Received: 24 January 2023 | Revised: 5 July 2023 | Accepted: 11 July 2023

DOI: 10.1111/faf.12783

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Biological life-history and farming scenarios of marine aquaculture to help reduce wild marine fishing pressure

Halley E. Froehlich[1,2] | Jamie C. Montgomery[3] | David R. Williams[4] | Casey O'Hara[3,5] | Caitlin D. Kuempel[6,7] | Benjamin S. Halpern[3,5]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California, USA

[2]Environmental Studies, University of California, Santa Barbara, California, USA

[3]Bren School of Environmental Science and Management, University of California, Santa Barbara, California, USA

[4]Sustainability Research Institute, School of Earth and Environment, University of Leeds, Leeds, UK

[5]National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California, USA

[6]Australian Rivers Institute, School of Environment and Science, Griffith University, Nathan, Queensland, Australia

[7]Coastal and Marine Research Centre, Griffith University, Nathan, Queensland, Australia

Correspondence
Halley E. Froehlich, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA.
Email: hefroehlich@ucsb.edu

Funding information
Zegar Family Foundation, 'Anticipating Climate Change Impacts on Ocean Aq

Abstract

Aquaculture (freshwater and marine) has largely supplemented fisheries, but in theory could help reduce fishing pressure on wild stocks. Although not the sole factors, some potential benefits depend on aquaculture pressures on fished species, including collection of wild 'seed' material—earlier to later life stages—for rearing in captivity and the capacity of aquaculture to increase. Here we first classify 203 marine (saltwater and brackish) animal species as being produced by either open-cycle *capture-based aquaculture* (*CBA*) or closed-cycle *domesticated aquaculture* (*DA*)—based on their likely reliance on wild seed—and assess the extent to which these forms of aquaculture could support seafood production and greater wild biomass. Using a data-limited modelling approach, we find evidence that current aquaculture practices are not necessarily helping reduce fishing to sustainable levels for their wild counterparts—consistent with emerging scientific research. However, if some wild capture species (87 equivalent spp.) were instead produced through CBA, almost a million extra tonnes could theoretically be left in the wild, without reducing seafood production. Alternatively, if reliance on wild seed inputs is further reduced by shifting to DA production, then a little less than doubling of aquaculture of the overexploited species in our study could help fill the 'production gap' to support fishing at maximum sustainable levels. While other ecological (e.g. escapes), social and economic considerations (e.g. market substitution) are important, we focused on a critical biological linkage between wild fisheries and aquaculture that provides another aspect on how to improve management alignment of the sectors.

KEYWORDS
ecosystem-based management, food security, integrated systems, MSY, sustainable development

1 | INTRODUCTION

Seafood from freshwater and marine systems is an essential part of global food security, providing an important source of protein and micronutrients for billions of people (FAO, 2020b; Golden et al., 2021; Hicks et al., 2019). For centuries, wild marine fisheries contributed the majority of global seafood supply, but now aquaculture is set to be the dominant aquatic production system for years to come, with freshwater aquaculture accounting for the majority (ca. 60%) of global production (FAO, 2020b). While some hoped farming would relieve fishing pressure on wild stocks (Anderson, 1985; Pomeroy et al., 2006), there is sparse evidence that the rapid growth of aquaculture globally has affected harvested populations (Cottrell et al., 2021; Diana, 2009; Longo et al., 2019). Instead, most recoveries of wild-fishery stocks can be attributed to improved management, rather than the meeting of demand through aquaculture (Anderson et al., 2019; FAO, 2020d; Hilborn et al., 2020; Hilborn & Ovando, 2014). If aquaculture is mentioned in a fisheries-management context, it is typically in relation to stock enhancement of wild populations through hatchery release efforts (e.g. Bostock et al., 2010; Lorenzen et al., 2021; Teletchea, 2017). Aquaculture has instead largely increased seafood supply, allowing global per capita consumption of aquatic protein to more than double in the last six decades, while total wild capture production has remained relatively stable (FAO, 2020b).

Although aquaculture is more often evaluated as an alternative or competing mode of seafood production to wild capture, the two systems are inherently linked, not only because they both meet demand for seafood, but also because numerous aquaculture species still rely on wild fisheries for feed (Alder et al., 2008; Froehlich, Jacobsen, et al., 2018) and seed (i.e. certain life stages captured in the wild for subsequent rearing in captivity) (Ottolenghi, 2008; Ottolenghi et al., 2004; Teletchea, 2015). A number of studies have investigated the ecosystem and conservation consequences of harvesting wild forage fish (e.g. herring, sardine, anchovy) for animal feed (Essington et al., 2015; Koehn et al., 2016; Pikitch et al., 2014; Smith et al., 2011), but far fewer have quantified the impacts of exploiting wild stocks for aquaculture brood stock and grow out (Ottolenghi, 2008; Ottolenghi et al., 2004; Teletchea, 2015). While some approaches of extraction on older stages can more likely add pressure on wild populations, for example, 'tuna ranching' (Lovatelli & Holthus, 2008; Teletchea, 2015; Volpe et al., 2013), others may have lower impacts because seed is taken at earlier life stages, before higher natural mortality occurs. Determining how and when different types of aquaculture alleviate or exacerbate pressures on wild stocks is a vital question for sustainable food production and more holistic management strategies. We also pay particular attention to life-history traits given they are highly influential at determining population resilience of wild species (Capdevila et al., 2022).

Aquaculture production can be generally classified as *capture-based aquaculture* (CBA) or *domesticated aquaculture* (DA), which differ based on whether they use wild 'seed' material (Figure 1), from earlier life stages to adults (Teletchea, 2015; Teletchea & Fontaine, 2014). CBA represents open-cycle practices where the cultivation of species relies on wild inputs, typically of earlier life stages, which are taken from the wild then raised to harvestable sizes (i.e. grow out; Teletchea levels 1–3). Earlier life stages (i.e. larvae and juveniles/subadults) of most aquatic species typically have higher natural mortalities (Figure 1). If CBA reduces mortality in earlier life stages post-capture, compared to wild populations, it theoretically allows the same level of production with lower impact on wild stocks compared to fisheries, which almost entirely target larger, older individuals that have survived the bulk of such stage-specific mortality (Barnett et al., 2017; Jørgensen & Holt, 2013; Lorenzen, 2000) (Figure 1). Alternatively, DA—also known as hatchery-based aquaculture (FAO, 2001)—refers to species that have fully closed production cycles, with aquaculture itself producing seed for new generations (Lovatelli & Holthus, 2008; Teletchea, 2015; Teletchea & Fontaine, 2014) (Figure 1; Teletchea levels 4–5). Completely decoupling production from wild stocks means that DA potentially provides both a means to increase production without impacting wild stocks through seed collection and a way to compensate for reduced catches, for example, from stock collapses or production gaps due to the implementation of more sustainable harvest control rules (Costello et al., 2016; Stoeckl et al., 2017; Walsh et al., 2018). A necessary first step in evaluating the potential impacts and benefits of aquaculture is therefore to identify which species are potentially produced by CBA compared to DA. However, there has been no comprehensive evaluation beyond finfish (*see* Teletchea, 2015, 2019).

