**, 106691 (2020).
28. K. Richerson, J. Leonard, D. S. Holland, Predicting the economic impacts of the 2017 West Coast salmon troll ocean fishery closure. *Mar. Policy* **95**, 142–152 (2018).
29. J. S. Stoll, E. Fuller, B. I. Crona, Uneven adaptive capacity among fishers in a sea of change. *PLoS One* **12**, e0178266 (2017).
30. S. A. Levin, J. Lubchenco, Resilience, robustness, and marine ecosystem-based management. *Bioscience* **58**, 27–32 (2008).
31. J. E. Cinner, O. Bodin, Livelihood diversification in tropical coastal communities: A network-based approach to analyzing "livelihood landscapes." *PLoS One* **5**, e11999 (2010).
32. C. M. Dewees, K. Sortais, M. J. Krachey, S. C. Hackett, D. G. Hankin, Racing for crabs: Costs and management options evaluated in Dungeness crab fishery. *Calif. Agric.* **58**, 186–189 (2004).
33. K. Richerson, A. E. Punt, D. S. Holland, Nearly a half century of high but sustainable exploitation in the Dungeness crab (Cancer magister) fishery. *Fish. Res.* **226**, 105528 (2020).
34. M. Barnes *et al*., The social structural foundations of adaptation and transformation in social-ecological systems. *Ecol. Soc.* **22**, 16 (2017).
35. F. Meng, G. Fu, R. Farmani, C. Sweetapple, D. Butler, Topological attributes of network resilience: A study in water distribution systems. *Water Res.* **143**, 376–386 (2018).
36. S. K. Moore *et al*., Impacts of climate variability and future climate change on harmful algal blooms and human health. *Environ. Health* **7** (suppl. 2), S4 (2008).
37. A. J. Lewitus *et al*., Harmful algal blooms along the North American west coast region: History, trends, causes, and impacts. *Harmful Algae* **19**, 133–159 (2012).
38. B. J. McCay, W. Weisman, C. Creed, "Coping with environmental change: Systemic responses and the roles of property and community in three fisheries" in *World Fisheries: A Social-Ecological Analysis*, R. E. Omner, R. I. Perry, K. Cochrane, P. Cury, Eds. (Blackwell Publishing, 2011), pp. 381–400.
39. C. Folke *et al*., Resilience thinking: Integrating resilience, adaptability and transformability. *Ecol. Soc.* **15**, 43 (2010).
40. B. J. McCay, Systems ecology, people ecology, and the anthropology of fishing communities. *Hum. Ecol.* **6**, 397–422 (1978).
41. J. Ritzman *et al*., Economic and sociocultural impacts of fisheries closures in two fishing-dependent communities following the massive 2015 US West Coast harmful algal bloom. *Harmful Algae* **80**, 35–45 (2018).
42. J. A. Santora *et al*., Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nat. Commun.* **11**, 536 (2020).
43. N. Bednaršek *et al*., Exoskeleton dissolution with mechanoreceptor damage in larval Dungeness crab related to severity of present-day ocean acidification vertical gradients. *Sci. Total Environ.* **716**, 136610 (2020).
44. J. E. Cinner, Social-ecological traps in reef fisheries. *Glob. Environ. Change* **21**, 835–839 (2011).
45. J. Platt, Social traps. *Am. Psychol.* **28**, 641–651 (1973).
46. R. Mearns, A. Norton, *Social Dimensions of Climate Change: Equity and Vulnerability in a Warming World* (The International Bank for Reconstruction and Development / The World Bank, Washington, D.C., 2010).
47. S. L. Jardine, M. C. Fisher, S. K. Moore, J. F. Samhouri, Inequality in the economic impacts from climate shocks in fisheries: The case of harmful algal blooms. *Ecol. Econ.* **176**, 106691 (2020).
48. T. Young *et al*., Adaptation strategies of coastal fishing communities as species shift poleward. *ICES J. Mar. Sci.* **76**, 93–103 (2019).
49. J. Wang, D. G. Brown, A. Agrawal, Climate adaptation, local institutions, and rural livelihoods: A comparative study of herder communities in Mongolia and inner Mongolia, China. *Glob. Environ. Change* **23**, 1673–1683 (2013).
50. D. S. Holland *et al*., Impact of catch shares on diversification of fishers' income and risk. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 9302–9307 (2017).
51. S. M. Russell, M. V. Oostenburg, A. Vizek, Adapting to catch shares: Perspectives of West Coast groundfish trawl participants. *Coast. Manage.* **46**, 603–620 (2018).
52. W. N. Adger, Social vulnerability to climate change and extremes in coastal Vietnam. *World Dev.* **27**, 249–269 (1999).
53. L. L. Colburn *et al*., Indicators of climate change and social vulnerability in fishing dependent communities along the Eastern and Gulf Coasts of the United States. *Mar. Policy* **74**, 323–333 (2016).
54. D. Campbell, C. Beckford, Negotiating uncertainty: Jamaican small farmers' adaptation and coping strategies, before and after hurricanes—A case study of Hurricane Dean. *Sustainability* **1**, 1366–1387 (2009).

55. R. X. Valdez *et al*., Perceptions of resilience in fishery-dependent Bahamian communities following a category 4 hurricane. *Fisheries (Bethesda, Md.)* **44**, 515–523 (2019).
56. S. K. Moore *et al*., Harmful algal blooms and coastal communities: Socioeconomic impacts and actions taken to cope with the 2015 US West Coast domoic acid event. *Harmful Algae* **96**, 101799 (2020).
57. W. N. Adger, K. Vincent, Uncertainty in adaptive capacity. *C. R. Geosci.* **337**, 399–410 (2005).
58. J. A. Ekstrom, S. K. Moore, T. Klinger, Examining harmful algal blooms through a disaster risk management lens: A case study of the 2015 US West Coast domoic acid event. *Harmful Algae* **94**, 101740 (2020).
59. J. R. Wilson *et al*., Adaptive comanagement to achieve climate-ready fisheries. *Conserv. Lett.* **11**, e12452 (2018).
60. F. Berkes *et al*., Globalization, roving bandits, and marine resources. *Science* **311**, 1557–1558 (2006).
61. J. Birkmann *et al*., Framing vulnerability, risk and societal responses: The MOVE framework. *Nat. Hazards* **67**, 193–211 (2013).
62. N. Deporte, C. Ulrich, S. Mahevas, S. Demanche, F. Bastardie, Regional métier definition: A comparative investigation of statistical methods using a workflow applied to an international otter trawl fishery in the North Sea. *ICES J. Mar. Sci.* **69**, 331–342 (2012).
63. M. Rosvall, C. T. Bergstrom, Maps of random walks on complex networks reveal community structure. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1118–1123 (2008).
64. G. Csardi, T. Nepusz, The Igraph software package for complex network research. *InterJournal.* **1695**(4), 1–9 (2006).
65. C. Spearman, The proof and measurement of association between two things. *Am. J. Psychol.* **15**, 72–101 (1904).

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ORIGINAL ARTICLE

Footprints of fixed-gear fisheries in relation to rising whale entanglements on the U.S. West Coast

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Abstract

On the U.S. West Coast, reports of whales entangled in fishing gear increased dramatically in 2014. In this study, a time series of fishing activity maps was developed from 2009 to 2016 for the four fixed-gear fisheries most commonly implicated in entanglements. Maps were generated using vessel monitoring system (VMS) data linked to port-level landings databases, which were related to entangled whale reports over the same time period and with modelled distributions of humpback whales *Megaptera novaeangliae* Borowski. Over the full study period, neither marked increases in fishing activity nor changes in fisheries footprints within regions with high whale densities were detected. By contrast, a delayed fishery opening in California due to a harmful algal bloom in spring of 2016 led to ~5–7 times average levels of Dungeness crab *Metacarcinus magister* (Dana) fishing activity, which was consistent with a high rate of entanglement in that year. These results are consistent with current hypotheses that habitat compression caused by a marine heatwave increased the overlap of whales with fishing activity, despite minimal changes in the fisheries themselves. This study adds to literature on bycatch of protected species in otherwise sustainable fisheries, highlighting the value of using VMS data for reducing human–wildlife conflict in the ocean.

KEYWORDS
California current ecosystem, fisheries bycatch, resource conflict, spatial analysis, vessel monitoring system, whale entanglement

1 | INTRODUCTION

Commercial fisheries operations can have many types of indirect impacts on marine ecosystems, such as changes in trophic structure, habitat alteration, and interactions of marine species with actively fished and derelict fishing gears (Watling and Norse, 1998; Worm and Tittensor, 2011; Arthur *et al.*, 2014; Gilman, 2015). Bycatch—incidental catch of non-targeted species—is of particular concern. Bycatch of lower trophic-level species, such as forage fish, has the potential to affect demographic rates of dependent predators, whereas bycatch of higher trophic-level species can influence the dynamics of prey species and their roles in an ecosystem/food web (Bonfil, 1994; Myers and Worm, 2003; Pikitch *et al.*, 2012). High-profile examples of fisheries bycatch leading to species declines or preventing recovery include the endangered North Atlantic right whale (*Eubalaena glaciali*), baiji (*Lipotes vexillifer*), vaquita (*Phocoena sinus*) and New Zealand sea lion (*Phocarctos hookeri*, (Breen *et al.*, 2003; Johnson *et al.*, 2005; Turvey *et al.*, 2007; Jaramillo-Legorreta *et al.*, 2017)). Larger marine mammals are especially vulnerable to bycatch, owing to their

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[Correction added on 30 March 2021, after first online publication: The copyright line was changed.]

size, long lifespan, low fecundity and late age at maturity (Lewison *et al*., 2004). The risk posed by bycatch is increasing globally and is considered “the single greatest threat to cetaceans from human activities” (Smith *et al*., 2014; IWC, 2018).

On the west coast of the United States, whale entanglement with commercial fishing gear—especially fixed-gear types—has been a low-level chronic problem (Hanson *et al*., 2019). However, reports of entangled whales increased substantially beginning in 2014, especially for humpback whales, *Megaptera novaeangliae* Borowski (Lebon and Kelly, 2019; Saez *et al*., 2020). The timing of this uptick in reports of entangled whales coincided with a marine heatwave of unprecedented scale, which lasted from 2014 to 2016 (Di Lorenzo and Mantua, 2016). Several non-mutually exclusive factors could explain this increase in reports of entangled whales, including increased size of whale populations, changes in the behaviour and spatial distribution of whales, increased effort devoted to observing entanglements, and increases in the overall amount and/or spatial distribution of fishing activity (O’Connor *et al*., 2009; Calambokidis *et al*., 2017; Santora *et al*., 2020). While other studies have addressed some of these factors, there is surprisingly little quantitative information available regarding fine-scale, spatio-temporal dynamics of the fixed-gear fishing fleets most often implicated in whale entanglements on the U.S. West Coast (Santora *et al*., 2020). Such information could reveal the extent to which shifts in overall fishing activity and the spatial footprints of fisheries could affect risk of whale entanglement.

Humpback whales typically aggregate in feeding grounds off the U.S. West Coast during summer/late autumn months and then migrate to breeding grounds for the winter before returning the following spring (Calambokidis *et al*., 2000; Barlow and Forney, 2007; Calambokidis *et al*., 2015). This behaviour likely kept humpback whales and Dungeness crab fishing activity separated in space and time, but the marine heatwave that began in 2014 caused humpback whales to linger off the west coast much later than usual. In addition, new biophysical evidence suggests that the marine heatwave, which lasted from 2014 to 2016, compressed the prey field of humpback whales closer to the coast and may have contributed to the recent rise in observed entanglements of humpback whales in the California Dungeness crab *Metacarcinus magister* (Dana) fishery (Santora *et al*., 2020), which tends to operate primarily in shallower depths (<150 m; Feist et al. *unpublished*). While shifts in the distribution of humpback whales and dynamics of the marine heatwave have been previously studied, the spatio-temporal dynamics of the actual footprint of fisheries in whale habitat has been poorly resolved. In this paper, this knowledge gap is addressed by quantifying the spatial and temporal variability of fishing activity across the full U.S. West Coast from 2009 to 2016. Specifically, a time series of fishing activity maps were developed in California, Oregon and Washington for four major pot- and trap-based fisheries, using landings informed vessel monitoring system (VMS) data from 2009 to 2016. Fishing activity was then related to modelled whale species distributions and observed entanglements across the same domain, which offers new insight into the potential causes of increased entanglements.

2 | MATERIALS AND METHODS

2.1 | Overview

Reports of entangled whales collected off the west coast of the United States from 2009 through 2016 were analysed to identify general spatio-temporal patterns in entangled whale sightings, and to determine whether there was a significant change in reporting that occurred starting in 2014. The data were also examined for correlations with gear type and whale species. Next, spatio-temporal patterns of pot- and trap-based fishing activity were characterised across the same study area and time period by linking port-level vessel landings data to VMS data to generate time-series maps of fishing activity. In addition, patterns of overlap between humpback whales and fishing fleets were characterised using modelled whale distributions. Comparisons were made before and after 2014, as these time periods comport with a major shift in ocean conditions as a result of an unprecedented marine heatwave (Bond *et al*., 2015; Whitney, 2015; Di Lorenzo and Mantua, 2016) and reports of entangled whales had been relatively low prior to 2014 (see below). Refer to Supplement (1.1–1.3) for further details regarding the spatial analyses referenced in subsequent sections.

2.2 | Data sources and analyses

2.2.1 | Entangled whale reports

A comprehensive, spatially explicit database of reports of entangled whales (Saez *et al*., 2020) was analysed to evaluate trends in the number of reported entanglements by species, location and gear type, from 2009 to 2016. Gear types were grouped into four categories: (1) Dungeness pots/traps; (2) other pots/traps; (3) gillnet, net and other; and (4) unknown. Given humpback and grey (*Eschrichtius robustus* Lilljeborg) whales accounted for the majority of entangled whale reports, all other species, which included blue (*Balaenoptera musculus* (L.)), fin (*Balaenoptera musculusphysalus* (L.)), minke (*Balaenoptera acutorostrata Lacépède*), killer (*Orcinus orca* (L.)), sperm (*Physeter microcephalus* L.) and unidentified whales, were grouped into a single “other” species category. It is important to note that the entangled individuals reported were not observed becoming entangled; the observation was merely one of a cetacean already entangled in fishing gear and the entanglement time and location was unknown in most cases. Further, cetaceans may travel hundreds or thousands of kilometres with gear attached to them, so the time and location of the actual entanglement may have occurred months previously at a location distant from the observation of the entangled whale (Moore and van der Hoop, 2012; Bradford and Lyman, 2015).

Two types of analyses were done with the entangled whale report data. First, descriptive statistics and general spatial patterns were characterised. Specifically, data were mapped pre- and post-2014 for each species category (humpback, grey and other) and gear type (Dungeness pots/traps; other pots/traps; gillnet, net and other; and unknown) described above. The second analysis quantified associations between the number of entangled whale reports and gear type, time period (pre- and post-2014) and species (humpback, grey, and other). A generalised linear model was applied assuming a Poisson distribution using a log-link function (library lme4 [v1.1-23] in R [v3.6.3, R Core Team (2019)]). Stepwise AIC (stepAIC function in library MASS [v7.3- 51.6] in R) was used to compare the full model (all interactions included) to reduce models, and the model with the lowest AIC was chosen as the best one. In this case, the full model and all reduced models were ecologically meaningful, as the interaction terms allowed evaluation of whether the number of entanglement reports in the earlier or later time periods differed for some species or gear types, but not others.

2.2.2 | Mapping fishing activity

Since pot and trap gear is most often associated with humpback whale entanglement (Saez *et al.*, 2020), analyses were limited to four commercially important species that were caught using this class of gear: Dungeness crab, spot prawn *Pandalus platyceros* Brandt, California spiny lobster *Panulirus interruptus* (Randall) and sablefish *Anoplopoma fimbria* (Pallas).

VMS data (NOAA, 2016) from January 2009 through June 2016 were used to track fishing vessel locations over time. VMS is used by enforcement agencies to track the locations of a subset of fishing vessels to determine whether they are fishing in closed areas. Vessels are monitored continuously, regardless of whether or not they are actively fishing, and their position, vessel identification number, velocity and time are transmitted every 30 to 60 min to remote monitoring stations on land. VMS data do not include information about which species are being targeted by fishing vessels, nor do they specify when fishing is occurring. To determine target fish species for each fishing trip, port-level vessel landings data, compiled by the Pacific Fisheries Information Network (PacFIN, 2017), were linked to the VMS data using a vessel ID number common between the two databases. The landings data provide detailed information about every fishing trip that offloaded catch at a given port, including vessel ID, date, time, species landed and corresponding biomass (see Supplement: 1.2). By linking these two datasets, it was possible to identify where fishing vessels were operating in the days preceding offloading a given catch. To identify spatio-temporal patterns of fishing activity for each of the four target species across the study area, the landings informed VMS points were then overlaid on a 5-km resolution grid and heatmaps were generated in 4-month intervals from November 2010 through June 2016 (see Supplement: 1.3).

Given a subset of fishing vessels are equipped with VMS transponders, an analysis of VMS representativeness in each fishery and by vessel size class was conducted. Representativeness was characterised by calculating the proportion of vessels and the proportion of landed biomass by VMS equipped vessels, relative to all vessels and landed tonnes in each corresponding fishery. The proportion of fishing activity that occurred aboard VMS equipped vessels was summarised by state and by vessel size class for each of the four target species. Twelve metres was used as the break point between large (≥12 m) and small (<12 m) vessel size classes. The 12 m length cut-off is commonly used to differentiate between small and large fishing vessels (Kasperski and Holland, 2013; Jardine *et al.*, 2020). Small vessels were tracked separately in these analyses, as they have less storage space and potentially place less gear in the water. Therefore, small vessels may present lower risk of entanglement to whales.

Because Dungeness crab are the dominant pot- and trap-based fishery on the U.S. West Coast, and since gear from this fishery is the most easily and often identified in reports of whale entanglements, trends in the size of the areas most fished for Dungeness crab were assessed for each state. Specifically, statistically significant hot spots were identified within the footprint of the Dungeness crab fishery for each 4-month interval using the Getis-Ord Gi* criterion (Getis and Ord (1992); see Supplement: 1.3.2 for details) and the Hotspot Analysis tool in ArcGIS. Total area of these hot spots for each 4-month interval for each state were calculated, and the size of these areas was compared pre- and post-2014. A 2-tailed *t*-test with unequal variance was used to test for significance between the two time periods.