Here we provide a global classification of marine (saltwater and brackish) aquaculture animals as likely produced by CBA or DA and

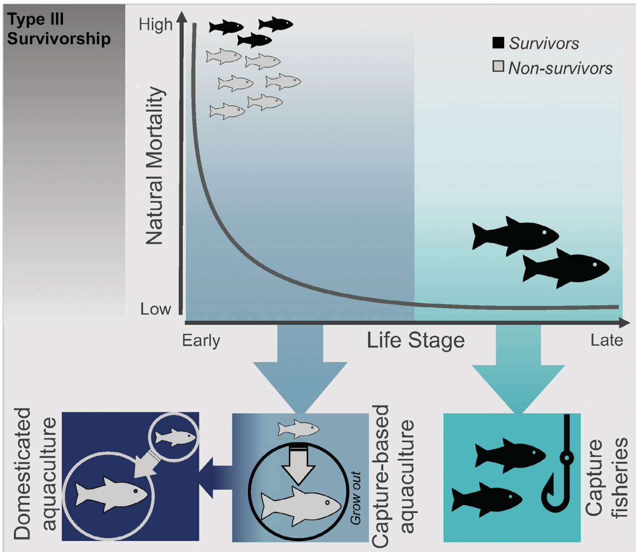

FIGURE 1 Conceptual model of *Type III survivorship* and generalized relationship with wild capture fisheries, capture-based aquaculture (CBA) and domesticated aquaculture (DA). *Non-survivors* (*grey*) are the proportion of the earlier life-stage wild population which *would have* succumbed to natural mortality but instead are collected and used in capture-based aquaculture grow out. *Survivors* (*black*) are the proportion of the wild population which reach older and larger adult stages and are typically targeted by wild capture commercial fisheries. Domesticated aquaculture, depicted in *dark blue*, originates from *CBA*, but eventually the life cycle is fully closed and thus no longer relies on wild life stages to 'seed' grow out. Note, for some species, smaller numbers of older, mature individuals can be captured for egg and sperm collection. This may result in mortality, but collection of earlier life-stage 'seed' material means that much early mortality is avoided, supporting the depicted generalized framework (*see* Methods for details).

simulate two potential scenarios of increased production of these forms of aquaculture to better align in helping wild caught species and food security. We focused on marine species because they account for the vast majority of fisheries landings (FAO, 2020b) and are important contributions to overall seafood production (Costa-Pierce et al., 2021; Pernet & Browman, 2021). First, we categorized 203 farmed marine species (104 finfish, 76 molluscs and 23 crustaceans) as produced through either CBA or DA, based on a probability-threshold model guided by previously published domestication criteria (Teletchea, 2015; Teletchea & Fontaine, 2014). While we simplify the differentiation between the two forms, it is important to note aquaculture and fisheries lie on a spectrum and the data limitations of most species preclude absolute certainty in farming designation in a given region, especially transitional phases using both wild and hatchery seed (Klinger et al., 2013; Olesen et al., 2015; Teletchea, 2019; Teletchea & Fontaine, 2015). Next, to explore where aquaculture may help relieve fishing pressure on wild caught species we used a data-limited approach to match and compare current aquaculture with wild caught production trends (FAO, 2020a) and regional stock status of the same wild species (Rosenberg et al., 2014, 2018). Finally, focusing on the most overexploited stocks according to the data-limited model, we simulated the potential benefits of aquaculture for fisheries conservation and food security by (1) evaluating when CBA production could help achieve sustainable management of wild populations by replacing some wild caught production; and (2) assessing the degree to which DA could provide a buffer against production losses if fisheries reform were to be implemented for the overexploited regional stocks in this study.

2 | MATERIALS AND METHODS

2.1 | Classification of species

To assess the potential for aquaculture to affect fisheries management we first classified the type of aquaculture cultivation (CBA or DA) for all marine species of interest (Table S1). We used the criteria developed by Teletchea and Fontaine (2014) as the primary approach to identify and model whether species were produced by CBA (reliant on wild seed) versus DA (no wild seed required). These criteria focus on quantity and longevity of annual production since 1950 to predict status, with greater tonnage and a longer history of production assumed to equate to a species being more likely to be domesticated. We used three production durations to categorize species: <5, 5–10 and >10 years. We classified species as produced by CBA if global production had occurred for collectively fewer than 5 years or if the species is a grouper, tuna, eel, yellowtail or mussel—species groups currently unlikely to be produced by DA due to cost, quality and/or challenges to close the life cycle (Kamermans & Capelle, 2019; Lovatelli & Holthus, 2008; Nakada, 2008; Ottolenghi, 2008; Ottolenghi et al., 2004; Wegner et al., 2018). This assumption is not to imply that these groups of species cannot transition from CBA to DA, but rather that CBA is still more common due to documented bottlenecks in the sector (e.g. technology and knowledge transfer) (Galparsoro et al., 2020; Jones et al., 2015; Kumar et al., 2018). In addition, we classified species as CBA if production has occurred for more than a total of 5 years, but production is below a threshold of 2900 tonnes annually and is declining over time. This threshold was derived from a logistic generalized linear model that predicted the probability that a species is produced via DA given the level of production, based on the qualitative categorization from Teletchea and Fontaine (2014) for finfish (Figure S1); the 2900-tonne threshold was where the predicted probability of a (finfish) species being DA reached greater than 50%, on average. If a species was collectively produced between 5 and 10 years and had either an increasing production trend or production levels above 2900 tonnes, we checked the status against primary and grey literature. We classified the remainder of species with production longevity greater than 10 years and 2900 thousand tonnes of global production per year as DA. Geoduck and abalone were designated as DA due to known wild seed limitations (Roodt-Wilding, 2007; Viet Le, 2016). Note, using finfish as the baseline to inform the threshold model approach may result in some misclassification for other taxonomic groups. However, we have tried to correct where necessary for some of the more well-documented cases.