2.2.3 | Humpback whale distribution map

A habitat-based spatial model of humpback whales developed by Becker *et al.* (2016) was used to determine overlap of the four fixed-gear fisheries with prime whale habitat. The model predicts average whale density on a 0.05 degrees grid throughout the U.S. West Coast Exclusive Economic Zone (EEZ). Predictions are based on a variety of environmental covariates as well as line-transect whale survey data collected from June through November at two- to five-year intervals from 1991 to 2009. Although the timing of these surveys does not overlap with the entirety of the fishing season for all four fixed-gear fleets considered here, the high-density areas correspond to known, persistent feeding areas classified as Biologically Important Areas (Calambokidis *et al.*, 2015), which are considered to represent areas where humpback whales are likely to occur. Grid cells from this model were classified into two density categories: high, defined as greater than two standard deviations above the mean, *sensu* Redfern *et al.* (2017), and low-to-medium (hereafter “low”), defined as less than two standard deviations above the mean.

2.2.4 | Spatio-temporal overlap of fishing with humpback whales

The degree of spatial overlap between fishing activity and humpback whales was estimated to evaluate the hypothesis that spatio-temporal changes in commercial fishing activity contributed to the increase in reporting of entangled whales that began in 2014. If changes in fishing activity were the predominant cause of the dramatic increase in whale entanglements that began around 2014, one would expect to see an increase in the overall magnitude and/or spatio-temporal distribution of commercial fishing activity within whale habitat. The landings informed VMS points for each of the four fisheries target groups were overlaid with the humpback whale distribution map and summarised in monthly time steps for both of the whale density categories (high and low). Years began in November instead of the conventional January of the standard Gregorian calendar to better synchronise with the 13 November start of the Dungeness crab fishing season on the U.S. West Coast. A two-way ANOVA was used (effects included fishery type, time period, pre- or post-2014 and state) to test for statistical significance of the difference in fishing activity overlap in the high-density humpback whale regions.

3 | RESULTS

3.1 | Entangled whale reports

3.1.1 | Descriptive statistics and general spatial patterns

Between 2009 and 2016, there were 187 confirmed reports of entangled whales off the U.S. West Coast: 109 humpback, 52 grey and 26 for all other species combined (unidentified = 11; blue = 4; fin = 5; killer = 2; minke = 2; sperm = 2, hereafter collectively "other"). The vast majority of the reports occurred in California (~85%), with Oregon and Washington each accounting for about 7.5% of all entangled whale reports (Figure 1 maps). Across all species and years, the type of gear involved in the entanglement was unknown in the majority of reports (~55%). For those reports where the gear type could be identified (~45% of all entangled whale reports), pot- and trap-based gear together (Dungeness, and other trap/pot) accounted for the majority (~71%) of the gear observed on entangled whales (Figure 1a-c). For humpback and the other whale species categories, Dungeness crab gear types were identified on entangled whales in 50 to 65% of the cases (Figure 1a,c).

3.1.2 | Annual entanglement by gear type, pre- and post-2014 and species

The analysis of whether annual entanglement reports differed among gear types, time periods or species (*glm*; Table S4) showed that the differences between time periods in annual entanglement reports were primarily due to an increase for humpback whales in 2014–2016 and that there were significant differences among gear types in the number of entangled whales reported across the full study period (Table S4). Comparing 2009–2013 with 2014–2016, mean annual reports of entangled humpback whales increased nearly 10-fold, from 3.4 to 30.7 (interaction term

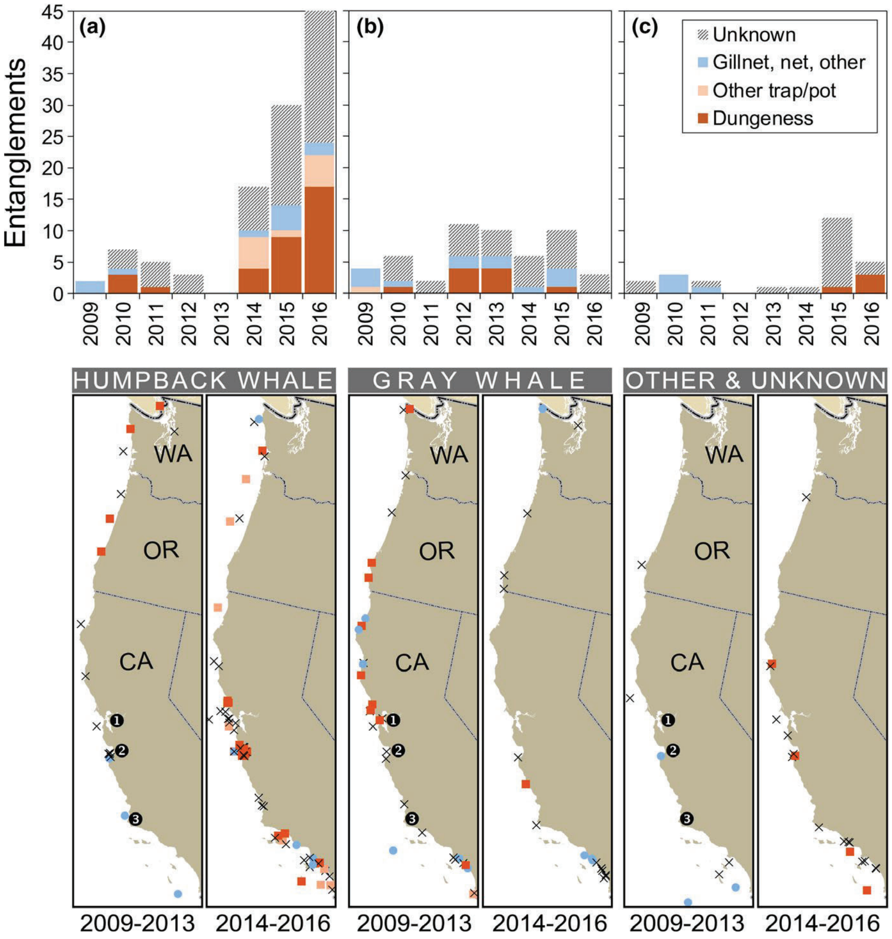

FIGURE 1 Cumulative annual number of confirmed entangled (a) humpback, (b) grey, and (c) all other whale species (including unidentified) reported on the west coast of the United States from 2009 to 2016 by gear type: Dungeness crab gear (dark orange); all other trap/pot gear (light orange) [sablefish, California spiny lobster and spot prawn]; gillnet, net or other gear (blue); and unknown or unidentified gear (hatched grey). For reference, maps below each figure indicate approximate locations along the U.S. West Coast where the entangled whales were observed, by gear and year range (2009-13 and 2014-16). Note, colours of site markers on maps correspond to plots, with Xs denoting unknown gear type. Circled numbers indicate geographic reference locations referred to in the results section, which include (1) San Francisco Bay; (2) Monterey Bay; and (3) Point Conception

between humpback and time period; Table S4). However, this change in annual entanglement reports between time periods was not evident for grey whales (mean 6.6 and 6.3) or the other whale species (mean 2.0 and 6.0) category considered. Across the full study period, annual entanglement reports were significantly higher for unknown gear than for pot- and trap-based gear, significantly higher for pot- and trap-based gear than for gillnet gear, and significantly higher for gillnet gear than for the other pot- and trap-based gear category (Table S4).

3.2 | Mapping fishing activity

3.2.1 | Representativeness of VMS data

From 2009 to 2016 for the fixed-gear fleets that targeted the four species analysed, there were 892,509 port-level landings records from 6,321 vessels. A total of 264,081 (29.59%) of those records came from 1221 (19.32%) boats equipped with VMS transponders. Across the four fisheries, the representativeness of fishing activity from vessels equipped with VMS varied considerably in terms of biomass landed and number of boats (Figure S1). The vast majority (>90%) of sablefish were landed from VMS equipped boats. For spot prawn, spiny lobster and Dungeness crab the representativeness ranged from 10 to 35% (Figure S1). With regard to vessel length, larger vessels were more likely to be equipped with VMS, so smaller vessels were usually under-represented (Figures S2–S4). Across seasons and fishing fleets, the proportion of vessels equipped with VMS transponders remained relatively constant from 2009 to 2016 (right side plots in Figures S2–S4). The exception was Washington spot prawn boats, where VMS coverage dropped essentially to zero starting in the 2012–13 season (Figures S3E,F), possibly because those few boats that had been fishing for spot prawn and were

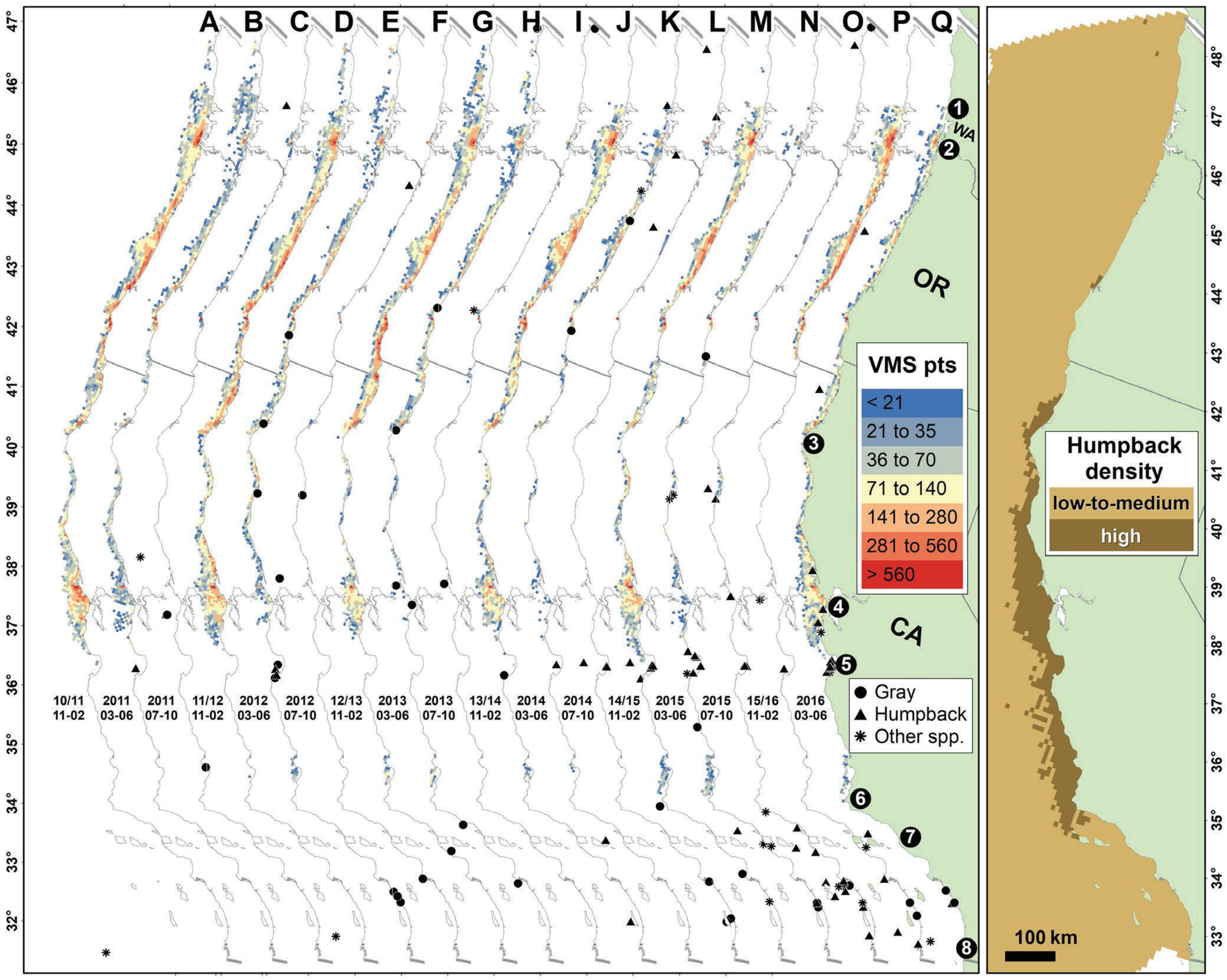

FIGURE 2 Spatial distribution of landings informed VMS data for vessels targeting Dungeness crab from November 2010 through June 2016, summarised in four-month intervals (maps A – Q). Map on far right illustrates the high and low-to-medium modelled humpback whale density regions used in the overlap analyses (from Becker *et al.*,2016). For reference, points are locations of confirmed reports of entangled whales within the corresponding four-month interval across all gear types. Circled numbers indicate geographic reference locations referred to in the results section, which include (1) Grays Harbor, (2) Columbia River, (3) Cape Mendocino, (4) San Francisco Bay, (5) Monterey Bay, (6) Point Conception, (7) Channel Islands and (8) San Diego

equipped with VMS transponders stopped fishing for spot prawn in Washington after the 2011–12 season, or they did not have their VMS transponders activated while fishing for spot prawn.

3.2.2 | Spatio-temporal patterns of fishing activity

The Dungeness crab fleet was the dominant fixed-gear fishery amongst the fleets that were analysed, in terms of biomass landed, number of vessels involved and total activity (Figure 2). From the beginning of the season in mid-November in any given year to February of the following year, activity was intense and nearly continuous across much of the west coast from Point Conception, California, to just north of Grays Harbor in Washington (Figure 2, maps A, D, G, etc.). Activity generally diminished from March through June each year, ceased completely by July off California, but continued at low levels in late spring and summer off the coasts of Oregon and Washington (Figure 2). Due to a domoic acid closure that delayed the 2015–16 crab season by up to 5 months in California, there was essentially no crab fishing from November 2015 through February 2016, a time period when the majority of crab fishing typically occurs (Figure 2, map P). Once the fishery eventually opened in California, there was anomalously high fishing activity from March through June 2016 (Figure 2, map Q).

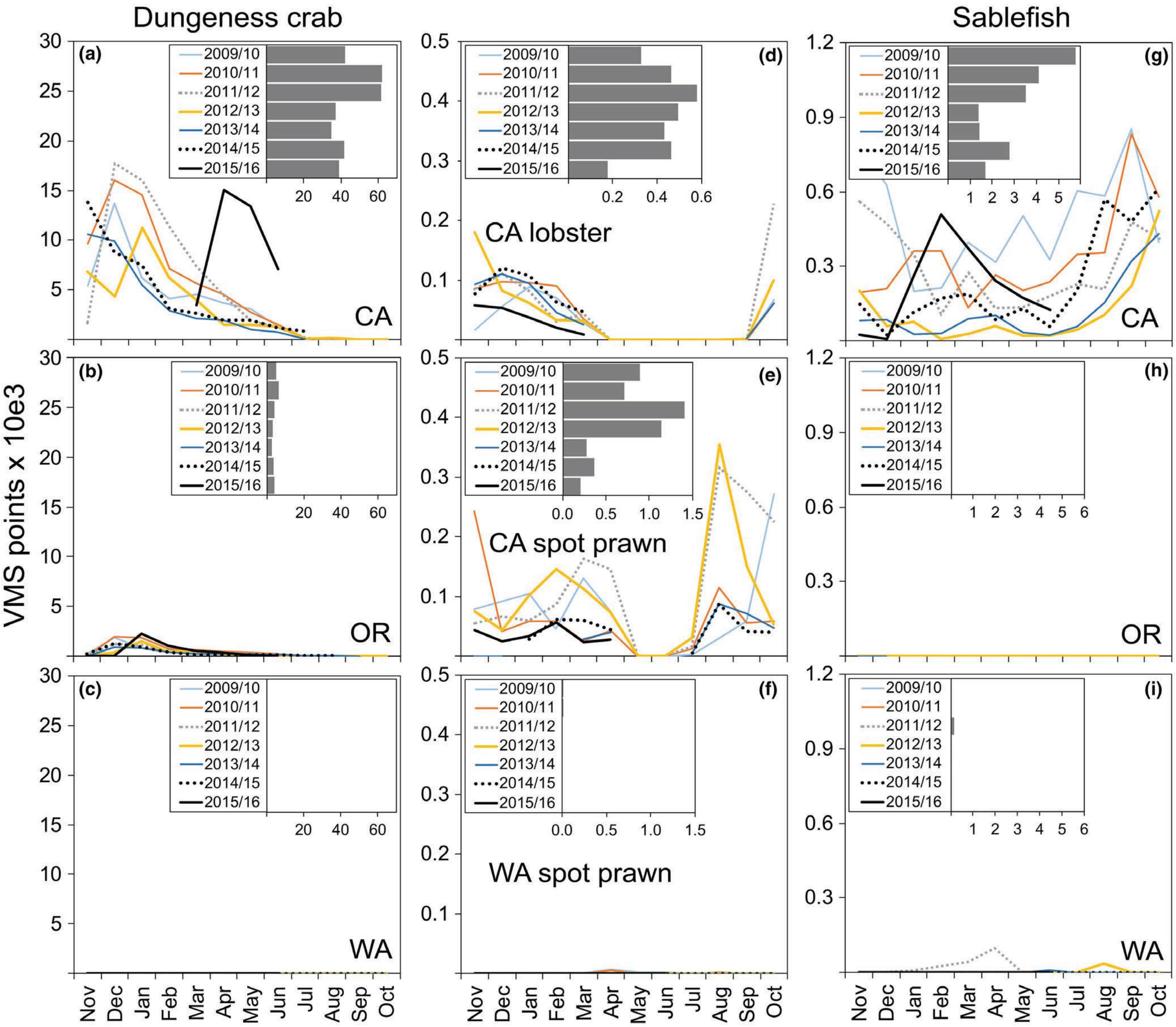

FIGURE 3 Cumulative monthly and annual (individual inset bar charts) landings informed VMS points that fell within high whale density regions (overlaid on humpback whale density map from Becker *et al.*,2016) for pot- and trap-based fisheries in Washington, Oregon and California from November 2009 to June 2016. (a) California Dungeness crab; (b) Oregon Dungeness crab; (c) Washington Dungeness crab*; (d) California spiny lobster; (e) California spot prawn; (f) Washington spot prawn*; (g) California sablefish; (h) Oregon sablefish*; and (I) Washington sablefish. *zero or negligible number of VMS points overlap in high humpback whale density regions for this fishery in this state

Based on the Dungeness crab hot spot mapping, the total area of the most intense fishing activity for pre-2014 (Nov 2009–Oct 2013) compared with post-2014 (Nov 2013–Jun 2016) decreased in California and Washington, and increased in Oregon. However, none of these changes in the total area of these hot spot patches were statistically significant (Table S5).