2.2 | Species matching and catch-MSY

We matched aquaculture and wild capture production by individual species. Nearly all species of interest are data limited or yet to be assessed, with only 7% in the RAM Legacy Stock Assessment Database (Ricard et al., 2012) (Table S1), meaning that we were unable to use fisheries reference points from formal stock assessments to determine the state of the wild stocks. We therefore followed other data-limited analyses and used the *catch-MSY* data-limited approach to assess FAO regional species stocks with at least 20 years of data and annual production above 1000 tonnes—the threshold for this modelling approach—resulting in 90 species and 143 regional stocks which we could model (Rosenberg et al., 2018). We applied the *catch-MSY* method (Martell & Froese, 2013; Rosenberg et al., 2018) that assumes a fish population (in our case, represented by a regional FAO fishing area) can be described by the Schaefer equation:

$$B_{t+1} = B_t + rB_t\left(1 - \frac{B_t}{K}\right) - C_t \tag{1}$$

where B is biomass at year $t+1$, r is the intrinsic population growth rate, K is carrying capacity and C is catch at year t. Catch data were input into the *catch-MSY* model using the *datalimited* package developed for R (Anderson et al., 2016) to estimate *MSY* and B/B_{MSY}. This version of *catch-MSY* is slightly modified by Rosenberg et al. (2014) to estimate biomass (B) and biomass reference points (B/B_{MSY}). We ran the model 100,000 times from an assumed uniform distributions of r and K, in accordance with previous studies (Anderson et al., 2016), to calculate median, upper (Q_{75}) and lower (Q_{25}) bounds for each species stock reference point. Subsequently, we estimated F/F_{MSY} based (where F is fishing mortality) on the functional properties of the Schaefer equation, where $MSY=0.25rK$, $B_{MSY}=0.5K$ and $F_{MSY}=0.5r$. We treated regional stocks as *overfished* if median $B/B_{MSY}<1$ and those experiencing *overfishing* when median $F/F_{MSY}>1$. Collectively, we referred to a stock as *overexploited* if they were both overfished *and* experiencing overfishing, as defined. We then used data-limited model outputs to assess if species with aquaculture, CBA or DA, tend to be more or less overexploited, assuming that if aquaculture was relieving fishing pressure there should hypothetically be more sustainable stocks, on average.

Data-limited approaches have been found to be imprecise and biased when estimating biomass (Free et al., 2020; Ovando et al., 2022; Walsh et al., 2018). More robust stock-status estimates of the species evaluated here would require formal stock assessments, especially at a local level; however, the method is reasonably suited for estimating *MSY* (Ovando et al., 2022). Nearly all species in this study are not formally assessed—which is notable in and of itself—so we performed a qualitative, semi-validation approach for the regional stocks categorized as *overexploited* (median $B/B_{MSY}<1$ and $F/F_{MSY}>1$; $N=73$) by looking through scientific literature and reports for any evidence of overfishing or overfished status, documented declines of concern, and/or depressed recovery of stocks of the regional species. Not surprisingly, strength of evidence varied, but we were able to find at least five of the 73 *catch-MSY* identified *overexploited* (7%) regional stocks were not in fact overfished or experiencing overfishing (Table S2). Additionally, we found 15 regional stocks with potential (e.g. overfishing reported as common in a given region) or no evidence (21%) and 53 (73%) with some evidence of negative fishing impacts (Table S2). The five regional stocks with clear contradictory evidence were not included in our overexploited analyses (i.e. MSY scenario). While our approach provides some validation measures, it is not a substitute for more rigorous assessments. Ultimately, the data-limited wild capture outputs provide a means to simulate our marine aquaculture scenarios to draw generalized conclusions about coordinating marine aquaculture and wild capture management based on species life history and farming practices.

2.3 | Capture-based aquaculture replacement scenario

To test the full scope of CBA to keep more biomass in the wild for a given fished cohort, compared to typical fishing methods of the same species, we simulated the replacement of all country-level catches of 87 identified CBA species reported in 2016 with CBA production (FAO, 2020a). Such an approach tests the feasibility (i.e. countries with and without CBA) and potential savings (tonnage) of pursuing such replacement. Note, we did not limit our calculations to overexploited CBA stocks due to the much smaller sample size ($n=38$).

Potential biomass spared (i.e. remains in the wild) by CBA, compared to traditional fishing, in a given time period (fishing year) for a specific species can be calculated using the following equation, an expanded method of Volpe et al., 2013, assuming differing stage-specific mortalities:

$$L_{\text{current}} = \left(C - Cm_l\right) + \frac{P\left(1 - m_e\right)\left(1 - m_l\right)}{S} \tag{2}$$

$$T = P + C \tag{3}$$

$$L_{\text{replace}} = \frac{T\left(1 - m_e\right)\left(1 - m_l\right)}{S} \tag{4}$$

$$\tau = L_{\text{current}} - L_{\text{replace}} \tag{5}$$

where tonnage (τ) left in the wild is a function of amount of loss (L) due to current CBA production (P), total catch (C), stage-based natural mortality ($m_{e\text{ or }l}$, e=earlier stage, l=later stage) and post-capture aquaculture survival (S) prior to harvest (where $S>0$). Total production (T) is the summation of catch and aquaculture. Thus, we adjusted both aquaculture and wild capture extraction relative to losses from earlier and/or later-stage natural mortality. Note, we accounted for an additional time-step of later-stage natural mortality (m_l) for aquaculture under the assumption that this is more comparable to the catch tonnage because earlier stages need to grow to harvestable sizes. Production and catch were based on country FAO 2016 estimates in tonnes (FAO, 2020a).

We collected natural mortalities for each aquaculture species in two ways. First, for finfish, we compiled life-history parameters using the FishLife package in *R* (Thorson et al., 2017), including asymptotic length (L_∞), von Bertalanffy growth coefficient (*K*), maximum age (t_{max}) and natural mortality (*M*; discrete). Second, for crustaceans and molluscs we used SeaLifeBase (Palomares & Pauly, 2019) to extract the same life-history parameters; although only 14 species (all molluscs) had *M* values. If *M* was missing, we estimated it using the following equations (Then et al., 2015):

$$M = 4.899\, t_{max}^{-0.916} \quad (6)$$

$$M = 4.118 K^{0.73} L_\infty^{-0.33} \quad (7)$$

We used the more accurate t_{max}-based estimator (Equation 6) where possible, otherwise we used the growth-based method (Equation 7). For the 38 species where no information was available, we used the average of the associated ISSCAAP group.

Natural mortality and survival are notoriously challenging to estimate regardless of stage or age-based assumptions (e.g. Maunder et al., 2023; Punt et al., 2021). To capture the savings reflected in the time of harvest between CBA versus typical fishing we assumed a *Type III* survivorship relationship, the common association reported in the literature (Barnett et al., 2017; Jørgensen & Holt, 2013; Lorenzen, 1996, 2000) (Figure 1), by increasing discrete natural mortality by 0.2 for earlier life stages. The increase in mortality is conservative (Lorenzen, 1996), influenced by the conventional assumption commonly made when natural morality is unknown for a given stock (i.e. $M \sim 0.2\,\text{year}^{-1}$) (Punt et al., 2021). We held natural mortalities constant for tuna species, which we assumed were captured for CBA at later life stages (i.e. 'ranching'). Post-capture survival data are also sparse, but can range between 20% and 95%, when available (Buentello et al., 2016; Engle et al., 2017; FAO, 2020c, 2020d; Humborstad et al., 2016; Masuma et al., 2008, 2011). Assuming adoption and use of practices supporting better survival than random chance (50%) and reflective of the overall improved survivorship reported in the literature, we randomly sampled across a uniform range of 50%–90% for our simulations.

With this information, we ran the CBA replacement scenario 10,000 times and report the median, upper (Q_{75}) and lower (Q_{25}) bounds of the outputs. With these outputs, we further explored the relationship between per cent wild biomass spared and discrete earlier life-stage mortality, the most pertinent life-history trait for comparing CBA and fishing.

In addition to 'ranching', older mature individuals can also be captured for brood stock to either remain in captivity for repeated spawns, milked and released, or fully stripped resulting in direct mortality. Even though some adults are captured, the eggs and sperm are the 'seed' material for production, thus still consistent with the generalized framework depicted in Figure 1. While the exact technique for any given regional stock cannot be determined, the number of adult individuals taken for initial spawning is typically orders of magnitude smaller than wild capture fishing and does not necessarily occur on an annual basis. Our generalized model therefore still provides a plausible understanding of CBA's potential. That said, in order to test the sensitivity of our model to natural mortality values, we also ran the CBA scenario assuming all species have later stage, thus lower mortality levels across the board (vs. the 0.20 adjusted described above) and compared the results.

2.4 | Domesticated aquaculture production gap scenario

We next simulated the feasibility of using DA to allow reform of potentially overexploited wild stocks. Theoretically, DA production could 'replace' all wild production without the trade-offs of CBA because it is not reliant on wild seed. However, given that wild fisheries are socially and culturally significant, this is unlikely to be politically or economically desirable, so we instead focused on only those fisheries that need reform. This more constrained DA consideration also better highlights a trade-off of fisheries reform: production gaps may open after implementation of new harvest control rules and strategically using DA to offset that production loss is a new way of thinking about the intersection of fisheries and aquaculture.

We compared three scenarios of wild and farmed production of the 50 overexploited species (across 68 regional stocks) in our dataset. First, we summed current landings from potentially overexploited stocks (2016) and compared that to all aquaculture production of the same species. We combined CBA and DA here because all full domestication starts as capture based. For these scenarios, we thus assume either all of these species become completely domesticated (currently 30 are CBA, and 20 DA) or more generalized DA production (e.g. 'white fish') replaces the wild supply. Second, we assessed how much DA would have to increase to fill the lost production if a moratorium was to be placed (temporarily or permanently) on all the overexploited fisheries' stocks. Third, we calculated the amount of DA needed to replace lost production if all fishing is restricted to MSY. Lastly, we further investigated the importance of the production gap by combining the latter two fishery management approaches (a 1-year moratorium and fishing at MSY thereafter) in a simple 50-year surplus-production simulation (based on estimated *catch-MSY* Schaefer parameters). This allowed us to explore how long, under the best-case scenario (e.g. 100% compliance, no extreme environmental variability or regime shifts), it takes to recover the overexploited stocks to ecologically sustainable levels (B/B_{MSY} >1).

It is important to note that we applied simplified methodologies to assess proximal biomass savings and recoveries. A more accurate and detailed approach would require assessing population dynamics, including stock structure (e.g. age or size) and possibly other context-dependent abiotic (e.g. physical forcing) and biotic (e.g. predators) ecosystem factors. However, our approach allows broad patterns in species and traits to be revealed, and highlights where more data are needed. We hope that this in turn will spur further collection of both the biophysical data required for more specific modelling and the socioeconomic data vital for translating recommendations into viable policies. All analyses were performed using *R v3.4.1* (R Core Team, 2018), colour palette *beyonce*.

3 | RESULTS AND DISCUSSION

3.1 | Current trends

The 203 marine aquaculture animal species, produced in 125 countries, accounted for ca. 17 million tonnes of production in 2016 (61% of marine animal aquaculture); the remaining marine cultured production was not categorized at the species level (i.e. 'not elsewhere included') and was thus excluded from the species-specific analyses (FAO, 2020b). As a result, the findings we report are likely conservative outcomes. Most species (137 spp.) have had some level of aquaculture production for at least a decade, with a median, non-consecutive time of production of 17 years ($Q_{25\%}=6.5$; $Q_{75\%}=36$). Only 61 of the 203 species we classified as produced through DA, but these accounted for 94% of all (2016) species-identifiable marine aquaculture production. Indeed three species—Manila clam (*Ruditapes philippinarum*, Veneridae), Whiteleg shrimp (*Penaeus vannamei*, Penaeidae) and Atlantic salmon (*Salmo salar*, Salmonidae)—contributed to over half of total DA production, highlighting production gains from domestication that parallel patterns in the livestock and poultry sectors (Teletchea & Fontaine, 2014).

Next, we assessed whether the farmed marine species were also commercially fished and possibly overexploited. Of the 203 farmed species, 143 were also captured in wild caught fisheries, a number of which may be overexploited (Tables S1 and S2), accounting for a total of ca. 7 million tonnes in 2016 (12% of total marine wild capture). The data-limited model, paired with the qualitative, semi-validation effort, estimated 48% of the regional stocks as overfished and experiencing overfishing based on estimated biomass (*B*) and fishing mortality (*F*), where a stock is *overfished* when median stock biomass levels are less than maximum sustainable biomass (B/B_{MSY} <1) and is experiencing *overfishing* when fishing mortality is greater than maximum sustainable levels (F/F_{MSY} >1; Figure 2). Again, we define overexploited as species which are overfished *and* experiencing overfishing. Although these reference points allow us to explore certain theoretical scenarios here, they should be used with caution due to inherent imprecision and biases of the method previously highlighted (Free et al., 2020; Martell & Froese, 2013; Ovando et al., 2022). The majority of potentially overexploited species were finfish (60%) and CBA (60%) produced, which constitute the largest proportion of the respective groups (Table S1). That said, species with DA counterparts appeared to experience overexploitation levels as well.