Spiny lobster fishing activity only occurred off the coast of southern California, concentrated primarily around the Channel Islands and San Diego (Figure S5). The fishery was most active from October of any given season through to the following February (Figure S5, maps A, D, G,). The fixed-gear based sablefish fishery was generally limited to a small region just south of Cape Mendocino, California, and in the vicinity of the Columbia River mouth at the border of Oregon and Washington (Figure S6). Unlike the Dungeness and spiny lobster fisheries, the sablefish fishery did not have as punctuated a season, so the patterns were more consistent over time (Figure S6). The spatial extent of the spot prawn fishery was extremely limited and the patchiest of all the fisheries examined, with most activity in the vicinity of the Channel Islands (results not shown due to data confidentiality restrictions).

3.2.3 | Spatio-temporal overlap of fishing with humpback whales

From 2009 to 2016, across all four fisheries operating within areas of both high and low humpback whale densities, there was considerable monthly variation of fishing activity within years (Figures 3 and 4 line

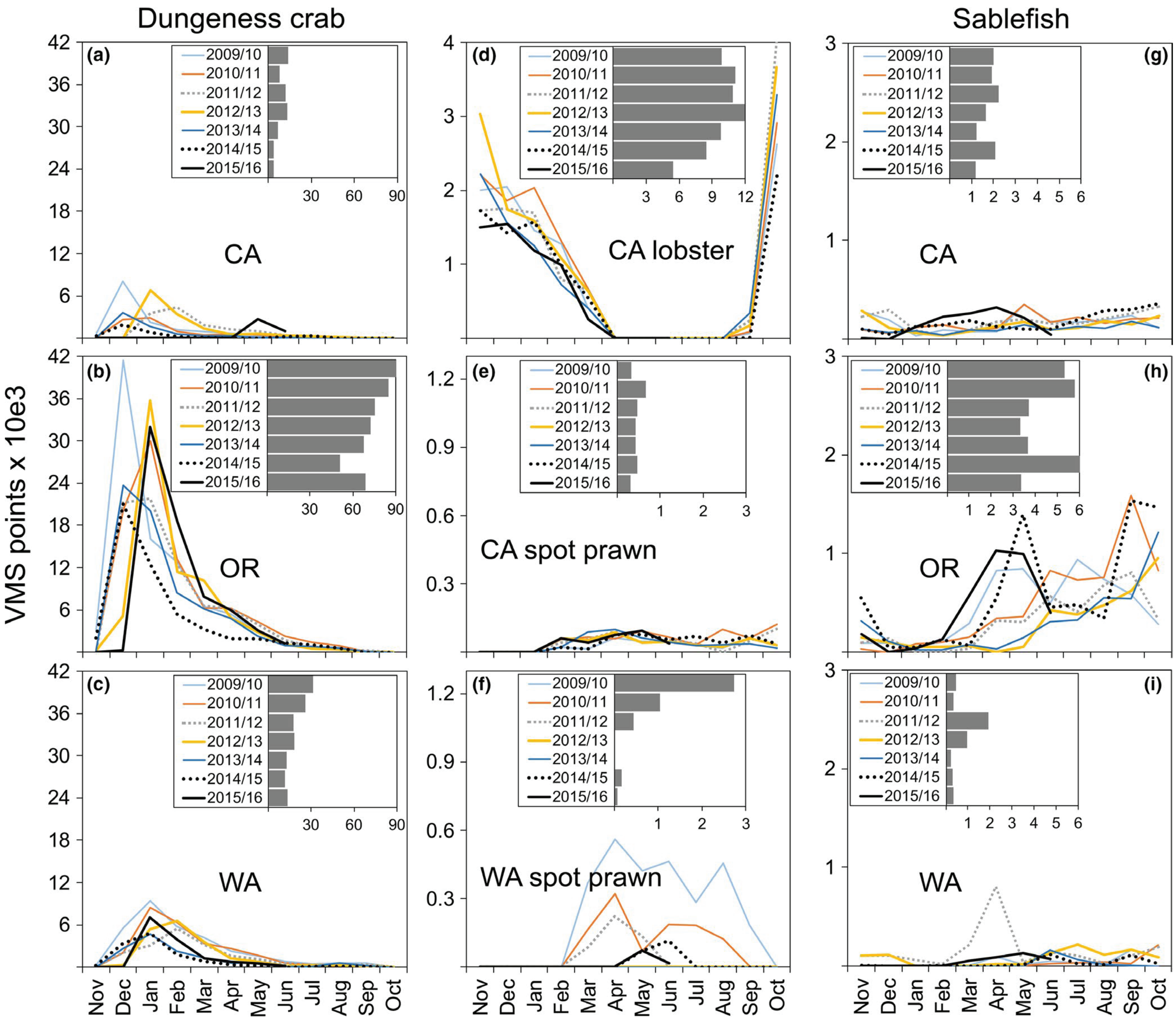

FIGURE 4 Cumulative monthly and annual (individual inset bar charts) landings informed VMS points that fell within low-to-medium whale density regions (overlaid on humpback whale density map from Becker *et al.*,2016) for pot- and trap-based fisheries in Washington, Oregon and California from November 2009 to June 2016. (a) California Dungeness crab; (b) Oregon Dungeness crab; (c) Washington Dungeness crab; (d) California spiny lobster; (e) California spot prawn; (f) Washington spot prawn; (g) California sablefish; (h) Oregon sablefish; and (i) Washington sablefish

plots). However, there was not an overall annual increase in activity that would be expected given the rise in humpback whale entanglements that began in 2014 (Figures 3 and 4 insets).

In the highest humpback density regions off the west coast, the Dungeness crab fishery was the most active of the four pot- and trap-based fisheries that were evaluated. Note scale of *y*-axis in Figures 3 and 4 compared with *y*-axis of other fixed-gear fisheries, and the scale of the *x*-axis in the horizontal bar chart insets. Nearly all of the Dungeness fishing activity that overlapped with the highest humpback density regions occurred off the coast of California (Figure 3a), with no overlap in Washington (Figure 3c) and minimal overlap in Oregon (Figure 3b). Overlap in low-density humpback whale regions in California was far less (Figure 4a).

There was a marked peak of fishing activity off California in both the high whale density (Figure 3a black monthly line, see also Figure 2 map Q) and low whale density regions (Figure 4a black monthly line). Owing to the 5-month domoic acid closure that occurred in the 2015–2016 Dungeness crab season, activity was ~5–7 times greater than mean levels for the months of April, May and June in high whale density regions. In the low whale density regions, May was the only month with above normal fishing activity (Figure 4a black monthly line). The vast majority of Dungeness crab fishing activity off the coasts of Washington and Oregon occurred in the low humpback density regions (Figure 4c,b, respectively). The Dungeness crab fishery off the coasts of Oregon and Washington did not have the same late season peak observed in California in either of the whale density regions (Oregon: Figures 3b and 4b black lines; Washington: Figures 3c and 4c black lines).

The vast majority of California spiny lobster fishing activity occurred in regions with low densities of humpback whales (Figures 3d and 4d). The spot prawn fishery had a relatively small footprint compared with Dungeness crab, where the majority of activity occurred in regions with high humpback whale density off the coast of California (Figure 3e), but fishing declined in this region over time (Figure 3e inset). There was no overlap with spot prawn within high-density humpback whale habitat in Washington (Figure 3f insets) and in low regions activity declined (Figure 4f inset). For the pot- and trap-based sablefish fishery most of the overlap in high humpback whale density regions occurred off California (Figure 3g), although activity diminished starting in 2012-13 (Figure 3g inset). There was no overlap and minimal overlap in Oregon (Figures 3h and 4h) and Washington (Figures 3i and 4i), respectively.

Pre- and post-2014 comparisons in high-density humpback whale habitats

While there was an anomalous uptick of Dungeness crab fishing activity that corresponded to the 5-month delay in the opening of the California crab season, there was no statistically significant increase in fishing activity before and after 2014 in high-density whale regions (Table S6). Based on the 2-way ANOVA of pre- and post-2014 fishing activity in high-density whale regions for each state, there was a decrease in overall fishing activity (Table S6). However, this decrease was only statistically significant for the spot prawn and sablefish fisheries in California (Table S6).

4 | DISCUSSION

Fisheries interactions with protected species are a chronic problem globally and a central issue related to conservation, particularly for marine mammals (Read, 2008; Reeves *et al.*, 2013; Smith *et al.*, 2014). Whale entanglements in fishing gear, in particular, generate a large amount of public interest and concern, along with raising issues in the United States surrounding management of the problem under the Endangered Species Act (ESA, 1972) and Marine Mammal Protection Act (MMPA, 1972). The substantial rise in entanglements on the U.S. West Coast in recent years may involve a number of factors, including changes in oceanographic conditions that compressed the humpback whale prey field closer to shore, concentrating the whales in closer proximity to pot- and trap-based fleets (Santora *et al.*, 2020). Prior to this study, however, the spatial dynamics of changes in fishing activities that may have increased the likelihood of entanglements had not been quantified. Here, these analyses add to an understanding of this environmental problem by characterising the spatio-temporal dynamics of pot- and trap-based fishing fleets operating off the U.S. West Coast on how those patterns have contributed to the whale entanglement phenomenon.

Based on the analyses of four commercial pot- and trap-based fisheries from 2009 through 2016, there were no increases in fishing activity in areas with historically high mean annual whale densities, or increased fishing in general, that could explain the dramatic increase in entangled whale reporting that occurred starting around 2014. However, there was anomalously high Dungeness crab fishing activity in spring of the 2015–2016 season. This was caused by a delay in the opening of the fishery as a result of persistent elevated domoic acid concentrations in crab viscera, a consequence of a massive harmful algal bloom (Moore *et al.*, 2019). This anomalously high Dungeness crab fishing activity in California in the spring of 2016 likely placed crab fishing gear in the same place at the same time with foraging humpback whales that had returned from their winter breeding areas off Mexico and Central America. In all other years, the majority of Dungeness crab fishing was typically completed well before the arrival of humpback whales in the system, which generally occurs in spring (Calambokidis *et al.*, 2000).

In 2014–2015, there were no dramatic increases in fishery activity for pot- and trap-based gear, which suggests that large whales moved into closer proximity to long-standing fisheries footprints. Evidence to date suggests that a marine heat wave that persisted from 2014 through mid-2016 compressed humpback whale habitat (Di Lorenzo and Mantua, 2016; Hobday *et al.*, 2018). A key consequence of this anomalous warming was that total biomass of the prey field available to humpback whales was reduced and what remained was limited to nearshore regions (Santora *et al.*, 2020). These insights about changing whale distributions provide a more complete picture of the impacts of fishing on whale entanglement. They also highlight a drawback of the static models of humpback whale distributions that were analysed here, which represent average long-term foraging areas. Future analyses that incorporate dynamic whale distribution models will more accurately reflect spatio-temporal patterns of whale distributions, and could perhaps even use near real-time environmental data such as remotely sensed sea surface temperature and chlorophyll to better understand overlap with fishing activity (Maxwell *et al.*, 2015).

There were at least two limitations to this study that warrant discussion. First, the coarse temporal grain (locations every 30 to 60 min) of the VMS data presents challenges to identifying accurately where pot- and trap-based gear was deployed. The use of depth filters helps to refine estimates, but vessel speed filters may not be as effective as they are for vessels deploying more speed sensitive fishing gear such as bottom- and mid-water trawl nets (Jennings and Lee, 2012; Charles *et al.*, 2014). Pot- and trap-based fishing fleets generally deploy their gear at rapid speeds, and slow to retrieve gear. However, they do not reduce their speed for hours at a time, as trawl-based vessels do, so detecting active fishing locations is not as accurate. Despite the approach used for filtering out VMS points that did not represent active fishing, these methods are in line with previous studies, so they likely afford a reasonable estimate of fishing activity (Mullowney and Dawe, 2009; Charles *et al.*, 2014).

Second, given VMS transponders are not present on all fishing vessels (with the exception of the sablefish boats), these analyses and conclusions therein regarding where and when fishing is occurring are based on a sub-sample of vessels that fish for the respective fish species. Further, there is likely a bias in this sub-sample, given VMS transponders are more prevalent on larger vessels. Thus, these analyses based on the landings informed VMS data likely adequately represent the patterns of larger vessels, while under-represent the behaviour and influence of smaller vessels.

While the present analyses were mainly focused on contemporaneous overlap between fishing activity and entanglement sightings, there may also be lagged impacts of fisheries on whales due to derelict gear. Derelict fishing gear poses a chronic threat to marine organisms, including cetaceans, that persists even after active fishing has ceased and may be increasing in magnitude over time (Arthur *et al.* (2014); Stelfox *et al.* (2016); Richardson *et al.* (2019), but see Asmutis-Silvia *et al.* (2017) and Stelfox (2017)). On the west coast of the United States, there are approximately 400,000 Dungeness crab traps fished each year and the annual loss rate is estimated to be up to 10% (Pacific Fishery Management Council, 2013). Indeed, within the whale entanglement data analysed in this paper, there was at least one entangled whale report where derelict gear was the known source and the buoy tags from the gear were two to three years old (Saez *et al.*, 2020). To worsen the problem, fishing gear can become entangled with other gear, which increases the probability that the gear becomes lost and irretrievable (see Gilman, 2015). While it does not appear that the majority of entanglements with whales involve derelict gear, mapping out fishing activity, as has been done in these analyses, is also useful for developing risk management plans with regard to entanglement with derelict gear (Brown and Niedzwecki, 2020).

4.1 | The future for reducing the risk of whale entanglement

Identifying where and when threats and stressors to a given species occur is a critical first step in assessing the overall risk a given perturbation poses (Halpern *et al.*, 2008). Whale entanglement with commercial fishing gear is a global problem that poses a significant risk to populations (Read *et al.*, 2006; Smith *et al.*, 2014; Kraus *et al.*, 2016). Minimising the risk of entanglements to ensure compliance with conservation laws and also sustaining thriving fisheries is a complex balancing act that requires the involvement of stakeholders, close integration between managers and researchers, a robust framework for incorporating new information and adaptive management (Borggaard *et al.*, 2017). Future research can build upon the results from these analyses by explicitly incorporating the overlap or exposure between the threat and the target species and assessing the consequences of the stressor to the target organism. Output from these analyses could be used for spatial planning directed at strategic areas where cetaceans are most likely to experience entanglement with fishing gear, which would provide insight at finer spatial and temporal scales into how management measures will influence not only risk of entanglement for whales, but also economic impacts on fishing fleets. Finally, efforts to incorporate emerging technologies (Bradley *et al.*, 2019), as well as dynamic, near real-time forecasts of large whale distributions, fishery target species (sensu Kaplan *et al.* (2016)) and harmful algal blooms (Smith *et al.*, 2018; Trainer *et al.*, 2019) would greatly enhance the utility of risk assessments by arming managers with multiple management options before environmental conditions have precipitated a fishing closure.

The patterns that were observed in this study add to a growing body of evidence related to bycatch of protected species in otherwise sustainable fisheries (e.g. North Atlantic right whales and lobster fisheries off the U.S. East Coast, (Borggaard *et al.*, 2017; Ingeman *et al.*, 2019)) and demonstrate the importance of developing novel methods to model spatio-temporal fishing activity using existing data sources and analyses in order to reduce human–wildlife conflict in the ocean (Guerra, 2019). And the techniques for generating time-series maps of fishing activity using existing remote sensed and landings data are critical for managing fisheries that pose risk to other marine organisms. Developing a risk assessment of whale entanglement with commercial fishing gear on the west coast that also incorporates human social or economic components could give resource managers a richer tool set for managing this phenomenon. Therefore, analyses that consider approaches to simultaneously minimise risk to whales and economic vulnerability of commercial fishermen may help to find a more forward-looking, long-term solution to continue the recoveries of protected cetaceans and sustain fisheries. Beyond the

U.S. West Coast, integrative studies that seek to understand the causes and consequences of climate-driven distributional changes in bycatch species and fisheries, and evaluate trade-offs associated with alternative management measures intended to mitigate negative consequences for fisheries species, protected species and dependent human communities, will help to create fisheries that are more climate-ready in the face of continued change (Wilson *et al*., 2018; Holsman *et al*., 2019).

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REFERENCES

Arthur, C., Sutton-Grier, A.E., Murphy, P. & Bamford, H. (2014) Out of sight but not out of mind: Harmful effects of derelict traps in selected U.S. coastal waters. *Marine Pollution Bulletin*, *86*, 19–28. https://doi.org/10.1016/j.marpolbul.2014.06.050

Asmutis-Silvia, R., Barco, S., Cole, T., Henry, A., Johnson, A., Knowlton, A. *et al*. (2017) Rebuttal to published article "A review of ghost gear entanglement amongst marine mammals, reptiles and elasmobranchs" by M. Stelfox, J. Hudgins, and M. Sweet. *Marine Pollution Bulletin*, *117*, 554–555. https://doi.org/10.1016/j.marpolbul.2016.11.052

Barlow, J. & Forney, K.A. (2007) Abundance and population density of cetaceans in the California Current ecosystem. *Fishery Bulletin*, *105*, 509–526.

Becker, E., Forney, K., Fiedler, P., Barlow, J., Chivers, S., Edwards, C. *et al*. (2016) Moving towards dynamic ocean management: How well do modeled ocean products predict species distributions? *Remote Sensing*, *8*, 149. https://doi.org/10.3390/rs8020149

Bond, N.A., Cronin, M.F., Freeland, H. & Mantua, N. (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, *42*, 3414–3420. https://doi.org/10.1002/2015gl063306

Bonfil, R. (1994) *Overview of world elasmobranch fisheries*. Rome, Italy: Food and Agriculture Organization.

Borggaard, D.L., Gouveia, D.M., Colligan, M.A., Merrick, R., Swails, K.S., Asaro, M.J. *et al*. (2017) Managing U.S. Atlantic large whale entanglements: Four guiding principles. *Marine Policy*, *84*, 202–212. https://doi.org/10.1016/j.marpol.2017.06.027

Bradford, A.L. & Lyman, E.G. (2015). *Injury determinations for humpback whales and other cetaceans reported to NOAA response networks in the Hawaiian Islands during 2007–2012*, in: NOAA Tech. Memo. (Honolulu, HI: United States Department of Commerce).