The potentially overexploited status of most of the wild species we assessed would suggest that aquaculture production independent of fisheries management does not necessarily lead to sustainable fishing levels, consistent with other recent studies (Cottrell et al., 2021; Longo et al., 2019). However, we cannot definitively say whether aquaculture unlinked from fisheries management does or does not relieve fishing pressure on wild species. In addition to the inherent bias of the data-limited approach, we also lack a robust counterfactual—incorporating the complex market and social dimensions of fisheries and food demand—to determine the level of fishing in the absence of aquaculture (Diana, 2009). Despite the absent counterfactual, our results suggest that aligning aquaculture policy and practice with fisheries management would likely be more effective than relying on passive replacement of wild capture fisheries.

3.2 | Replacement with capture-based aquaculture

In the first scenario, we explored the results of completely replacing current landings of wild caught CBA species for a given year with the same tonnage of the same species (87 spp.), but solely produced through CBA. The simplified scenario thus assumed fisheries management only permits collection of earlier life stages for most species for the purpose of controlled grow out of these species. After accounting for natural mortality, we found that, for these 87 species, approximately 29% ($Q_{range}=18\%–37\%$) of currently fished tonnage could remain in the ocean with no loss of production. This equates to an additional 714,000 tonnes ($Q_{25}=438{,}000$, $Q_{75}=921{,}000$) left in the wild (Figure 3), with 98% of species likely to see some level of positive median gain (range biomass spared = 1%–34%). The sensitivity

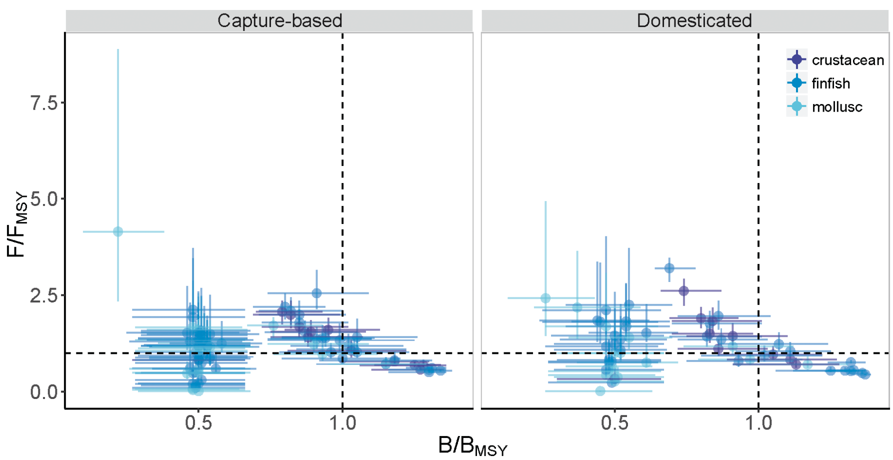

FIGURE 2 Median (plus 25% and 75% quartiles) FAO regional stock status (*MSY* = maximum sustainable yield, *B* = biomass, *F* = fishing mortality) of wild capture species that could be assessed using *catch-MSY* methods, relative to the classifications of species that can be produced by CBA (left) and DA (right).

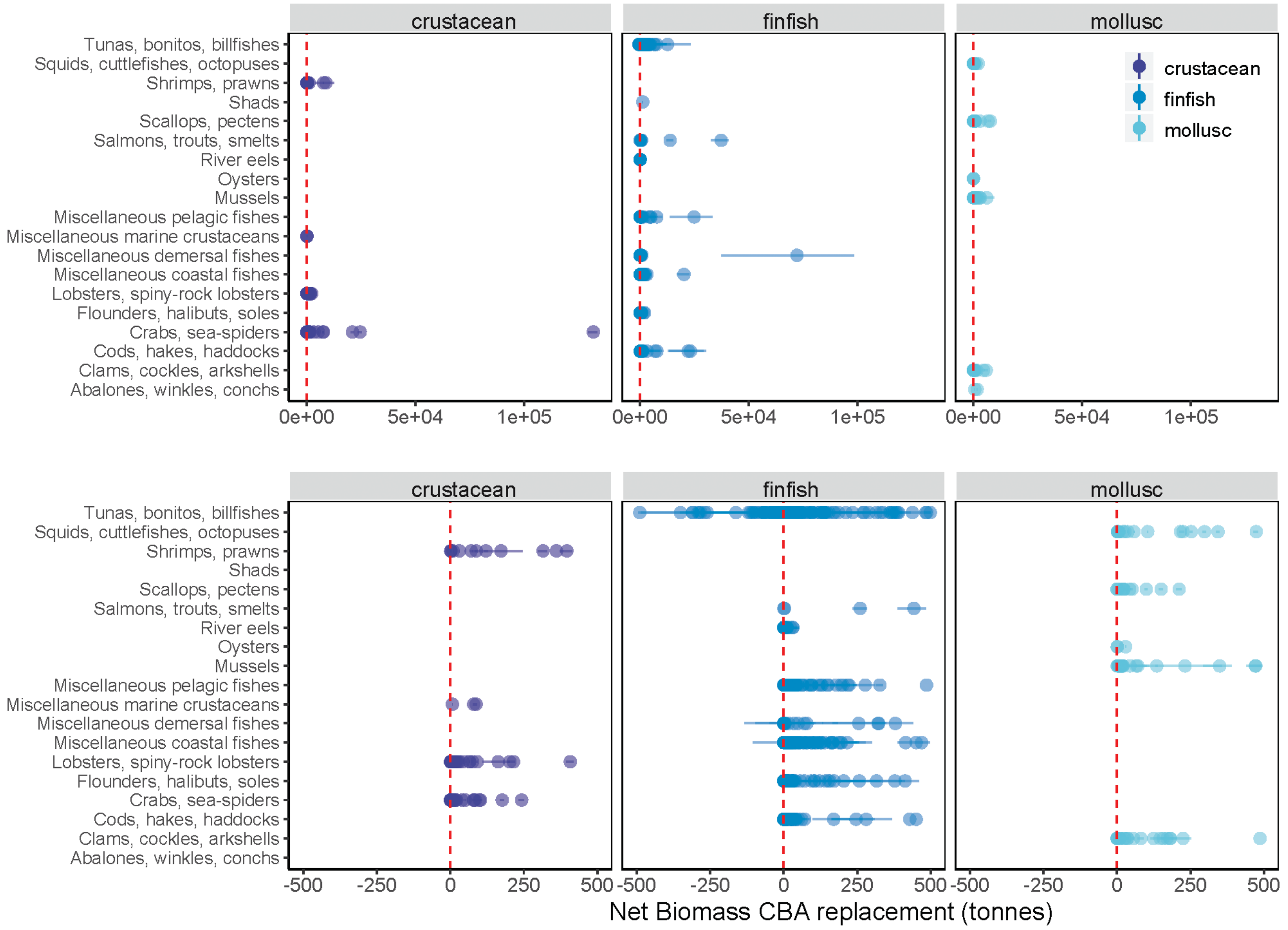

FIGURE 3 Median net biomass (tonnes) and lower and upper quartiles (25% and 75%) remaining in the wild for each species in a given FAO region and country if CBA replaces the equivalent wild landings for crustaceans (*purple*), finfishes (*blue*), and molluscs (*aqua*). *Bottom panels* are zoomed in results of *top panels*. *See Figure S2 for comparable sensitivity results.*

test of assuming later-stage mortality levels for CBA capture for all species produced comparable, though as expected, reduced beneficial outcomes (70% of species to likely see net positive gains; median = 302,000, Q_{25} = −42,000, Q_{75} = 561,000; Figures S2 and S3). Presently, 125 of the 159 countries which landed CBA species in the wild have not produced any of them through aquatic farming; this means that integrating CBA alongside national-scale fisheries management would require these countries to either begin aquaculture production or import seafood from other countries that do farm to fill the production gap—raising questions about the practicality and feasibility of this scenario. Indeed, landings are not only about direct food production, but also about livelihoods and culture, which would be affected under this scenario (Levine et al., 2015). Alternatively, if only the 35 countries practicing CBA replaced their fishing of these species with mariculture, then results would be more modest, but still positive (64,000 tonnes, Q_{25} = 29,000 Q_{75} = 91,000). Importantly, however, increasing extraction of seed for CBA without reducing wild capture fisheries simply increases fishing pressure on wild stocks, meaning that aligning aquaculture–fisheries policy and management is key to realizing the potential ecological benefits explored here, and, perhaps more importantly, accounting for the socioeconomic tradeoffs that may result, for example, Xuan & Armstrong, 2017.

Biomass savings were strongly dependent on earlier life-stage (discrete) natural mortality of the farmed CBA species: in aggregate, savings were projected to occur in all species with earlier life-stage natural mortality greater than 0.30, and peaking in those with mortalities of approximately 0.78 (Figure 4; df_2 = 769, p < .001, R^2_{adj} = 0.98). Similar thresholds were found in the later-stage natural mortality CBA sensitivity test (Figure S3; 0.30–0.65). This result is intuitive: harvesting earlier life stages before they experience the majority of natural mortality and growing them to maturity in a farm with lower mortality allows for much greater adult biomass to be produced from the same biomass of seed. Invertebrates, particularly crab species (m_{range} = 0.46–0.93), appeared to benefit the most based on relative tonnage spared versus catch (median 239,000 tonnes spared). Conversely, species which were not projected to benefit from CBA were those with lower natural mortality during the extraction stage for aquaculture, possibly exacerbated by lower post-capture survival. A notable example was Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae), an extremely high value species

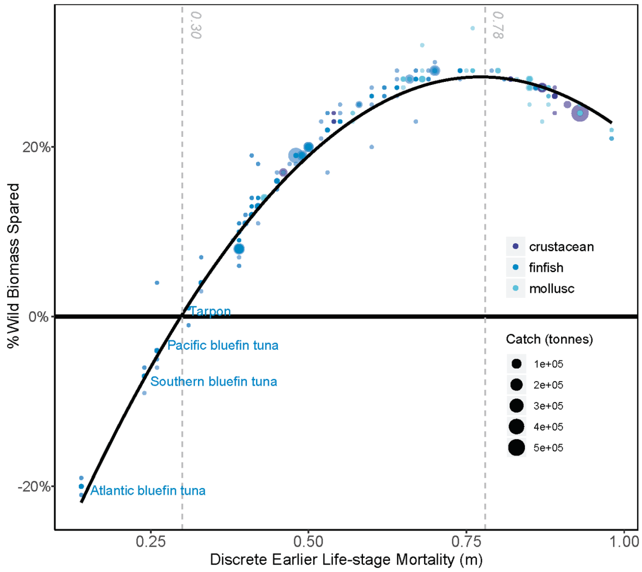

FIGURE 4 Average ($p < .001$, $R^2_{adj} = 0.98$) percent wild biomass spared versus discrete earlier life-stage (larvae and juveniles) mortality of all taxonomic groups: crustacean (*purple*), finfish (*blue*), and mollusc (*aqua*). Average limits for increasing percent biomass savings are depicted with *grey dashed lines*. Data points are scaled relative to total wild catch. *See Figure S3 for comparable sensitivity results*.

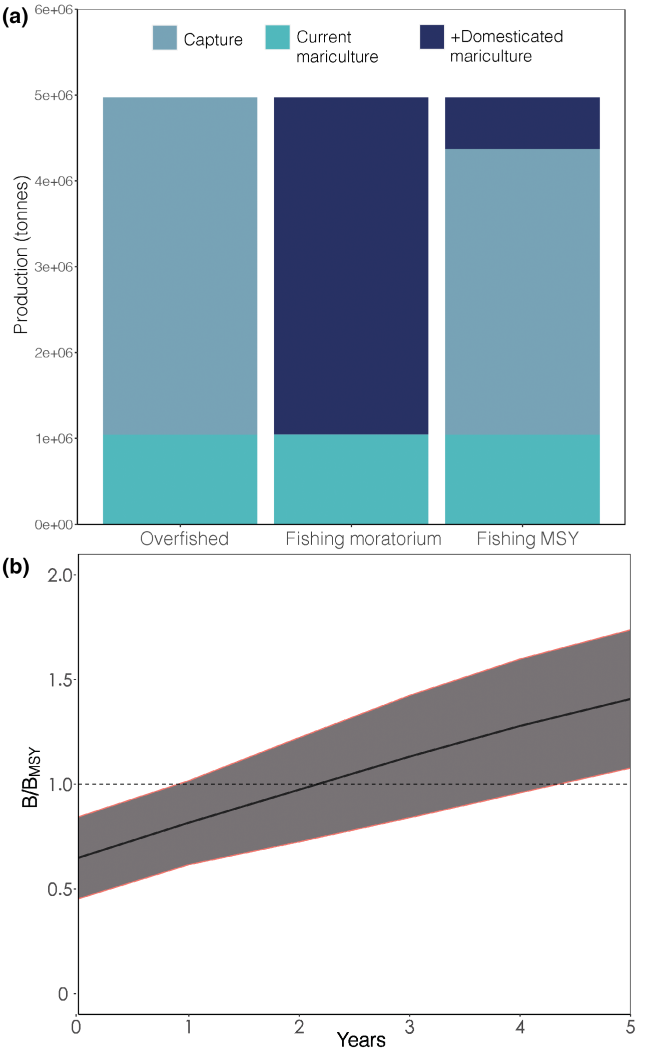

FIGURE 5 Panel (a) shows total tonnage of production under three scenarios: contribution from species overexploited (50 spp, 68 regional stocks) by marine capture fisheries (*light blue*) and equivalent species production from current marine aquaculture (CBA and DA combined, *aqua*), how much added marine DA (*dark blue*) would be needed to fill a moratorium production gap, and finally respective contributions if fisheries were managed at maximum sustainable yield (MSY). Panel (b) depicts the average number of years (± SD) to recover the *overexploited* stocks under best-case scenario.