Bradley, D., Merrifield, M., Miller, K.M., Lomonico, S., Wilson, J.R. & Gleason, M.G. (2019) Opportunities to improve fisheries management through innovative technology and advanced data systems. *Fish and Fisheries*, *20*, 564–583. https://doi.org/10.1111/faf.12361

Breen, P.A., Hilborn, R., Maunder, M.N. & Kim, S.W. (2003) Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 527–541. https://doi.org/10.1139/f03-046

Brown, A.H. & Niedzwecki, J.M. (2020) Assessing the risk of whale entanglement with fishing gear debris. *Marine Pollution Bulletin*, *161*, 111720. https://doi.org/10.1016/j.marpolbul.2020.111720

Calambokidis, J., Barlow, J., Flynn, K., Dobson, E. & Steiger, G.H. (2017) *Update on abundance, trends, and migrations of humpback whales along the US West Coast*. International Whaling Commission.

Calambokidis, J., Steiger, G.H., Curtice, C., Harrison, J., Ferguson, M.C., Becker, E. *et al*. (2015) 4. Biologically Important Areas for selected cetaceans within U.S. waters – West coast region. *Aquatic Mammals*, *41*, 39–53. https://doi.org/10.1578/AM.41.1.2015.39

Calambokidis, J., Steiger, G.H., Rasmussen, K., Urbán, R.J., Balcomb, K.C., Ladrón de Guevara, P. *et al*. (2000) Migratory destinations of humpback whales that feed off California, Oregon and Washington. *Marine Ecology Progress Series*, *192*, 295–304. https://doi.org/10.3354/meps192295

Charles, C., Gillis, D. & Wade, E. (2014) Using hidden Markov models to infer vessel activities in the snow crab (*Chionoecetes opilio*) fixed gear fishery and their application to catch standardization. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 1817–1829. https://doi.org/10.1139/cjfas-2013-0572

Di Lorenzo, E. & Mantua, N. (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, *6*, 1042–1047. https://doi.org/10.1038/nclimate3082

ESA. (1972) *"Endangered Species Act of 1973"*, in: 16 U.S.C. § 1561 et seq. (eds.) United States & USFWS.

Getis, A. & Ord, J.K. (1992) The analysis of spatial association by use of distance statistics. *Geographical Analysis*, *24*, 189–206. https://doi.org/10.1111/j.1538-4632.1992.tb00261.x

Gilman, E. (2015) Status of international monitoring and management of abandoned, lost and discarded fishing gear and ghost fishing. *Marine Policy*, *60*, 225–239. https://doi.org/10.1016/j.marpol.2015.06.016

Guerra, A.S. (2019) Wolves of the Sea: Managing human-wildlife conflict in an increasingly tense ocean. *Marine Policy*, *99*, 369–373. https://doi.org/10.1016/j.marpol.2018.11.002

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C. *et al*. (2008) A global map of human impact on marine ecosystems. *Science*, *319*, 948–952. https://doi.org/10.1126/science.1149345

Hanson, M.B., Good, T.P., Jannot, J.E. & McVeigh, J. (2019) *Estimated humpback whale bycatch in the U.S. West Coast Groundfish Fisheries 2002–2017*. Seattle, WA: National Marine Fisheries Service.

Hobday, A.J., Oliver, E.C.J., Sen Gupta, A., Benthuysen, J.A., Burrows, M.T., Donat, M.G. *et al*. (2018) Categorizing and naming marine heatwaves. *Oceanography*, *31*, 162–173. https://doi.org/10.5670/oceanog.2018.205

Holsman, K.K., Hazen, E.L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S.J. *et al*. (2019) Towards climate resiliency in fisheries management. *ICES Journal of Marine Science*, *76*(5), 1368–1378. https://doi.org/10.1093/icesjms/fsz031

Ingeman, K.E., Samhouri, J.F. & Stier, A.C. (2019) Ocean recoveries for tomorrow's Earth: Hitting a moving target. *Science*, *363*, eaav1004. https://doi.org/10.1126/science.aav1004

IWC. (2018) Report of the Scientific Committee. *Journal of Cetacean Research and Management (Supplement)*, *19*, 44–48.

Jaramillo-Legorreta, A., Cardenas-Hinojosa, G., Nieto-Garcia, E., Rojas-Bracho, L., Ver Hoef, J., Moore, J. *et al.* (2017) Passive acoustic monitoring of the decline of Mexico's critically endangered vaquita. *Conservation Biology*, *31*, 183–191. https://doi.org/10.1111/cobi.12789

Jardine, S.L., Fisher, M.C., Moore, S.K. & Samhouri, J.F. (2020) Inequality in the economic impacts from climate shocks in fisheries: The case of Harmful Algal Blooms. *Ecological Economics*, *176*, 106691. https://doi.org/10.1016/j.ecolecon.2020.106691

Jennings, S. & Lee, J. (2012) Defining fishing grounds with vessel monitoring system data. *ICES Journal of Marine Science*, *69*, 51–63. https://doi.org/10.1093/icesjms/fsr173

Johnson, A., Salvador, G., Kenney, J., Robbins, J., Kraus, S., Landry, S. *et al.* (2005) Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science*, *21*, 635–645. https://doi.org/10.1111/j.1748-7692.2005.tb01256.x

Kaplan, I.C., Williams, G.D., Bond, N.A., Hermann, A.J. & Siedlecki, S.A. (2016) Cloudy with a chance of sardines: forecasting sardine distributions using regional climate models. *Fisheries Oceanography*, *25*, 15–27. https://doi.org/10.1111/fog.12131

Kasperski, S. & Holland, D.S. (2013) Income diversification and risk for fishermen. *Proceedings of the National Academy of Sciences*, *110*, 2076–2081. https://doi.org/10.1073/pnas.1212278110

Kraus, S.D., Kenney, R.D., Mayo, C.A., McLellan, W.A., Moore, M.J. & Nowacek, D.P. (2016) Recent scientific publications cast doubt on north Atlantic right whale future. *Frontiers in Marine Science*, *3*, 137. https://doi.org/10.3389/fmars.2016.00137

Lebon, K.M. & Kelly, R.P. (2019) Evaluating alternatives to reduce whale entanglements in commercial Dungeness Crab fishing gear. *Global Ecology and Conservation*, *18*, e00608. https://doi.org/10.1016/j.gecco.2019.e00608

Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution*, *19*, 598–604. https://doi.org/10.1016/j.tree.2004.09.004

Maxwell, S.M., Hazen, E.L., Lewison, R.L., Dunn, D.C., Bailey, H., Bograd, S.J. *et al.* (2015) Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, *58*, 42–50. https://doi.org/10.1016/j.marpol.2015.03.014

MMPA. (1972). *"Marine Mammal Protection Act of 1972"*, in: 16 U.S.C. § 1361 et seq. (eds.) United States, NOAA & USFWS.

Moore, S.K., Cline, M.R., Blair, K., Klinger, T., Varney, A. & Norman, K. (2019) An index of fisheries closures due to harmful algal blooms and a framework for identifying vulnerable fishing communities on the U.S. West Coast. *Marine Policy*, *110*, 103543. https://doi.org/10.1016/j.marpol.2019.103543

Moore, M.J. & van der Hoop, J.M. (2012) The painful side of trap and fixed net fisheries: Chronic entanglement of large whales. *Journal of Marine Biology*, *2012*, 1–4. https://doi.org/10.1155/2012/230653

Mullowney, D.R. & Dawe, E.G. (2009) Development of performance indices for the Newfoundland and Labrador snow crab (Chionoecetes opilio) fishery using data from a vessel monitoring system. *Fisheries Research*, *100*, 248–254. https://doi.org/10.1016/j.fishres.2009.08.006

Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, *423*, 280–283. https://doi.org/10.1038/nature01610

NOAA. (2016) *VMS database management system*. Silver Spring, MD: NOAA Office of Law Enforcement.

O'Connor, S., Campbell, R., Cortez, H. & Knowles, T. (2009) *Whale Watching Worldwide: Tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare*. (Yarmouth, MA, USA: prepared by Economists at Large).

PacFIN. (2017) *Pacific Fisheries Information Network (PacFIN) Data Explorer*. Pacific States Marine Fisheries Commission.

Pacific Fishery Management Council. (2013) *Pacific Coast Fishery Ecosystem Plan for the U.S. Portion of the California Current Large Marine Ecosystem*. Portland, OR: Pacific Fishery Management Council.

Pikitch, E., Boersma, P.D., Boyd, I., Conover, D., Cury, P., Essington, T. *et al.* (2012) *Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs*. Washington, DC: Lenfest Ocean Program.

R Core Team. (2019) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Read, A.J. (2008) The looming crisis: Interactions between marine mammals and fisheries. *Journal of Mammalogy*, *89*, 541–548. https://doi.org/10.1644/07-mamm-s-315r1.1

Read, A.J., Drinker, P. & Northridge, S. (2006) Bycatch of marine mammals in U.S. and global fisheries. *Conservation Biology*, *20*, 163–169. https://doi.org/10.1111/j.1523-1739.2006.00338.x

Redfern, J.V., Moore, T.J., Fiedler, P.C., de Vos, A., Brownell, R.L. Jr, Forney, K.A. *et al.* (2017) Predicting cetacean distributions in data-poor marine ecosystems. *Diversity and Distributions*, *23*, 394–408. https://doi.org/10.1111/ddi.12537

Reeves, R.R., McClellan, K. & Werner, T.B. (2013) Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011. *Endangered Species Research*, *20*, 71–97. https://doi.org/10.3354/esr00481

Richardson, K., Asmutis-Silvia, R., Drinkwin, J., Gilardi, K.V.K., Giskes, I., Jones, G. *et al.* (2019) Building evidence around ghost gear: Global trends and analysis for sustainable solutions at scale. *Marine Pollution Bulletin*, *138*, 222–229. https://doi.org/10.1016/j.marpolbul.2018.11.031

Saez, L., Lawson, D. & DeAngelis, M.L. (2020) *Large whale entanglements off the U.S. West Coast, from 1982–2017*, in: NOAA Tech. Memo. Silver Spring, MD: United States Department of Commerce.

Santora, J.A., Mantua, N.J., Schroeder, I.D., Field, J.C., Hazen, E.L., Bograd, S.J. *et al.* (2020) Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nature Communications*, *11*, 536. https://doi.org/10.1038/s41467-019-14215-w

Smith, J., Connell, P., Evans, R.H., Gellene, A.G., Howard, M.D.A., Jones, B.H. *et al.* (2018) A decade and a half of *Pseudo-nitzschia* spp. and domoic acid along the coast of southern California. *Harmful Algae*, *79*, 87–104. https://doi.org/10.1016/j.hal.2018.07.007

Smith, Z., Gilroy, M., Eisenson, M., Schnettler, E. & Stefanski, S. (2014) *Net loss: The killing of marine mammals in foreign fisheries*. New York, NY: Natural Resources Defense Council.

Stelfox, M. (2017) Review of "Rebuttal to published article "A review of ghost gear entanglement amongst marine mammals, reptiles and elasmobranchs" by M. Stelfox, J. Hudgins, and M. Sweet". *Marine Pollution Bulletin*, *117*, 556–557. https://doi.org/10.1016/j.marpolbul.2016.11.053

Stelfox, M., Hudgins, J. & Sweet, M. (2016) A review of ghost gear entanglement amongst marine mammals, reptiles and elasmobranchs. *Marine Pollution Bulletin*, *111*, 6–17. https://doi.org/10.1016/j.marpolbul.2016.06.034

Trainer, V.L., Moore, S.K., Hallegraeff, G., Kudela, R.M., Clement, A., Mardones, J.I. *et al.* (2019) Pelagic harmful algal blooms and climate change: Lessons from nature's experiments with extremes. *Harmful Algae*, *91*, 101591. https://doi.org/10.1016/j.hal.2019.03.009

Turvey, S.T., Pitman, R.L., Taylor, B.L., Barlow, J., Akamatsu, T., Barrett, L.A. *et al.* (2007) First human-caused extinction of a cetacean species? *Biology Letters*, *3*, 537–540. https://doi.org/10.1098/rsbl.2007.0292

Watling, L. & Norse, E.A. (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology*, *12*, 1180–1197.

Whitney, F.A. (2015) Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific. *Geophysical Research Letters*, *42*, 428–431. https://doi.org/10.1002/2014gl062634

Wilson, J.R., Lomonico, S., Bradley, D., Sievanen, L., Dempsey, T., Bell, M. *et al*. (2018) Adaptive comanagement to achieve climate-ready fisheries. *Conservation Letters*, *11*, e12452. https://doi.org/10.1111/conl.12452

Worm, B. & Tittensor, D.P. (2011) Range contraction in large pelagic predators. *Proceedings of the National Academy of Sciences*, *108*, 11942–11947. https://doi.org/10.1073/pnas.1102353108

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Agenda Item E.4
Attachment 1
April 2021

Catch-only projection of the Pacific sardine resource in 2021 for U.S. management in 2021-2022

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Introduction

The Pacific sardine resource is assessed annually in support of the Pacific Fishery Management Council's (PFMC) process of specifying annual catch levels for the U.S. fishery. The following catch-only projection was conducted to provide a biomass estimate for harvest specifications during the 2021-2022 fishing year. The projection model included finalized catches for calendar year 2019 and updated catches for 2020, semester 1, but does not include other fishery or survey data collected over the past year (there are no new survey data available). New years of fishery and survey data will be incorporated in the next update assessment.

Methods

The following catch-only projection for 2021 management is based on data and methods described by Kuriyama et al. (2020), as reviewed by a Stock Assessment Review Panel in February 2020 and the Scientific and Statistical Committee in April 2020. The assessment projection was conducted using Stock Synthesis (SS v.3.30.14).

The projection model included sardine landings (metric tons) from six major fishing regions: Ensenada (ENS), southern California (SCA), central California (CCA), Oregon (OR), Washington (WA), and British Columbia (BC). Catch data for the fisheries off ENS, SCA, and CCA were pooled into a single "MexCal" fleet, and catch data from OR, WA, and BC were combined and treated as a single "PacNW" fleet in the model. The sardine model is based on a July-June model year, with two semester-based seasons per year (S1-July to December and S2-January to June).

Table 1: Finalized catch values for fleet by model year-semester (bolded columns). Preliminary values used in the 2020 benchmark assessment are adjacent to the bolded columns. The values in bolded columns show updated and finalized catch values for model year 2019, and new finalized catch values for model-year semester 2020-1. These values are data and not assumed values based on previous fishing activity.

Calendar Y-S	Model Y-S	MexCal_S1	**MexCal_S1**	MexCal_S2	**MexCal_S2**	PNW	**PNW**
2018-2	2019-1	130.86	**223.61**	0	**0**	7.73	**8.198**
2019-1	2019-2	0	**0**	11819.4	**33070.23**	2.51	**0.06**
2019-2	2020-1	--	**764.00**	--	**0**	--	**0.418**

The 2020 benchmark assessment used F values (yr^{-1}; as opposed to catch) to forecast for 2021. The 2021 catch-only projection used this approach, and used similar assumptions to forecast for 2022. The values for model year-semester 2020-1 were data (indicated by bolding in Table 2), and the values for 2020-2, 2021-1, and 2021-2 assumed F values estimated from the most recent observations from 2019-2 (see Table 1). For model year-semesters 2020-2 and 2021-2 the most recent observations were from 2019-2. For model year-semester 2021-1, the most recent observations were from 2020-1. The F values used in the forecast file were those associated with catch values. The catch-only projection assumed, as in the 2020 benchmark assessment, that fishing activity remained constant from the most recent observations. Note, the F values estimated from the MexCal_S2 catch value (33,070 mt) were estimated to be 4.0, which is the upper bound in the model.

Table 2: Catch values and associated F values used in the forecast file for the 2021 catch-only projection. The values for model year-semester 2020-1 were data (indicated by bolding), and the values for 2020-2, 2021-1, and 2021-2 assumed F values estimated from the most recent years of observation. For model year-semesters 2020-2 and 2021-2 the most recent observations were from 2019-2. For model year-semester 2021-1, the most recent observations were from 2020-1.

		MexCal_S1		MexCal_S2		PNW	
Calendar Y-S	Model Y-S	Catch	F (yr^{-1})	Catch	F (yr^{-1})	Catch	F (yr^{-1})
2019-2	**2020-1**	**764**	**0.345**	**0**	**0**	**0.42**	**0**
2020-1	2020-2	--	0	--	4	--	0
2020-2	2021-1	--	0.345	--	0	--	0
2021-1	2021-2	--	0	--	4	--	0

In summary, details regarding the projection estimate are as follows:

- Updated catch values associated with model year-semester 2019-1 and 2019-2 in the data file.
- Updated F values in the forecast file. F values for 2020-1 were calculated from an assessment run with catch values input in the forecast file. The 2020-1 calculated F values were then input to the forecast file. F values for 2020-2, 2021-1, and 2021-2 were

assumed to be the same as the F values from most recent data values (2019-2 for 2020-2 and 2021-2 and 2020-1 for 2021-1).

- No other data or parameterization changes were made to the assessment model.

Results

Summary biomass (age 1+) for the 2021 fishing year is forecast to be 14,011 mt (Fig. 1), and recruitment is forecast to be 339 million age-0 fish (Fig. 2). The catch-only projection had a higher 2019 recruitment estimate than that from the 2020 benchmark assessment (Fig. 2), likely as a result of the finalized catch information from 2019. Specifically, the MexCal_S2 catch amount was 33,070 mt, an increase over the preliminary value of 11,819 mt used in the 2020 benchmark assessment (Table 1). The 2021 forecast recruitment was estimated from the stock-recruit relationship (Fig. 2).