(Figure 4). Atlantic bluefin tuna—one of the largest and most endangered of the tuna species in some regions—is consistently captured at larger, older stages, meaning that little earlier-stage natural mortality is avoided, and extraction for CBA instead merely adds to pressure from capture fisheries (Ottolenghi, 2008; Ottolenghi et al., 2004) and also risks removing individuals before they can reproduce (Barneche et al., 2018; Hixon et al., 2013). The CBA later-stage natural mortality sensitivity test did result in more species seeing no benefit ($n = 29$), especially finfishes (90%; Figures S2 and S3). These results provide important guidance for determining which species and aquaculture traits, that is, early capture and higher natural mortality, are more likely to result in savings of wild biomass and alleviation of fishing pressure from CBA.

There are also multiple species for which CBA may not bring sufficiently large savings to reduce extraction to sustainable levels, even when replacing 100% of wild landings. For example, only ca. 1% of biomass may be spared for a given Tarpon (*Megalops atlanticus*, Megalopidae) regional stock and most catches are less than 1000 tonnes (Figure 4). In this circumstance, and those previously highlighted, DA may be necessary to benefit wild caught species without reducing production.

3.3 | Filling production gaps with domesticated aquaculture

DA does not require wild inputs beyond feed for fed species and so eliminates that particular pressure on wild stocks. Assuming present DA species production can scale and/or some of the CBA species transition to DA, complete replacement of the 68 potentially overexploited regional stock tonnage in our theoretical scenario analysis would require a approximately fourfold increase in mariculture production (Figure 5a)—perhaps unlikely in the short term, even taking into account aquaculture's rapid growth. Note, this scenario does not necessarily assume a like-for-like species replacement (as in the CBA scenario), which does accommodate for more general seafood production but would likely require different shifts in demand. That said, lost tonnage from reducing fishing effort to MSY for these fisheries could be replaced by a little less than doubling (1.6x) of current DA production (Figure 5a), something global marine aquaculture has achieved 11 times in the last ca. 60 years (median 1.6x increase = 6 years; range = 3–9 years).

Finding socially, economically and politically feasible ways to cover the possible temporary or prolonged reductions in production necessitated by fisheries reform is a major but often overlooked challenge (Stoeckl et al., 2017). Even under the best-case scenario (e.g. 100% compliance, no extreme environmental variability or regime shift), recovery can take several years (Figure 5b), which could threaten the food security and economic wellbeing of people dependent on those resources. Our findings suggest that strategic investment in DA could be a tool for increasing the feasibility of fisheries reform by avoiding both temporary and long-term seafood production losses. In fact, closing the life cycle for the genetic improvement of aquatic species has recently been presented by the United Nation's Food and Agricultural Organization (FAO) to help support future sustainable food production (FAO, 2019). However, increasing existing DA production or closing the cycle of CBA species can be constrained if technology, finances, enabling policies and/or knowledge sharing in limited (Bartley et al., 2009; Gjedrem, 2010; Gjedrem et al., 2012; Olesen et al., 2015), making our results a likely best-case scenario globally.

3.4 | Aligning sustainable fisheries and aquaculture

While management of aquaculture has the potential to better align with fisheries, it still requires resources and space, with the other environmental impacts these imply. Of the 203 marine species we assessed, 135 (66%) are 'fed species' requiring direct feed inputs; the remaining species (all molluscs) are filter feeders (FAO, 2020b). Feed inputs largely come from forage fish (fishmeal and oil) and land-based crops. Given limits on the production of forage fish, sustainably increasing aquaculture would require increasing adoption of alternative feed ingredients, including crops, micro- and macroalgae, bacteria, yeast, insects and byproducts (Cottrell, 2021; Cottrell et al., 2020; Froehlich, Jacobsen, et al., 2018; Hua et al., 2019; Nagappan et al., 2021), likely imposing a small (compared to land–animal production) additional pressure on terrestrial food systems and environments (Froehlich, Runge, et al., 2018). In addition, while production of aquatic species generally requires less space compared to other food systems (Froehlich, Runge, et al., 2018; Gentry et al., 2017; Poore & Nemecek, 2018), it can still impact local species and environments (e.g. through pollution, escapes), necessitating strong regulatory and management practices to mitigate or reduce such threats (Clavelle et al., 2019; Edwards, 2015; Soto et al., 2008; Stentiford et al., 2020). A potentially important impact also arises specifically for CBA because of its reliance on wild seed. As discussed previously, this could negatively impact some target species, but could also have wider ecological impacts, including disruption to community assemblages (Piñeiro-Corbeira et al., 2018) or if earlier life stages are an important resource for local predators—something which has not been studied to date. Indeed, there is still much that needs to be evaluated when it comes to aquaculture, fisheries and ecosystem interactions, limiting our ability to plot certain sustainability pathways.

One important externality associated with aquaculture is escape risk of cultured species. Indeed, aquaculture species—especially those that can reproduce—can pose a risk to wild stocks due to introgression (Glover et al., 2020) and/or competition (Branch & Steffani, 2004) of escapes. Applying the data-limited modelling approach uncovered that some wild stocks of CBA species may be overexploited but are in fact invasive in many other regions around the world. Of note, the Green Mussel (*Perna viridis*, Mytilidae) in its native region of the Eastern Indian Ocean has some of the highest estimated median overexploitation levels ($B/B_{MSY}=0.22$, $F/F_{MSY}=4.2$; Figure 2), and has spread throughout the globe due initially to ship ballast and hull fouling transport, but later via deliberate aquaculture introductions (CABI, 2019). Such results underscore the need for strong regulatory and management frameworks (e.g. native or established species requirements, such as in the United States) as well as fundamental biological and ecological understanding of the species at hand to avoid negative impacts on native populations, harvested or otherwise, such as the One Health approach (Stentiford et al., 2020).