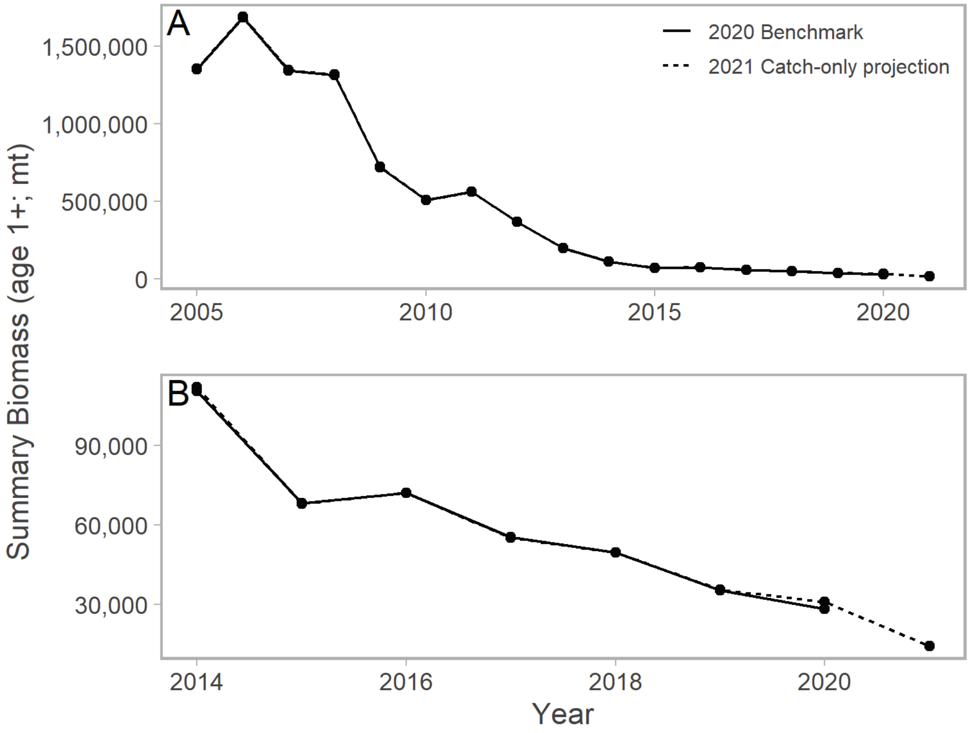

Figure 1: Time series of summary biomass (age 1+; mt) for the 2020 benchmark assessment (solid lines) and the 2021 catch-only projection (dashed lines). Panels are arranged by time series length (A: 2005-2021 and B: 2014-2021).

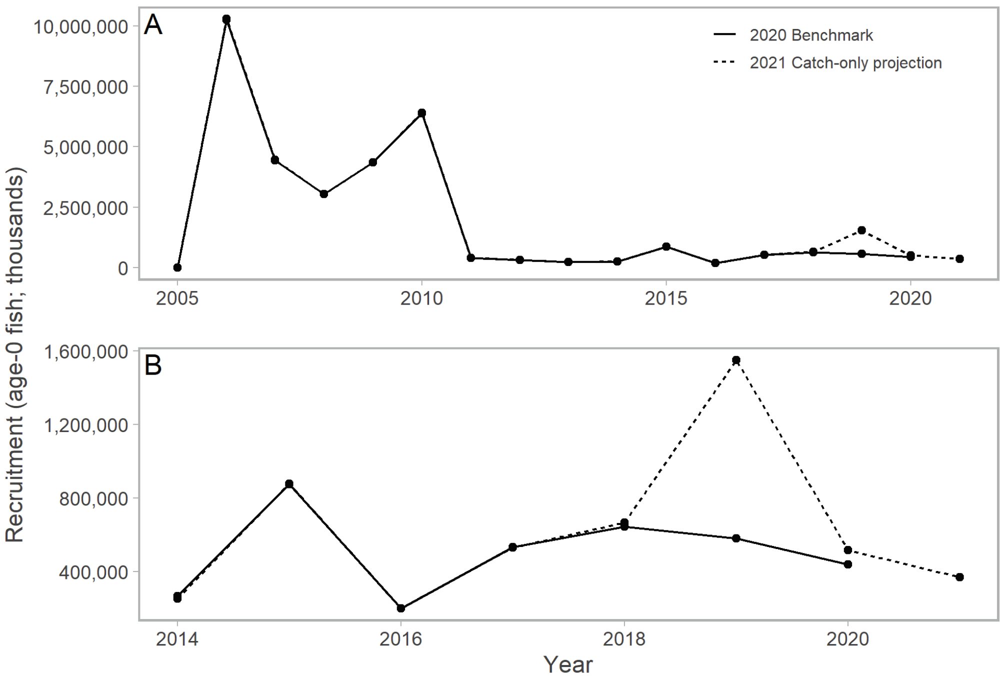

Figure 2: Time series of recruits entering the population (thousands of age-0 fish) for the 2020 benchmark assessment (solid lines) and the 2021 catch-only projection (dashed lines). Panels are arranged by time series length (A: 2005-2021 and B: 2014-2021).

Sensitivities

Sensitivities accounting for alternative assumptions about recruitment and uncertainties regarding MexCal catch values were evaluated. Two recruitment sensitivities assumed average recruitment from the years 2005-2019 (Avg. R 05-19) and from the years 2010-2019 (Avg. R 10-19). In the 2021 catch-only projection, recruitment was that calculated from the stock-recruit relationship. These recruitment scenarios represented the two recruitment scenarios evaluated in the sardine rebuilding plan (Hill et al. 2020). Another sensitivity run assumed that F values used in the forecast file were the same as those used in the 2020 benchmark (Base F). In this sensitivity, the primary change was that MexCal_S2 F value was assumed to be 1.95 (value used for forecast in 2020 benchmark) instead of 4 (value calculated from updated data).

Summary biomass (age 1+) estimates were 32,647 mt for the Avg. R 05-19 scenario, 14,456 mt for the Avg. R 10-19 scenario, and 21,678 mt for the constant F scenario (Fig. 3). The summary biomass estimate from the 2021 catch-only projection was 14,011 mt.

The Avg. R 05-19 sensitivity is perhaps the least likely sensitivity scenario, as it calculates an average recruitment from a period that included high recruitment events in 2005-2010 (Fig. 2). Biomass levels are low, and it is likely that recruitment will continue to be low in the near term. The constant F scenario is more realistic, given potential uncertainties associated with recent catches from the MexCal fleet. In prior assessments, the preliminary and final reported catch values have been comparatively close, and the recent difference (11,819 mt vs. 33,070 mt) is anomalous.

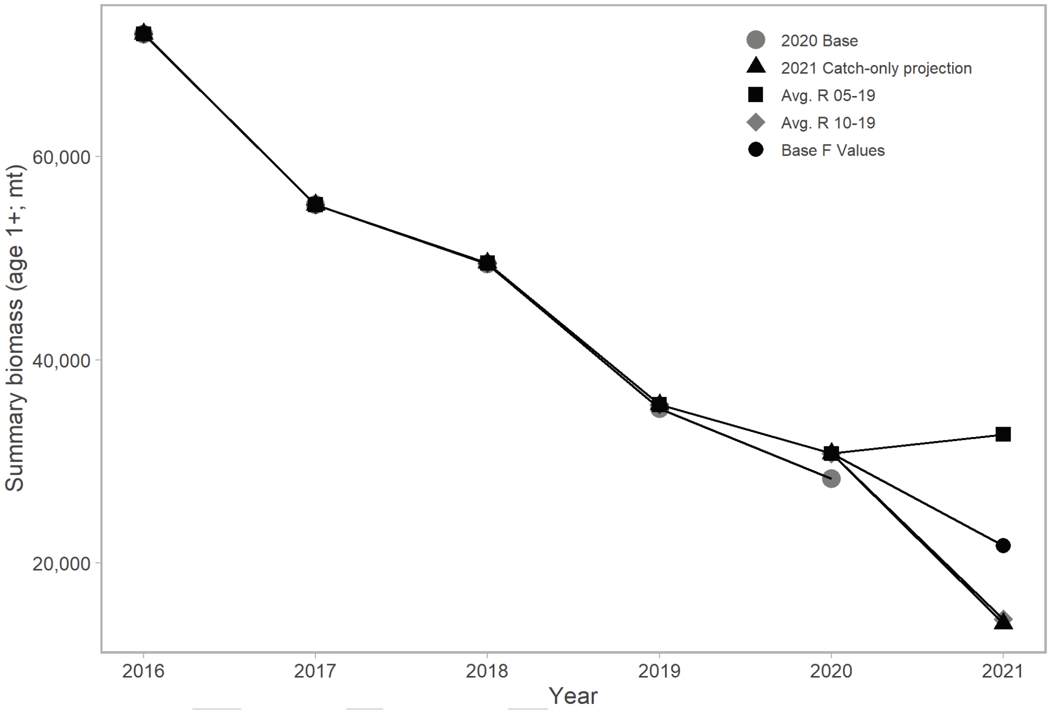

Figure 3: Time series of summary biomass (age 1+; mt) for the 2020 benchmark assessment (grey circles), 2021 catch-only projection (triangles), Avg. R 05-19 (squares), Avg. R 10-19 (grey diamonds), and Base F values (black circles). The 2021 catch-only projection and Avg. R 10-19 summary biomass values for 2021 are nearly identical and plotted on top of each other here.

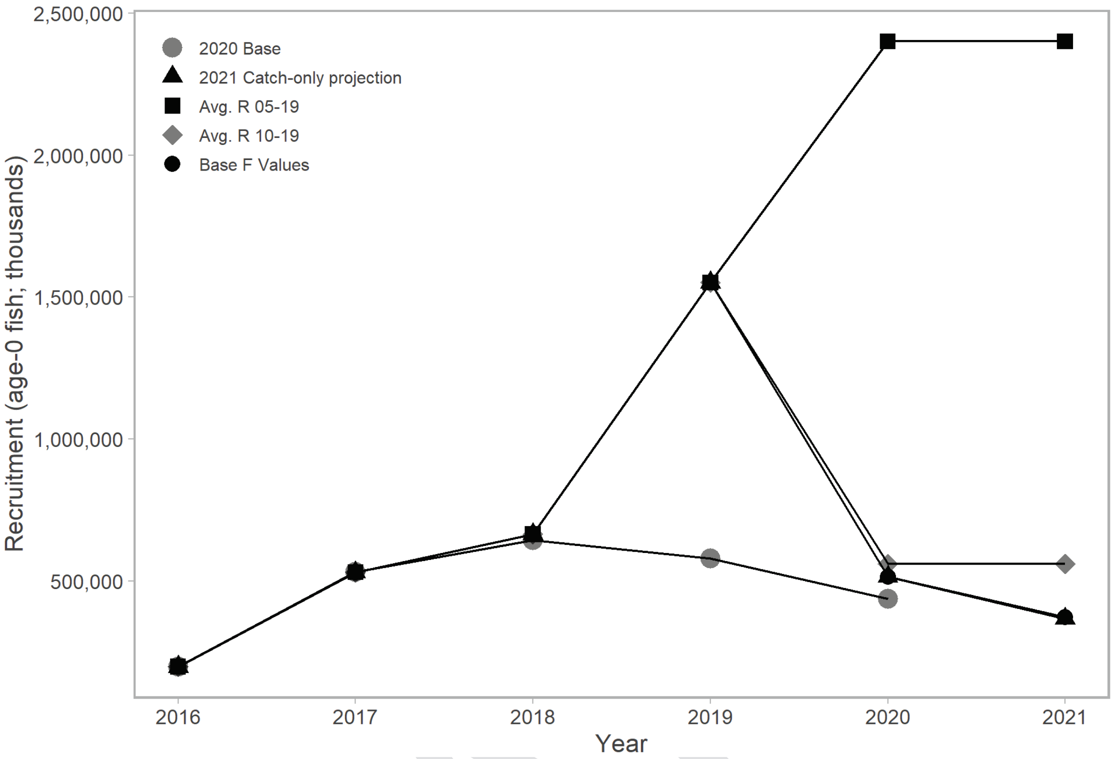

Figure 4: Time series of recruits entering the population (thousands of age-0 fish) for the 2020 benchmark assessment (grey circles), 2021 catch-only projection (triangles), Avg. R 05-19 (squares), Avg. R 10-19 (grey diamonds), and Base F values (black circles).

Exploitation status

Exploitation rate is defined as the calendar year catch divided by the total mid-year biomass (July-1, ages 0+). Based on the latest model and historic catches, the U.S. exploitation rate approached 2% and total exploitation (including Mexico and Canada landings) was about 67% during 2020. Catches from Mexico account for nearly all of the 2020 harvest, and have an exploitation rate of 65% (Fig. 5).

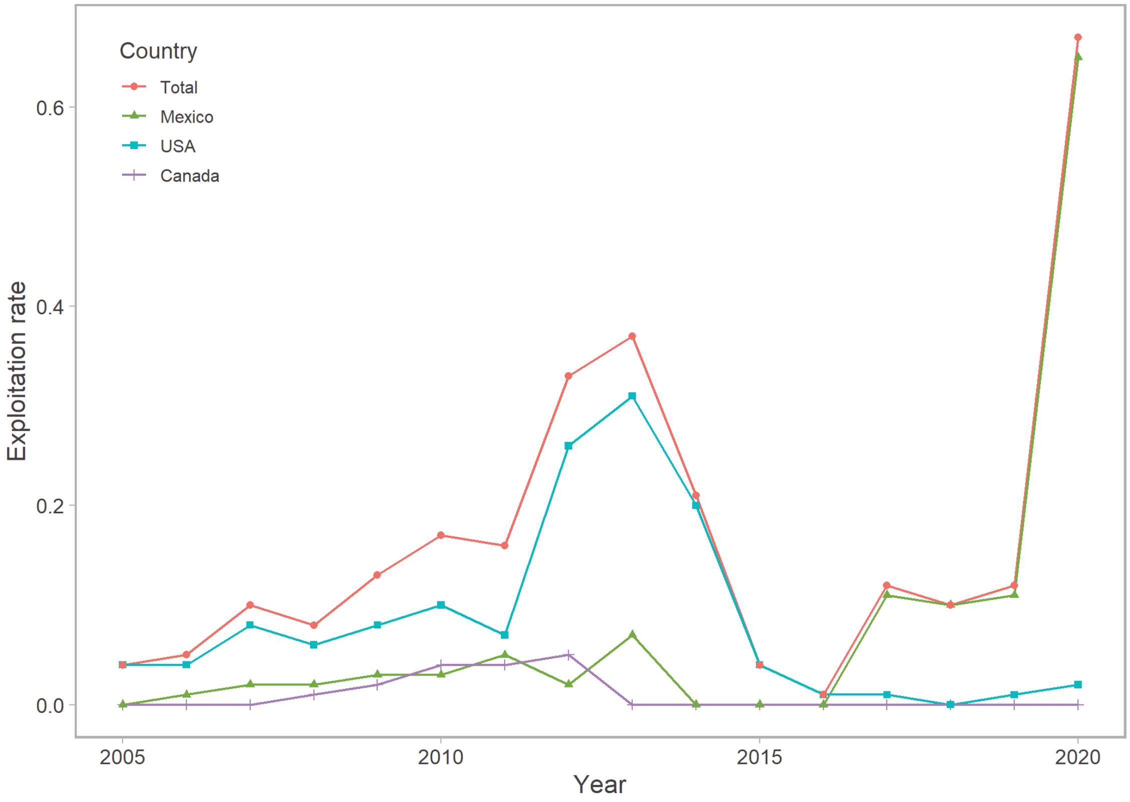

Figure 5: Plots of total exploitation rate (red) and exploitation rate by country. Countries shown are Mexico (green), U.S. (blue), and Canada (purple).

Harvest control rules

The harvest guidelines are shown in the table below, based on the age 1+ biomass of 14,011 mt. The stock is below the 150,000 mt management threshold and the harvest guideline is 0 mt for the 2021 – 2022 fishing year. Acceptable biological catches for a range of P-star values are also shown in the table below (Tier 1 σ=0.605; Tier 2 σ=1.0).

Harvest Control Rule Formulas

OFL = BIOMASS * E_{MSY} * DISTRIBUTION;   where E_{MSY} is bounded 0.00 to 0.25
$\text{ABC}_{\text{P-star}}$ = BIOMASS * $\text{BUFFER}_{\text{P-star}}$ * E_{MSY} * DISTRIBUTION;   where E_{MSY} is bounded 0.00 to 0.25
HG = (BIOMASS - CUTOFF) * FRACTION * DISTRIBUTION;   where FRACTION is E_{MSY} bounded 0.05 to 0.20

Harvest Formula Parameters

BIOMASS (ages 1+, mt)	**14,011**								
P-star	0.45	0.40	0.35	0.30	0.25	0.20	0.15	0.10	0.05
ABC Buffer(Sigma 0.582228)	0.93228	0.86817	0.80653	0.74631	0.68635	0.62523	0.56083	0.48914	0.39938
ABC BufferTier 2	0.88191	0.77620	0.68023	0.59191	0.50942	0.43101	0.35472	0.27761	0.19304
ABC BufferTier 3	0.77777	0.60248	0.46272	0.35036	0.25950	0.18577	0.12582	0.07707	0.03726
CalCOFI SST (2018-2020)	16.0140								
EMSY	0.239680								
FRACTION	0.200000								
CUTOFF (mt)	150,000								
DISTRIBUTION (U.S.)	0.87								

Harvest Control Rule Values (MT)

OFL =	**2,922**								
ABC(Sigma 0.607) =	2,724	2,537	2,356	2,180	2,005	1,827	1,639	1,429	1,167
ABCTier 2 =	2,577	2,268	1,987	1,729	1,488	1,259	1,036	811	564
ABCTier 3 =	2,272	1,760	1,352	1,024	758	543	368	225	109
HG =	**0**								

Recent management performance

US landings in the past years have remained below the annual catch limits (or annual catch targets, when applicable; Table 3). The 2020-2021 annual catch target for Pacific sardine, based on the 2020 benchmark assessment, was 4000 mt for Pacific sardine (Table 4). Landings-to-date of the northern subpopulation in the U.S. were 764 mt for 2020, 19% of the annual catch target. Note, March 2021 is still within the 2020-2021 fishing year.

Table 3: Summary biomass (age 1+), overfishing limit (OFL), allowable biological catch (ABC), annual catch limit (ACL), and annual catch target (ACT) values for recent fishing years. All units are in mt.

Fishing-year	Summary Biomass	OFL	ABC	ACL	ACT
2017-2018	86,586	16,957	15,497	8,000	
2018-2019	52,065	11,324	9,436	7,000	
2019-2020	27,547	5,816	4,514	4,514	4,000
2020-2021	28,276	5,525	4,288	4,288	4,000

Table 4: Annual catch limit (ACL), annual catch target (ACT) values, and catches from USA, Mexico, and Canada for recent fishing years. All units are in mt.

Fishing-year	ACL	ACT	USA	Mexico	Canada
2017-2018	8,000		372	6,032	0
2018-2019	7,000		655	11,210	0
2019-2020	4,514	4,000	705	32,589	0
2020-2021	4,288	4,000	764	0	0

Uncertainties

The high 2019 catch from Mexico and lack of 2020 biomass estimates due to cancellation of fishery-independent surveys in the past year contribute to the uncertainty of the catch-only projection. As a result, the uncertainties discussed in the 2020 benchmark assessment, such as the amount of nearshore biomass and proportion of northern subpopulation in Mexican waters remain. Specifically, the MexCal_S2 F value of 4 is a major uncertainty, and the sensitivity assuming an F of 1.95 (also a very high number) provides a range of potential forecast biomass levels, both of which are below the 50,000 mt management threshold.

The 2021 summary biomass (age 1+) forecast from the 2020 benchmark assessment was 28,276 mt, and the MexCal_S2 catches (applied to model year-semester 2019-2) were updated to be 33,070 mt. These numbers may seem to be biologically implausible but there are a number of factors to take into account. The 2021 catch-only projection estimated a larger recruitment event in 2019, and many of these recruits were then removed by the fishery.

The 2021 catch-only projection estimated a larger recruitment value for 2019 to fit to the updated catch values for 2019 (Table 5). The 2019-1 total biomass was estimated to be 103,697 mt in the 2021 catch-only projection instead of 60,689 mt as in the 2020 benchmark. Catch amounts were removed from the population according to the fleet-specific selectivity curves, which targeted primarily age-0 and age-1 fish (Fig. 6). The total biomass values for 2020-1 more similar than those from 2019-1, and the summary biomass values for 2019-1 and 2020-1 are also similar (Table 5).

Table 5: Total biomass (TB; age 0+) and summary biomass (SumB; age 1+) estimated from the 2020 benchmark assessment (2020bench) and 2021 catch-only projection (2021proj). All values are in mt.

Model Y-S	TB-2020bench	TB-2021proj	SumB-2020bench	SumB-2021proj
2018-1	62,012	62,516	49,449	49,528
2018-2	44,264	44,793	27,003	26,954
2019-1	60,689	103,697	35,186	35,591
2019-2	38,008	64,179	22,444	22,628
2020-1	47,548	53,428	28,276	30,758
2020-2	29,698	32,017	17,936	18,186
2021-1	NA	30,196	NA	14,011
2021-2	NA	18,626	NA	8,752

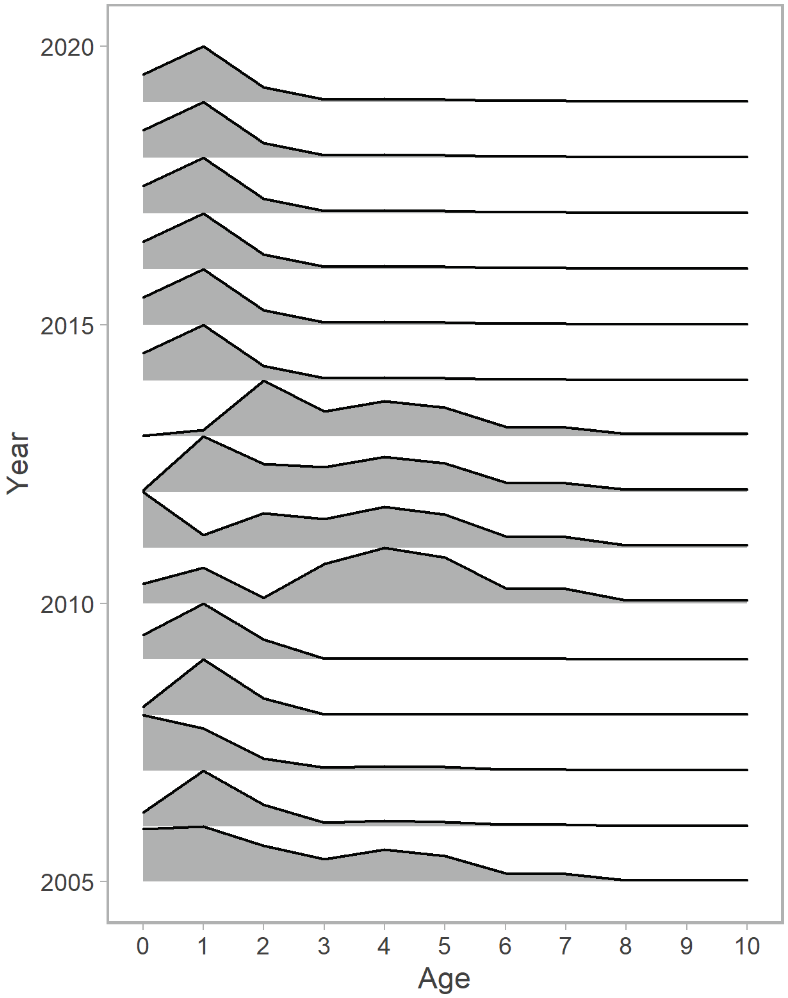

Figure 6: Time-varying age-based selectivity patterns for MexCal S2 fishing fleet in the 2020 benchmark assessment (Figure 24 in Kuriyama et al. 2020).

Research and data needs

There have been no updates to the acoustic-trawl fishery data, thus uncertainty regarding nearshore biomass remains. There were no updates to the CCPSS aerial survey. The recommendations for the aerial survey included the need to coordinate visual estimates with randomly sampled purse-seine point sets, temporal rather than spatial replication, and sufficient biological sampling on mixed anchovy and sardine schools. The 2021 spring and summer acoustic-trawl surveys will make strides toward increasing nearshore coverage using acoustics in collaboration with the fishing industry.

References

Hill, K.T., Kuriyama P. T., Crone, P.R. 2020. Pacific sardine rebuilding analysis based on the 2020 stock assessment. Pacific Fishery Management Council. Portland, OR.

Kuriyama, P.T., Zwolinski, J.P., Hill, K.T., Crone, P. R. 2020. Assessment of the Pacific sardine resource in 2020 for U.S. management in 2020-2021, U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-628.

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Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific

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Marine heatwaves (MHWs) have occurred in all ocean basins with severe negative impacts on coastal and ocean ecosystems. The northeast Pacific 2013–2015 MHW in particular received major societal concerns. Yet, our knowledge about how MHWs impact fish stocks is limited. Here, we combine outputs from a large ensemble simulation of an Earth system model with a fish impact model to simulate responses of major northeast Pacific fish stocks to MHWs. We show that MHWs cause biomass decrease and shifts in biogeography of fish stocks that are at least four times faster and bigger in magnitude than the effects of decadal-scale mean changes throughout the 21st century. With MHWs, we project a doubling of impact levels by 2050 amongst the most important fisheries species over previous assessments that focus only on long-term climate change. Our results underscore the additional challenges from MHWs for fisheries and their management under climate change.

Marine heatwaves (MHWs) - persistent extremely warm ocean temperatures - are already impacting ecosystems worldwide[1–5]. Impacts from MHWs include range shifts of marine fishes and invertebrates[6–9], bleaching of coral reefs[2], mass mortality of kelp forest[4,10] and other coastal vegetation[11] and reduction in reproductive success and survivorship of marine animals[12]. Long-term ocean warming since the early 20th century due to human-induced increase in greenhouse emissions has led to widespread increases in MHW frequency, intensity and duration[13]. Globally, the frequency of MHWs has been doubled since 1982[14], and is projected to increase further under continued global warming[5,14,15].

In 2013, a large MHW in the northeast Pacific appeared off the coast of Alaska and subsequently expanded south to Baja California. This specific MHW, commonly known as the "Blob"[16], persisted through to the end of 2015 and was the largest MHW globally since 1982[17] with sea surface temperature (SST) anomalies of over 6 °C. This warm Blob affected ecosystems from the California Current in the South to the Gulf of Alaska and the Bering Sea in the North[9,18–20]. The anomalously high temperature enhanced the stratification of the upper ocean, leading to a decrease in nutrient supply to the surface ocean and causing a decrease in net primary production and community production[21,22]. Observational studies have reported ecological changes in the Northeast Pacific region, such as shifts in the horizontal and vertical distributions of marine species[8,19], as well as changes in pelagic micronekton and macrozooplankton communities and their species richness[18,23]. Such changes impacted also human activities such as fisheries[19]. Towards the end of 2019, a new MHW has emerged in the North Pacific[24], raising concerns that a similar MHW as the Blob in 2013–2015 may reappear in the near future. Due to the already low numbers of Pacific cod (*Gadus macrocephalus*) and the potential reappearance of the Blob, the United States' federal cod fishery in the Gulf of Alaska closed for the 2020 season as a precautionary measure[25]. The fisheries closure underscores the potential high impacts of such MHWs not only on marine ecosystems, but also on social-economic systems such as fisheries.

Simulating ecological changes of fish stocks and fisheries using modelling approaches can help elucidate and attribute the relative contribution of MHWs to observed changes in ecosystems[26] and assess future ecological risks under alternative scenarios of climate change[27]. However, projections of ecological impacts of MHWs have focused mainly on sensitive biogenic habitats such as coral reefs and intertidal systems[28,29]. In contrast, previous impact assessments on fish stocks and fisheries focused mainly on decadal-scale changes in mean conditions under climate change while the additional impacts of MHWs are more uncertain. Improved understanding of

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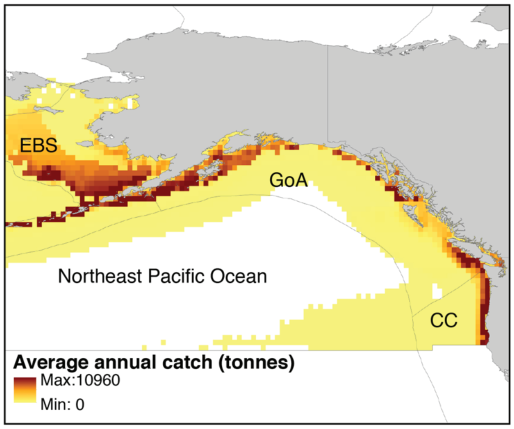

Figure 1. Average annual fisheries catches of the 22 studied fish stocks from 1981 to 2015 in the northeast Pacific Ocean and the three large marine ecosystems therein. Catches data were obtained from the Sea Around Us fisheries database (www.seaaroundus.org)[55]. The boundary of the northeast Pacific Ocean is based on the United Nations' Food and Agriculture Organization Statistical Area 67. The large marine ecosystems include: EBS - Eastern Bering Sea, GoA - Gulf of Alaska, and CC - California Current.

the futures of living marine resources will help inform dependent human communities, sectors and governance institutions to develop more effective climate-adaptation and risk-reduction measures.

Here, we aim to test the hypotheses that MHWs will add to the impacts of changes in mean ocean conditions under climate change, leading to additional anomalous shifts in biomass, distribution and potential catches of fish stocks in the northeast Pacific regions. Previous studies have applied species distribution models to project the effects of changing long-term mean ocean conditions on spatial distribution, abundance, community structure and the potential biomass production of fishes and invertebrates in this region[27,30,31]. In this study, we extend such modelling approaches to examine the consequences of MHWs on fish stocks and fisheries. Our analysis focused on the northeast Pacific Ocean and the Large Marine Ecosystems (LMEs) therein where most fishing took place (Fig. 1). We used the United Nations' Food and Agriculture Organization (FAO) Statistical Area (Area 67) to delineate the northeast Pacific region. This region includes three LMEs[32]: (a) Eastern Bering Sea, (b) Gulf of Alaska and (c) California Current. We examine the additional risk of MHWs on fish distribution[biomass] and and potential fisheries catches and explore whether and how the projected impacts of MHWs add to the decadal scale changes in mean ocean conditions. We also discuss the implications of the findings for ecosystem-based fisheries management.

We analyzed projected changes in annual mean Sea Surface Temperature (SST) in the northeast Pacific Ocean using a 10-member ensemble simulation of the Earth system model version 2 developed at the Geophysical Fluid Dynamics Laboratory (GFDL ESM2M[33–35]; see Materials and Methods). Each ensemble simulation was run over the 1950–2100 period under the same external forcing of historical changes before 2005 and Representative Concentration Pathway 8.5 (RCP8.5) thereafter. The RCP8.5 scenario represents a pathway of greenhouse gas concentrations for which radiative forcing reaches approximately 8.5 Wm^{-2} by 2100. We simulated changes in abundance and distributions of exploited fish stocks that are highly important to fisheries in the northeast Pacific region (Fig. 1) We included a total of 22 fish species that were reported in the fisheries statistics in the northeast Pacific region (www.seaaroundus.org). These species were important to fisheries in this region as they contributed up to 80% of the total observed catches from 2006 to 2015 (www.seaaroundus.org). We used the dynamic bioclimate envelope model (DBEM)[36,37], which is a spatially-explicit species distribution-population dynamic model, to simulate dynamical changes in biomass, and potential fisheries catch for each species on a 0.5° latitude × 0.5° longitude grid of the world ocean (see Methods for details). To identify MHWs, we calculated anomalies between the annual mean SST simulated by each of the individual 10 ensemble members and the ensemble-averaged SST (Fig. 2). We calculated four impact indicators to examine the ecological responses of fish stocks and their implications for fisheries during a MHW. These indicators are: (1) total biomass, (2) latitudinal centroid (average of the coordinates of grid cell weighted by the species' biomass), (3) depth centroid (average of bathymetry of grid cell weighted by the species' biomass), and (4) maximum catch potential [catch at fish stock-specific fishing mortality rate (F) that achieves maximum sustainable yield (MSY) i.e., $F = F_{MSY}$].

Results

We identified amongst the ten ensemble member simulations in total 149 MHWs in any of the three LMEs from 1981 to 2100. During these MHWs, the SST anomalies (i.e. mean annual intensity) are on average 0.99 °C (5th to 95th percentile = 0.55–1.49 °C) higher than the ensemble-mean SST (Fig. 3A). In comparison, the simulated average rate of SST change across the LMEs is 0.23 ± 0.04 °C (standard deviation) per decade (Fig. 3B). Thus, the average MHW SST anomalies, which are estimated annually, are about four times the mean warming per decade in the northeast Pacific LMEs. The intensity of MHWs is higher in the high latitude LMEs, i.e., Eastern Bering Sea and Gulf of Alaska, relative to that in California Current (Fig. 3A), because the SST variability is larger in Eastern Bering Sea and Gulf of Alaska than in California Current. Since we focused on annual means in SST, the modeled SST anomalies in all three LMEs are in general smaller than the observed peak SST anomalies during the Blob.

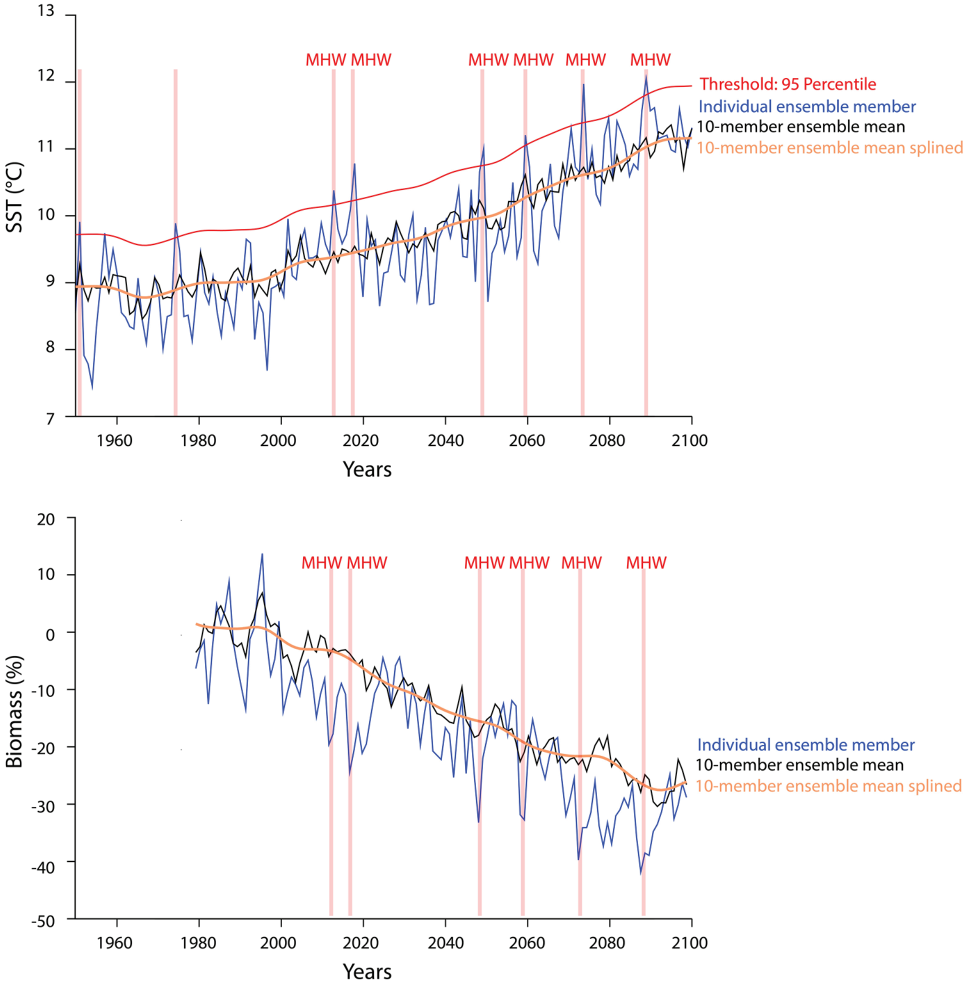

Figure 2. Schematic diagram explaining the characterization of Marine Heatwaves (MHWs) and their impacts on fish stocks. (**a**) The characterization of MHWs based on outputs from the 10 ensemble member projections of the GFDL ESM2M and (**b**) their impacts on biomass of the sockeye salmon (*Oncorhynchus nerka*) in the Gulf of Alaska large marine ecosystem. The red vertical bars in both panels indicate MHW events. Biomass changes are given as changes relative to 1986 to 2005.