In addition to ecological considerations, detailed socioeconomic analyses should be carefully considered with this type of production alignment between fisheries and aquaculture. As aquaculture grows, the question of whether it competes with, supplements or supports the resource-constrained fishing industry will be increasingly important. Emerging reports of fishers in the Northeast of North America (e.g. Maine lobstermen) taking up aquaculture in response to collapsed stocks and increasing pressure from climate change suggest some transitions from fishing to farming may be occurring (Stoll et al., 2019). Several countries have already experienced a 'blue transition' of aquaculture overtaking wild capture production, largely due to initial overexploitation of the fisheries, policies enabling aquaculture and rising globalization increasing the accessibility and demand of seafood (Cottrell et al., 2021). In fact, similar factors that drove people from hunting to farming on land (e.g. larger populations, climate change), appear to be aligning at a larger scale for transitions of fishing to farming to potentially become more common in the future (Kuempel et al., 2021). A few international bodies are trying to prepare for such changes through large, multidisciplinary projects (e.g. COEXIST, Bergh, 2013) assessing and offering guidelines to sustainable integration of aquaculture and fisheries. However, to date, there does not appear to be explicit accounting of such information into commercial fisheries management (e.g. Marshall et al., 2018). Our exploratory scenario-based study demonstrates a new perspective on how aquaculture and fisheries could theoretically align as the social and environmental landscapes affecting our seafood continue to change.

We constrained some of our scenario analyses (i.e. CBA simulation) to only allow like-for-like replacement of fisheries with aquaculture species, assuming that biophysical, regulatory and/or other social conditions would constrain production. However, consumption patterns show that some species can be interchanged. For example, aquaculture production of Atlantic salmon has increased to meet the growing demand for salmon in general, and now accounts for three quarters of global salmon production. Although wild and farmed markets can differentiate, wild salmon can be susceptible to substitution (Asche et al., 2005), including when labelling breaks down (usually in restaurants) (Cline, 2012). Cultured shrimp and whitefish (e.g. tilapia) are also produced in large quantities providing consistent, year around access of these broader categories of aquatic foods (Anderson et al., 2018), which can affect the price of wild items depending on the scale of the production and market (Asche et al., 2001). Ultimately, some of our results may be overly conservative, and many more wild stocks could be better managed if some fishing pressure is alleviated by the farming of substitutable species, with the explicit incorporation of this into management plans.

While our study focuses on marine species, freshwater comparisons could also be explored in the future, though will likely encounter more severe data limitations. Freshwater production accounts for the majority (ca. 60%) of total aquaculture, but only about 10% of total (reported) wild capture (Cooke et al., 2016; FAO, 2020b). Freshwater fisheries are critically important for regional food security and nutrition around the world, yet many species appear threatened by overfishing, pollution and habitat loss (Fluet-Chouinard et al., 2018; Pitcher, 2015; Vianna et al., 2020). Due to the comparatively smaller scale, most freshwater fisheries are undervalued and overlooked, resulting in sparse data and few quantified reference points (Cooke et al., 2016; Pitcher, 2015). Given the scale of freshwater aquaculture and importance of sustainable freshwater fisheries, as well as the similarity of data-poor conditions, the scenario approaches explored in this marine-based study could feasibly be applied to freshwater systems. The two systems are already tightly linked through enhancement practices (Lorenzen, 2014) and the theoretical aquaculture–fisheries alignments explored in this paper could be used to expand on existing freshwater-based frameworks for the two systems (Lorenzen et al., 2012). Again, the approaches employed here are no substitution for formal assessments, but in the absence of better data, the simulated, scenario-based approach can provide key insights into potential benefits and limitations of more actively integrating aquaculture and fisheries beyond enhancement.

Wild fisheries face a challenging future (FAO, 2018; Pinsky et al., 2018; Szuwalski & Hollowed, 2016; Teh et al., 2017). Multiple strategies have been proposed to combat these challenges, but have largely been developed independent of aquaculture (Anderson et al., 2019; Deroba & Bence, 2008). Even perfectly managed fisheries ultimately have a limit to the food they can provide, and this limit is not sufficient to meet anticipated future demand for seafood. Instead, many countries are looking to aquaculture expansion to provide additional production (Froehlich et al., 2017; Lester et al., 2018). We demonstrate how the strategic adoption of capture-based and domesticated marine aquaculture for different species could increase total seafood production with relatively lower extractive impact on wild fishery stocks, potentially supporting fisheries reform and increasing the sustainability of the seafood sector as a whole while avoiding a reduction in production—temporary or prolonged—that otherwise may occur under fisheries reform. We provide a framework for evaluating which species and types of aquaculture might provide the biggest ecological benefits, and which may perversely increase pressures on wild stocks. Moreover, explicitly considering aquaculture and fisheries together in a marine resource management framework could avoid confusion and conflict between the two, helping identify opportunities for synergistic alignment while acknowledging the trade-offs of these systems (e.g. Lester et al., 2018). Such alignment will be challenging, and its feasibility will depend on existing infrastructure and regulations, political will, social interest and available capital. Our study provides a more nuanced, biologically driven perspective of how aquaculture could be integrated more actively into fisheries management considerations, beyond hatcheries, demonstrating possible avenues and potential benefits to harmonizing aquaculture and fisheries for sustainable seafood growth in the future.

ACKNOWLEDGMENTS

This research was a collaborative endeavour and not explicitly funded by a single grant or agency. Authors HEF, JCM, CDK and BSH acknowledge funding from the Zegar Family Foundation through the 'Anticipating Climate Change Impacts on Ocean Aquaculture' and 'Environmental Impact and Sustainability of Global Food Systems' projects. HEF and DRW acknowledge funding from the University of California, Santa Barbara. Many thanks to Dr. Chris Free for providing a friendly review of the manuscript and paying particular attention to the use of data-limited modelling in this study. We also thank the numerous anonymous reviewers of this manuscript for their expertise and thoughtful insights that significantly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Code and data are available on Github: https://github.com/Froehlich-Lab/aqua_fish_CBA_DA.

ORCID

Halley E. Froehlich https://orcid.org/0000-0001-7322-1523
David R. Williams https://orcid.org/0000-0002-0379-1800
Casey O'Hara https://orcid.org/0000-0003-2968-7005
Caitlin D. Kuempel https://orcid.org/0000-0003-1609-9706
Benjamin S. Halpern https://orcid.org/0000-0001-8844-2302

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How to cite this article: Froehlich, H. E., Montgomery, J. C., Williams, D. R., O'Hara, C., Kuempel, C. D., & Halpern, B. S. (2023). Biological life-history and farming scenarios of marine aquaculture to help reduce wild marine fishing pressure. *Fish and Fisheries*, *24*, 1034–1047. https://doi.org/10.1111/faf.12783