The biomass of the 22 exploited fish stocks in the three northeast Pacific LMEs was projected to decrease by a median of −2.8% (5th to 95th percentile = −17.1 to 0.4%) during MHW events (Fig. 3C), with maximum decreases of up to 20%. Changes in maximum catch potential levels were almost the same as changes in biomass (Fig. S4–6). The biomass (and maximum catch potential levels; not shown) of almost all fishes in the California Current fish stocks were lower during MHWs for the majority of the fish stocks (median = −4.0%, 5th to 95th percentile from −18.3 to 0.0%). The direction of impacts of MHW on fish stock biomass in the Eastern Bering Sea (−0.8%, from −11.7 to 1.1%) and Gulf of Alaska (−3.0%, from −14.5 to 0.2%) were slightly more variable. These general decreases in biomass during MHWs added to the long-term climate change-induced changes in biomass. The decadal mean changes in biomass were projected to be more variable in the direction of changes than changes during the MHWs years across the LMEs (Fig. 3D). For the species with negative responses during MHWs, the decreases in biomass during MHWs were several factors higher than the rate of biomass decrease per decade from 1981 to 2100 under RCP8.5.

We also projected signature of MHWs on the biogeography of exploited fish stocks in the northeast Pacific (Figs. 3E,G). 70% of the fish stocks showed a poleward shift in the latitudinal distribution centroids during MHWs (Fig. 3E). The direction of shifts in the Gulf of Alaska were projected to be more variable across species (median = −0.76 km, 5th to 95th percentile from −7.6 to 19.9 km) than those in Eastern Bering Sea and California Current, with around half of the species shifting southward. On average, fish assemblages in Eastern Bering Sea and California Current were projected to shift poleward at a rate of 9.5 km (−4.0 to 23.9 km) and 5.8 km (−5.1 to 22.0 km) per year, respectively, for each MHW event, with maximum shifts of over 30 km relative to the mean distribution. The pattern and magnitude of the latitudinal shifts of the fish assemblages were similar to the average decadal-scale shifts under climate change (Fig. 3F). Bathymetric shifts with MHWs were projected to vary more substantially across the stock-ensemble members, particularly in Eastern Bering Sea (−0.8, −6.7 to 24.1 m) and California Current (−4.1, −14.4 to 26.1 m) compared to Gulf of Alaska (1.6, −16.1 to 8.1 m); note

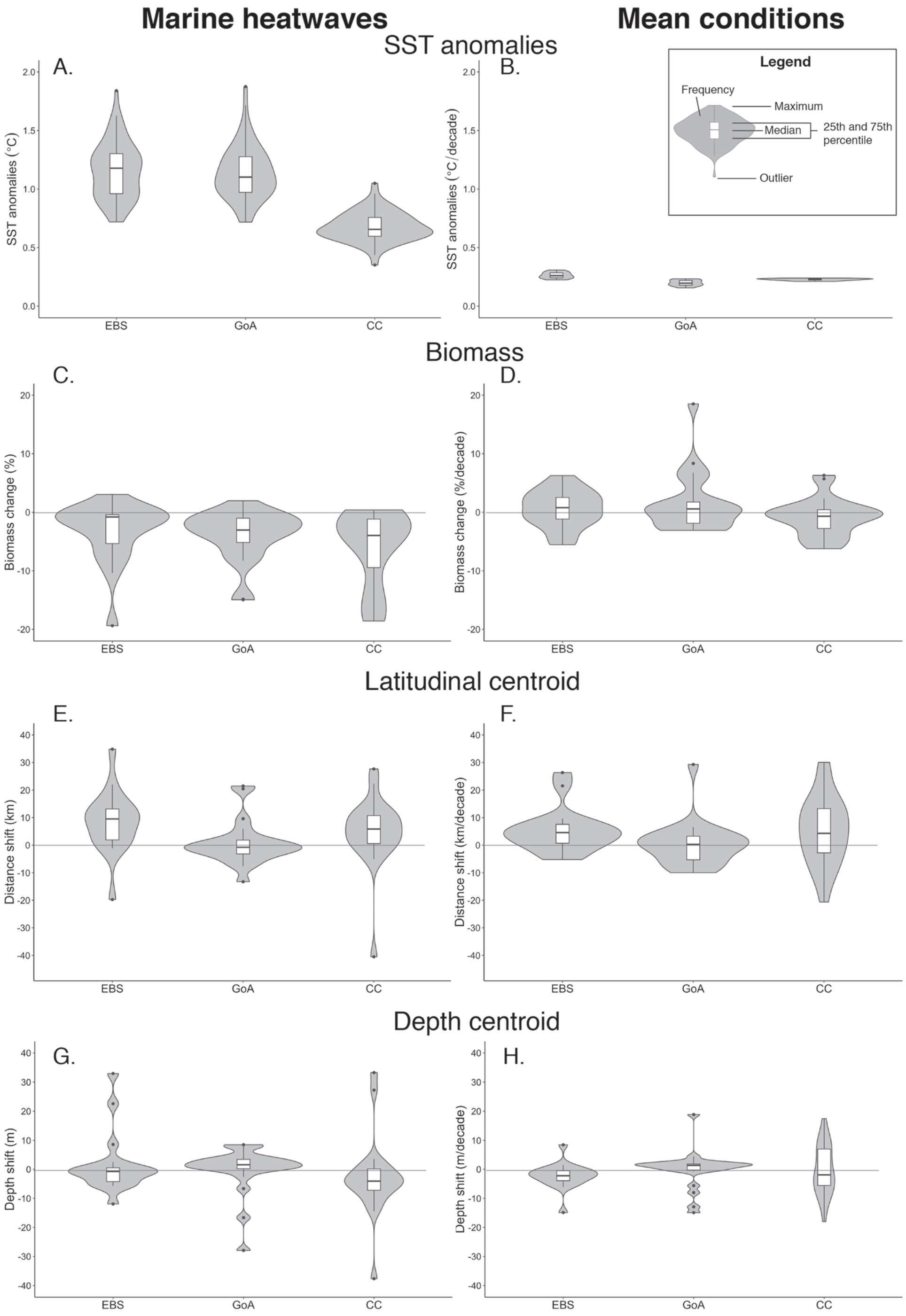

Figure 3. Projected changes in sea surface temperature (**A**,**B**) and the impact indicators (biomass, latitudinal centroid and depth centroid; **C**–**H**) of the 22 studied fish stocks in the three large marine ecosystems (Eastern Bering Sea - EBS, Gulf of Alaska - GoA, California Current - CC) of the northeast Pacific during MHWs (left panels) and due to long-term climate change from 1981 to 2100 (right panels). Changes in sea surface temperature and impact indicators during MHWs were expressed relative to the spline-smoothed ensemble-mean of the same time period. In contrast, long-term climate changes were calculated from linear regressions over the 1981–2100 period, with the rate of change (slope of the regression) expressed as change per decade. Negative depth centroid shifts in G-H indicate species' average distribution that were projected to be deeper.

negative values indicate shift to deeper waters). The pattern of shifts in depth centroids of fish assemblages were generally consistent between MHWs and long-term decadal-scale mean changes (Fig. 3G,H).

Amongst the 22 fishes, pelagic fish were projected to be most negatively impacted by MHWs, followed by Pacific salmon and groundfish (Fig. 4). Overall, almost all the studied pelagic fish showed significant decrease in

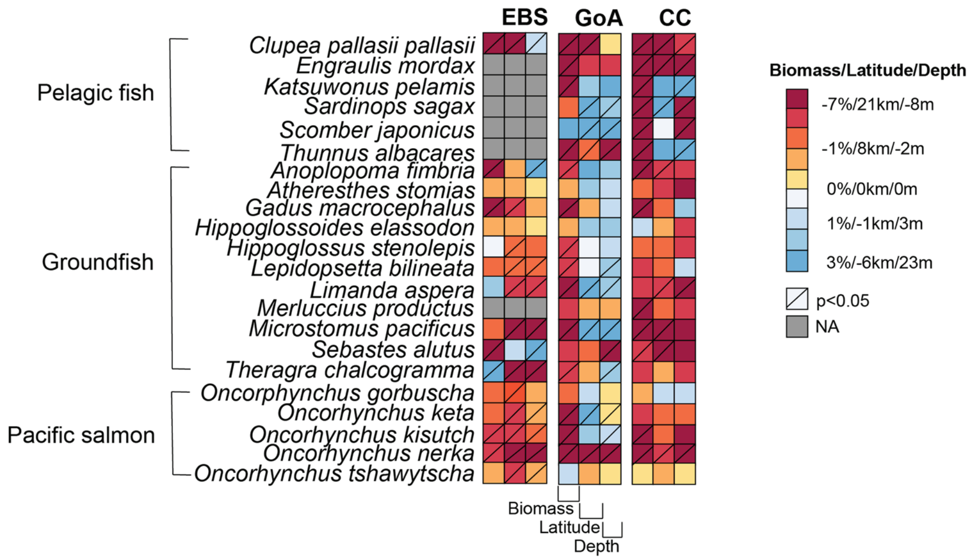

Figure 4. Projected mean changes in biomass, latitudinal and depth centroid of the 22 exploited marine fish stocks in the Eastern Bering Sea (EBS), Gulf of Alaska (GoA) and California Current (CC) during MHW years. NA - not available in catch record between 2006 and 2015.The different colour scales represent the projected changes in biomass, latitudinal centroid and depth centroid. Stripping of a cell represents changes at a significant level of below 0.05.

biomass (more than 7%) under MHWs relative to the mean conditions, except Pacific sardine (*Sardinops sagax*) and Japanese mackerel (*Scomber japonicus*) that did not show significant changes in Gulf of Alaska. Amongst the five studied Pacific salmon species, biomass of sockeye salmon (*Oncorhynchus nerka*) decreased most substantially and most consistently across LMEs under MHWs, followed by coho salmon (*O. Kisutch*). For groundfish, biomass of Pacific cod (*Gadus macrocephalus*), sablefish *(Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) were projected to decrease significantly under MHWs in all LMEs. Only Alaska pollock in the Eastern Bering Sea increased significantly in biomass under MHWs amongst all the 22 species and LMEs.

For MHW impacts on species' biogeography, the distribution centroids of Pacific hering (*Clupea pallasii pallasii*) and sockeye salmon were projected to shift poleward in all three LMEs (Fig. 4). More fish stocks in Gulf of Alaska than in Eastern Bering Sea or California Current shifted significantly equatorward, or in variable directions amongst ensemble members under MHWs. Direction of shifts in depth centroid also often differed between LMEs for the same species. For example, Pacific Dover sole (*Microstomus pacificus*) was projected to shift poleward in Eastern Bering Sea and California Current, but equatorward in Gulf of Alaska and to deeper waters in Eastern Bering Sea, while shifted shallower in Gulf of Alaska (Fig. 4).

We chose Pacific cod, sockeye salmon and Californian anchovy that were of particular interest to fisheries and coastal communities in the northeast Pacific region to highlight how MHWs will exacerbate impacts from long-term climate change (Fig. 5). Firstly, these species will experience ocean warming as a result of both the mean increase in SST under RCP8.5 as well MHWs (Fig. 5A–C). This will greatly exacerbate the warming hazards to these species. Secondly, biomass of these three fish stocks dropped approximately 5% for Pacific cod in Eastern Bering Sea to 30% for sockeye salmon in Gulf of Alaska and California anchovy in California Current during MHWs in addition to the decrease due to long-term mean changes under RCP8.5 (5%, 25% and 10% by 2100 relative to 2000; Fig. 5D–F). Similarly, shifts in biogeography, as indicated by the latitudinal centroids of the three selected species (Fig. 5G–I), added to the effects of the shifts due to changes in mean ocean conditions by as much as 100 km poleward during MHWs (e.g., California anchovy in California Current). As such, biomass decrease and biogeographic shifts during MHWs early in the 21st century were projected to be at a similar level as the decadal-scale average changes by around the 2050 s. This also means that MWHs will exert large impact 'shocks' while fish stocks are already impacted by long-term mean climate change. For example, with both MHWs and changes in mean conditions, biomass of sockeye salmon was projected to drop by more than 40% by 2100 relative to 2000 under RCP8.5.

Discussion

Our findings provide theoretical support to the empirical observations from scientific surveys and anecdotal accounts from fishers that fisheries important fish stocks such as Pacific cod and sockeye salmon had been impacted by the 2013–2015 northeast Pacific MHW[19]. In addition, we offer new insights into the combined impacts of MHWs and long-term climate change on the species distribution in the northeast Pacific. Specifically, we show that MHWs can more than double the magnitude of the impacts on fish stocks by 2050 due to long-term climate change. Previous vulnerability and impact assessments have therefore greatly underestimated the risk to future fish stocks and fisheries in the northeast Pacific under climate change.

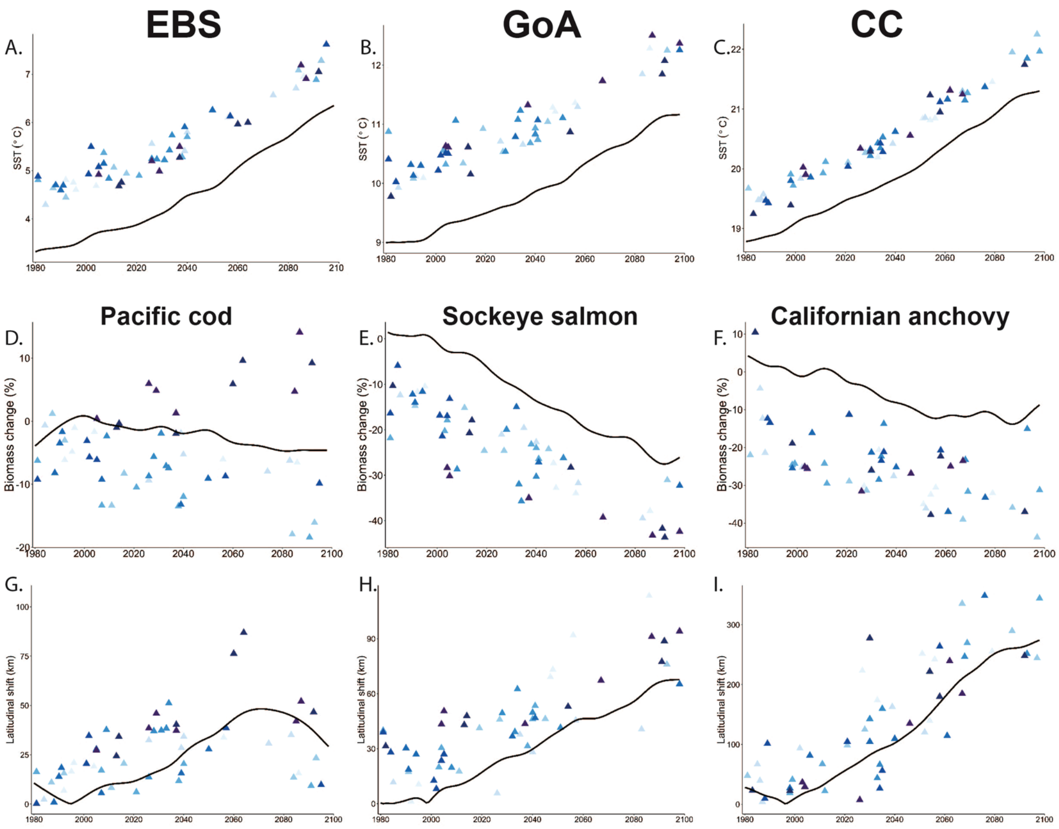

Figure 5. Projected time-series of changes in sea surface temperature (SST) (**A**–**C**), biomass (**D**–**F**) and latitudinal centroid (**G**–**I**): Pacific cod (*Gadus macrocephalus*) (**D**,**G**), sockeye salmon (*Oncorhynchus nerka*) (**E**,**H**) and Californian anchovy (*Engraulis mordax*) (**F**,**I**)) in the Eastern Bering Sea (EBS), Gulf of Alaska (GoA) and California Current (CC). The solid lines represent the average values across the 10 ensemble member simulations (smoothed with a cubic spline function); blue-colored triangles represent values during MHW years; the different intensity of blue color represents different ensemble member simulations (see Figs. S1–12 for results for all the large marine ecosystems and studied fish stocks).

Some fish stocks had already showed changes in biogeography during the recent Blob that are similar to the MHW impacts projected in this study. In Gulf of Alaska, analysis using data collected from scientific surveys showed that some groundfish species such as Pacific cod had shifted their distributions to deeper waters during anomalous warm temperature[8,9]. However, the directions of biogeographic shifts varied between species and across their life stages. Such shifts also differed between sub-regions due to different oceanographic conditions and bathymetric profiles[8]. These oceanographic and biological complexities could contribute to the large variability of our projected biogeographic shifts for groundfish between ensemble members.

Although shifts in biogeography associated with the Blob are more widely reported in literature[19], our results show that biomass decreases are more consistent in response to MHWs in the northeast Pacific relative to biogeographic shifts. Therefore, biomass of fish stocks may be a better impact indicator in detecting and assessing the impacts of MHWs as part of ecosystem-based management. However, as the magnitude of the projected biomass decrease and biogeographic shifts varied between species in our study, different sets of impact indicators that are species-specific can be used to more efficiently monitor and assess the impacts of MHWs.

The characteristic of the MHW impacts will result in a different set of challenges for management and conservation of living marine resources than those associated with the long-term mean change in climate. The rate of changes in biomass, potential catches and biogeography of fish stocks are much higher under MHWs than under long-term climate change. For example, in the California Current, Pacific sardine and California anchovy population are observed to show alternations of their abundance that are partly driven by changes in oceanographic regimes in the Pacific Ocean[38,39]. Particularly, warm regimes tend to favor sardine's recruitment and abundance while cool regimes favor anchovy. Thus, under decade-scale mean ocean warming, sardine was projected to increase in biomass while the opposite was projected for anchovy in the California Current. In contrast, poleward range expansion of sardine and anchovy was projected to result in long-term increase in their abundance in the Gulf of Alaska. However, the projected short-term rapid warming under MHWs pushed environmental temperature beyond those preferred by both sardine and anchovy, leading to a drop in their biomasses in both the California Current and Gulf of Alaska. Moreover, satellite data and model simulations suggest that MHWs are linked to and can be exacerbated by, multi-annual climate variability such as El Niño Southern Oscillation (ENSO), resulting in the particularly large and persistent biological impacts in the Northeast Pacific region from the Blob[13,19,40]. In any case, these complex biological responses of sardine and anchovy that inter-mixed between the effects of MHWs and decadal-scale warming therefore demand more rapid and short-term governance and adaptation responses such as alteration of fishing quota, shifts in fishing ground and targeted species[41]. The challenges from MHWs impact will thus put 'double strains' on sustainable management of living marine resources under climate change, pointing to the need for future research into the development of more robust adaptation and governance responses[42,43]. Previous studies have shown that global warming substantially increases the risks of MHWs to occur[14]. Our study additionally suggests that MHWs can strongly exacerbate the impact of decadal-scale mean ocean warming on fish stocks. A reduction of anthropogenic greenhouse gas emissions - the fundamental driver of global warming[44] – is therefore needed to limit the impacts of MHWs on fish stocks and fisheries[5].

Even though we consider the projected pattern of MHW impacts on fish stocks and the implications for understanding future risks on fisheries and their governance under climate change as robust, a number of caveats needs to be discussed. The global Earth system model used in this study (i.e. GFDL ESM2M) is able to adequately simulate mean states and trends in different marine heatwave metrics over the satellite 1982–2016 period[14]. However, the horizontal resolution (about 1°) of the ocean component of the Earth system model is too coarse to accurately represent some of the oceanographic dynamics in coastal and shelf seas such as upwelling or mesoscale eddy activity e.g.[45]. In addition, some of the biogeochemical processes in the high latitudes associated with sea ice are also not well resolved. The simulated net primary productivity in GFDL ESM2M, in particular, is highly uncertain[46], especially in regions with sea ice[47], because nutrient inputs during sea ice melt[48] or through rivers[49] are not included. The fish stock model assumes that historical species' biogeography reflects their environmental niches[50]. Variations in the projected pathways of changes in biomass and biogeography of species in this study were partly caused by the differences in species' temperature preferences calculated from different Earth system model ensemble members e.g., the increase in biomass under MHWs for Pacific cod in one of the ensemble members (dark purple diamonds in Fig. 5G). The fish stock model also did not account for interspecific interactions or evolutionary adaptation to epigenetic responses to environmental changes[51]. For instance, we projected a positive impact of MHWs on Alaskan pollock (*T. chalcogramma*) in Eastern Bering Sea. However, previous studies have suggested that anomalous warm temperature affects the availability of preferred nutritious prey that reduced the survivorship and recruitment of pollock in the Bering Sea[19]. Moreover, we only examined climate projections following the 'no mitigation' high greenhouse gas emissions scenario (RCP8.5) and including an 'idealized' fishing scenario i.e., assuming all fishing is at level to achieve maximum sustainable yield of each fish stock. The effects of scenario uncertainties associated with different greenhouse gas emission and pathways of fishing effort and their management on the impacts of MHWs on marine ecosystems need to be explored further. Future research can build on the foundation laid by this study to incrementally address these uncertainties[52]. For example, the number of ensemble members, Earth system models and fish models may be increased to explore a wider range of model uncertainties. The analysis can also be repeated using high resolution Earth system models, and fish models with trophic interactions and/or eco-evolutionary dynamics.

Overall, this study underscores the importance of considering MHWs in assessing climate risks and impacts. Previous risk and impact assessment that focused on the effects of long-term changes in mean conditions under climate change may have largely underestimated climate risks on fish stocks and fisheries. Moreover, the rapid rate of change and the prevalence of impacts across fisheries important fish stocks in the northeast Pacific point to the need to examine whether climate adaptation, designed mostly for dealing with long-term mean changes, would be sufficient to reduce the additional climate risks from MHWs. Without appropriate mitigation and adaptation measures, MHWs may pose additional risks on the long-term viability of marine species and the sustainability of their fisheries, and the associated benefits to dependent human communities such as food, economic benefits and livelihoods[11]. Our results also provide a foundation for further modelling efforts and analysis to build on and systematically explore different dimensions of uncertainties.

Methods

Earth system model.

We analyzed projected changes in annual mean SST in the northeast Pacific Ocean using a 10-member ensemble simulation of the Earth system model version 2 developed at the Geophysical Fluid Dynamics Laboratory (GFDL ESM2M[33–35]). The GFDL ESM2M is a fully coupled carbon cycle-climate model that consists of an ocean, atmosphere, sea ice, and land model, and includes land and ocean biogeochemistry. The nominal horizontal resolution of the ocean component is about 1° latitude × 1° longitude with 50 vertical levels[53].

Each ensemble simulation is run over the 1950–2100 period under the same external forcing of historical changes before 2005 and Representative Concentration Pathway 8.5 (RCP8.5) afterwards. The RCP8.5 is a high greenhouse gas emission scenario[54] that leads to a global atmospheric surface warming in ESM2M of 3.2 °C by 2081–2100 relative to preindustrial. All 10 ensemble members are run under the same external radiative forcing scenario, but are started from different initial conditions in January 1st of 1950. Spread in the ensemble members is generated by slightly perturbing the initial state of the Earth system at the start of each simulation. These initial perturbations cause each ensemble member to have a unique atmosphere and ocean state at each point in time, i.e. a different state of internal variability. As a specific example, the real ocean experienced an El Niño in 1997–1998. In the model, ensembles may have had a La Niña, El Niño or been neutral at this time.

Dynamic bioclimate envelope model.

We simulated changes in abundance and distributions of 22 exploited fish stocks that are highly important to fisheries in the northeast Pacific region using the dynamic bioclimate envelope model (DBEM)[36,37]. The DBEM is a spatially-explicit biomass dynamic model. It is driven by changes in ocean conditions that are obtained from the Earth system model simulations described above. Variables of ocean conditions include temperature, dissolved oxygen concentration, salinity, sea ice extent, surface advection and net primary production. Variables for surface and bottom were applied to model pelagic and demersal species, respectively. The DBEM model simulates changes in annual average biomass and catch potential of marine fishes and invertebrates on a 0.5° latitude × 0.5° longitude grid of the world ocean. Movement of adults and pelagic larvae is calculated by sets of advection and diffusion equations with diffusion rates vary according to gradients of environmental suitability for each modelled species and ocean currents[36]. Fishing mortality (F) was set at the level to achieve maximum sustainable yield (MSY). The projected annual catch for each species is hereafter termed maximum catch potential.

Identifying MHWs in the northeast Pacific. To identify MHWs, we calculated anomalies between the SST simulated by each of the individual 10 ensemble members and the ensemble-averaged SST (Fig. 2). First, for each ensemble member simulation, we calculated the annual average SST in each of the three LMEs within the northeast Pacific region (as defined in Fig. 1) from 1950 to 2100 (blue line in Fig. 2a). Second, for each year, we calculated the average SST across the temperatures simulated from the 10 ensemble members; i.e. the ensemble-averaged SST (black line in Fig. 2a). Third, we applied a cubic spline (using the R function "smooth.spline" with smoothing parameter = 0.6) to the ensemble mean SST to further minimize the contribution of changes in temperature due to internal variability (orange line in Fig. 2a). Thus, the resulting SST series show the long-term changes in mean conditions only. For each LME in the northeast Pacific region, we identified MHWs as the positive temperature anomalies that were above the 95th percentile of temperature anomalies from 1950 to 2100 (red line in Fig. 2a). For every MHW identified from each ensemble member, we characterized its magnitude (SST anomalies relative to the smoothed ensemble mean values) and occurrence year.

Modelling ecological responses to MHWs. We included a total of 22 fish species that were reported in the fisheries statistics in the northeast Pacific region (www.seaaroundus.org). These species were important to fisheries in this region as they contributed up to 80% of the total observed catches from 2006 to 2015 (www.seaaroundus.org). We calculated four impact indicators to examine the ecological responses of fish stocks and their implications for fisheries during a MHW. These indicators are: (1) total biomass, (2) latitudinal centroid (average of the coordinates of grid cell weighted by the species' biomass), (3) depth centroid (average of bathymetry of grid cell weighted by the species' biomass), and (4) maximum catch potential (catch at $F = F_{MSY}$). We used outputs from DBEM to calculate these indicators for each LME. Since the projected relative changes in biomass and maximum catch potential are similar, we presented simulation outputs for changes in biomass only.

For each of the four impact indicators, we calculated the annual anomalies with procedures similar to those applied to SST (Fig. 2). Firstly, we applied DBEM to simulate changes in spatial distribution of biomass and catches from 1950 to 2100 under changes in ocean conditions projected from each of the 10 Earth system model ensemble members (blue line in Fig. 2b). Secondly, for each year, we calculated the average values simulated from the 10 ensemble members (black line in Fig. 2b) and smoothed the averaged series with a cubic spline filter (orange line in Fig. 2b). We then calculated the annual anomalies of each impact indicator from the difference between each ensemble member simulation and the detrended series. Finally, we recorded the ensemble member-specific annual indicator anomalies in the year when the temperature anomalies had been characterized as MHWs (red bars in Fig. 2b). We focused on analyzing the simulated impact indicators from 1981 to 2100 to ensure that the detected signals are not due to model initialization during the early period of the simulation.

We tested the statistical significance of the effects of the occurrences of MHWs on the ecological impact indicators for exploited fish stocks in the northeast Pacific region using the glm function in R, with the occurrences of MHWs or non-MHW year as factor. The datasets for the information for accessing the projected temperature changes, MHWs and impacts on fish stocks are provided in the SI.

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References

1. Frölicher, T. L. & Laufkötter, C. Emerging risks from marine heat waves. *Nat. Commun.* **9**, 650 (2018).
2. Hughes, T. P. *et al*. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373 (2017).
3. Smale, D. A., Wernberg, T. & Vanderklift, M. A. Regional-scale variability in the response of benthic macroinvertebrate assemblages to a marine heatwave. *Mar. Ecol. Prog. Ser.* **568**, 17–30 (2017).
4. Wernberg, T. *et al*. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Chang.* **3**, 78 (2013).
5. Collins, M. *et al*. *Extremes, Abrupt Changes and Managing Risks*. (2019).
6. Pershing, A. J., Mills, K. E., Dayton, A. M., Franklin, B. S. & Kennedy, B. T. Evidence for adaptation from the 2016 marine heatwave in the Northwest Atlantic Ocean. *Oceanography* **31**, 152–161 (2018).
7. Caputi, N. *et al*. Management adaptation of invertebrate fisheries to an extreme marine heat wave event at a global warming hot spot. *Ecol. Evol.* **6**, 3583–3593 (2016).
8. Li, L. *et al*. Subregional differences in groundfish distributional responses to anomalous ocean bottom temperatures in the northeast Pacific. *Glob. Chang. Biol.* **25**, 2560–2575 (2019).
9. Yang, Q. *et al*. How "The Blob" affected groundfish distributions in the Gulf of Alaska. *Fish. Oceanogr.* **28**, 434–453 (2019).
10. Reed, D. *et al*. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nat. Commun.* **7**, 13757 (2016).
11. Bindoff, N. L. *et al*. *Changing Ocean, Marine Ecosystems, and Dependent Communities*. (2019).
12. Jones, T. *et al*. Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophys. Res. Lett.* **45**, 3193–3202 (2018).
13. Oliver, E. C. J. *et al*. Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* **9**, 1324 (2018).
14. Frölicher, T. L., Fischer, E. M. & Gruber, N. Marine heatwaves under global warming. *Nature* **560**, 360–364 (2018).
15. Darmaraki, S. *et al*. Future evolution of Marine Heatwaves in the Mediterranean Sea. *Clim. Dyn.* **53**, 1371–1392 (2019).
16. Bond, N. A., Cronin, M. F. & Freeland, H. & Mantua, N. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.* **42**, 3414–3420 (2015).
17. Laufkötter, C., Frölicher, T. L. & Zscheischler, J. High-impact marine heatwaves attributable to human-induced global warming (under review). *Science (80-)*.

18. Brodeur, R. D., Auth, T. D. & Phillips, A. J. Major Shifts in Pelagic Micronekton and Macrozooplankton Community Structure in an Upwelling Ecosystem Related to an Unprecedented Marine Heatwave. *Front. Mar. Sci.* **6**, 212 (2019).
19. Cavole, L. M. *et al*. Biological impacts of the 2013–2015 warm-water anomaly in the northeast Pacific: Winners, Losers, and the Future. *Oceanography* **29**, 273–285 (2016).
20. Leising, A. W. *et al*. State of the California Current 2014–15: Impacts of the Warm-Water "Blob". *Calif. Coop. Ocean. Fish. Investig. Reports* **56** (2015).
21. Whitney, F. A. Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific. *Geophys. Res. Lett.* **42**, 428–431 (2015).
22. Yang, B., Emerson, S. R. & Peña, M. A. The effect of the 2013–2016 high temperature anomaly in the subarctic Northeast Pacific (the "Blob") on net community production. *Biogeosciences* **15**, 6747–6759 (2018).
23. Santora, J. A. *et al*. Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem. *Mar. Ecol. Prog. Ser.* **580**, 205–220 (2017).
24. NOAA. New Marine Heatwave Emerges off West Coast, Resembles 'the Blob'. Available at: https://www.fisheries.noaa.gov/feature-story/new-marine-heatwave-emerges-west-coast-resembles-blob (2019).
25. Earl, E. Stock decline leads to historic shutdown for Gulf P-cod. *Alaska Journal of Commerce* (2019).
26. O'Connor, M. I. *et al*. Strengthening confidence in climate change impact science. *Glob. Ecol. Biogeogr.* **24**, 64–76 (2015).
27. Cheung, W. W. L., Brodeur, R. D., Okey, T. A. & Pauly, D. Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Prog. Oceanogr.* **130**, 19–31 (2015).
28. Gattuso, J.-P. *et al*. Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios. *Science (80-).* **349**, aac4722 (2015).
29. Portner, H. O. *et al*. Ocean systems. in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (eds. Field, C. B. *et al*.) 1–138 (2014).
30. Weatherdon, L. V., Ota, Y., Jones, M. C., Close, D. A. & Cheung, W. W. L. Projected scenarios for coastal First Nations' fisheries catch potential under climate change: management challenges and opportunities. *Plos One* **11**, e0145285 (2016).
31. Morley, J. W. *et al*. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *Plos One* **13**, e0196127 (2018).
32. Pauly, D. *et al*. Fisheries in large marine ecosystems: descriptions and diagnoses. *UNEP large Mar. Ecosyst. Rep. a Perspect. Chang. Cond. LMEs World's Reg. Seas. UNEP Reg. Seas Reports Stud*. 23–40 (2008).
33. Dunne, J. P. *et al*. GFDL's ESM2 global coupled climate-carbon Earth System Models. Part I: Physical formulation and baseline simulation characteristics. *J. Clim.* **25**, 6646–6665 (2012).
34. Rodgers, K. B., Lin, J. & Frölicher, T. L. Emergence of multiple ocean ecosystem drivers in a large ensemble suite with an earth system model. *Biogeosciences* **11**, 18189–18227 (2015).
35. Dunne, J. P. *et al*. GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part II: Carbon System Formulation and Baseline Simulation Characteristics. *J. Clim.* **26**, 2247–2267 (2013).
36. Cheung, W. W. L., Lam, V. W. Y. & Pauly, D. Dynamic bioclimate envelope model to predict climate-induced changes in distribution of marine fishes and invertebrates. in *Modelling Present and Climate-shifted Distributions of Marine* Fishes *and Invertebrates* (eds. Cheung, W. W. L., Lam, V. W. Y. & Pauly, D.) **16(3)**, 5–50 (University of British Columbia, 2008).
37. Cheung, W. W. L. *et al*. Structural uncertainty in projecting global fisheries catches under climate change. *Ecol. Modell.* **325**, 57–66 (2016).
38. Checkley, D. M. Jr. & Barth, J. A. Patterns and processes in the California Current System. *Prog. Oceanogr.* **83**, 49–64 (2009).
39. Lindegren, M., Checkley, D. M., Rouyer, T., MacCall, A. D. & Stenseth, N. C. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Natl. Acad. Sci.* **110**, 13672–13677 (2013).
40. Tseng, Y.-H., Ding, R. & Huang, X. The warm Blob in the northeast Pacific—the bridge leading to the 2015/16 El Niño. *Environ. Res. Lett.* **12**, 54019 (2017).
41. Barange, M. *et al*. *Impacts of climate change on fisheries and aquaculture*. (United Nations' Food and Agriculture Organization, 2018).
42. Miller, D. D., Ota, Y., Sumaila, U. R., Cisneros-Montemayor, A. M. & Cheung, W. W. L. Adaptation strategies to climate change in marine systems. *Glob. Chang. Biol.* **24**, e1–e14 (2018).
43. Pershing, A. J. *et al*. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science (80-)* **350**, 809–812 (2015).
44. Bindoff, N. L. *et al*. Detection and attribution of climate change: from global to regional. in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the INtergovernmental Panel on Climate Change* (Cambridge University Press, 2013).
45. Turi, G. *et al*. Response of O2 and pH to ENSO in the California Current System in a high-resolution global climate model. *Ocean Sci.* **14**, 69–86 (2018).
46. Laufkötter, C. *et al*. Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences* **12**, 6955–6984 (2015).
47. Vancoppenolle, M. *et al*. Future Arctic Ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent mechanisms. *Global Biogeochem. Cycles* **27**, 605–619 (2013).
48. Lancelot, C. *et al*. Spatial distribution of the iron supply to phytoplankton in the Southern Ocean: a model study. *Biogeosciences* **6**, 2861–2878 (2009).
49. Le Fouest, V., Babin, M. & Tremblay, J. E. The fate of riverine nutrients on Arctic shelves. *Biogeosciences* **10**, 3661–3677 (2013).
50. Luoto, M., Pöyry, J., Heikkinen, R. K. & Saarinen, K. Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Glob. Ecol. Biogeogr* **14**, 575–584 (2005).
51. Araujo, M. B. & Guisan, A. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **33**, 1677–1688 (2006).
52. Cheung, W. W. L., Pauly, D. & Sarmiento, J. L. How to make progress in projecting climate change impacts. *ICES J. Mar. Sci. J. du Cons* **70**, 1069–1074 (2013).
53. Griffies, S. M. *et al*. Problems and prospects in large-scale ocean circulation models. *Proc. Ocean* **9**, 410–431 (2009).
54. Riahi, K. *et al*. RCP 8.5-A scenario of comparatively high greenhouse gas emissions. *Clim. Change* **109**, 33–57 (2011).
55. Pauly, D., Zeller, D. & Palomares, M. D. *Sea Around Us Concepts, Design and Data* (www.seaaroundus.org). (2020).

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Author contributions

Both W.L.C. and T.L.F. contributed to the conception and design of the work, the acquisition, analysis and interpretation of data, and the writing of the manuscript. W.L.C. conducted the study as a visiting scholar at the Oeschger Centre for Climate Change Research and the Climate and Environmental Physics Division of the Physics Institute of the University of Bern, Bern, Switzerland.

Competing interests

The authors declare no competing interests.

Additional information

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