

Rapid and direct recoveries of predators and prey through synchronized ecosystem management

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One of the twenty-first century's greatest environmental challenges is to recover and restore species, habitats and ecosystems. The decision about how to initiate restoration is best-informed by an understanding of the linkages between ecosystem components and, given these linkages, an appreciation of the consequences of choosing to recover one ecosystem component before another. However, it remains difficult to predict how the sequence of species' recoveries within food webs influences the speed and trajectory of restoration, and what that means for human well-being. Here, we develop theory to consider the ecological and social implications of synchronous versus sequential (species-by-species) recovery in the context of exploited food webs. A dynamical systems model demonstrates that synchronous recovery of predators and prey is almost always more efficient than sequential recovery. Compared with sequential recovery, synchronous recovery can be twice as fast and produce transient fluctuations of much lower amplitude. A predator-first strategy is particularly slow because it counterproductively suppresses prey recovery. An analysis of real-world predator-prey recoveries shows that synchronous and sequential recoveries are similarly common, suggesting that current practices are not ideal. We highlight policy tools that can facilitate swift and steady recovery of ecosystem structure, function and associated services.

The unprecedented pace of change in the Anthropocene^{1–3} has added urgency to the task of recovering degraded ecosystems, focusing attention on the time it takes to achieve conservation goals, restoration successes and social-ecological sustainability^{4,5}. Restoration is a global priority of tremendous breadth, with recent international commitments to restore more than half a billion hectares of land⁶ as well as the >3,500 marine fisheries worldwide that remain overexploited⁷. The costliness of prolonged restoration efforts and mandates for rebuilding timelines make it all-the-more pressing to develop practical means to accelerate the speed of recoveries^{7–10}. Remarkably, the pace of recovery is often overlooked in ecosystem restoration. Here, we propose that the temporal sequence in which interventions are implemented can influence the pace of recovery, that this influence is often overlooked in ecosystem restoration, and that it is likely to play a critical role in shaping twenty-first century solutions to environmental issues.

Conventionally, ecosystem restoration was underpinned by the idea that reinstating a plant community would provide habitat for associated animals. There is now increasing appreciation for the roles animals can play in facilitating restoration (for example, nutrient cycling) and the value of considering their dynamics from the outset to achieve desired ecosystem composition¹⁰. Amplified attention to the significance of faunal dynamics in restoration is especially significant, because faunal dynamics have proven key to understanding patterns of ecosystem degradation. People have altered animal communities in a predictable sequence, with species higher on the food chain tending to be depleted before species lower on the food chain, a phenomenon referred to as 'trophic downgrading'¹¹. This predator-first sequence of species loss can

have disproportionate influences on the structure and function of ecosystems, altering food security, economic yields, species invasions, disease prevalence and carbon sequestration^{11–14}. Given the clear ecological and socioeconomic effects of trophic downgrading, a key unanswered question is: does sequence matter when it comes to the recovery of exploited food webs?

Many ecosystems are characterized by declines of one or more predator population and one or more prey population, with restoration actions implemented to counteract these effects. For instance, trophy hunting, the fur trade and industrial fisheries are wholly or partially responsible for population collapses of lions and wildebeest in Africa, Steller sea lions and Pacific herring in the temperate Pacific, and mink and muskrat in North America (Fig. 1). Harvest restrictions and protected-area management are two common strategies used to reverse these effects, resulting in recoveries that follow one of three pathways (Fig. 1): (1) predator-first recovery, (2) prey-first recovery or (3) roughly synchronous predator and prey recovery. Despite the qualitatively distinct characteristics of these recovery pathways, there is little theory or empirical analysis related to restoration sequence (though there are exceptions^{15–19}).

A focus on sequence provides key insights into across-ecosystem variation in the extent and frequency of documented recoveries^{8,18}. For example, prey may recover more slowly or not at all if abundant predators have strong effects at low prey abundance²⁰. Likewise, slow or failed recoveries may be the result of predator-first approaches in which specialist predators do not have access to a readily available and abundant prey base²¹. Therefore, intuition suggests that prey-first recovery should enhance predator recovery, and thereby

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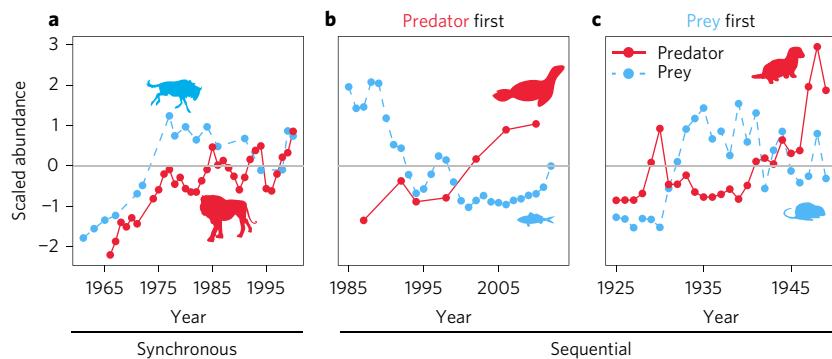


Figure 1 | Example time series illustrating that ecological communities can follow a predictable sequence of recovery to achieve trophic upgrades, following declines in predator and prey populations (trophic downgrades). **a**, Synchronous recovery in Serengeti National Park, Tanzania, where woodlands lions (*Panthera leo*; $n = 12$ counts yr^{-1}) and one of their favoured prey, blue wildebeest (*Connochaetes taurinus*; $n = 1$ count yr^{-1}) recovered at approximately the same time (mid-1970s; ref. ⁴⁸). **b**, Predator-first recovery in the Northeast Pacific near Haida Gwaii, British Columbia, Canada, where Steller sea lions (*Eumetopias jubatus*; data from $n = 15$ haul-out sites⁴⁹) recovered a decade before their Pacific herring prey (*Clupea pallasi*; based on data from two management regions representing $n = 11$ spawning locations⁵⁰). **c**, Prey-first recovery in Newfoundland, Canada, where muskrat (*Ondatra zibethicus*) recovered about 20 years before predatory mink (*Mustela vison*; reports from $n = 1$ fur trade post⁵¹). Note that all time series were standardized to zero mean and unit variance for the length of the time series presented, and we define recovery as a sustained return to a population size equal to or greater than the long-term mean.

recovery of the full community. However, we are not aware of a theory that has examined these possibilities formally.

Results

We analysed an apex predator–multiple prey model to evaluate the effectiveness and relative cost of synchronous versus sequential reductions in exploitation rates of predators and their prey (Box 1). Surprisingly, we find that synchronous recovery from sustainable exploitation levels produces recoveries of predator and prey populations that are faster than prey-first and predator-first strategies (Figs 2 and 3).

Analytical approximations and numerical sensitivity analysis demonstrate that synchronous recovery is universally the fastest strategy for a wide range of exploitation rates and species' productivity rates (Supplementary Figs 1–4). There is, however, one exception to this conclusion. In the case where the productivity of the focal prey is relatively low and the availability of alternative prey to the predator is relatively high, prey-first recovery is the fastest strategy (Supplementary Fig. 4). While there are certainly examples of this situation in nature²², it is unlikely to be common for the many communities in which prey productivity tends to exceed predator productivity²³.

For most stable and feasible parameter combinations, however, prey-first recovery is not fastest, and because it leads to transient prey release from predation and exploitation, this strategy causes summed predator and prey densities to peak at levels much higher than their eventual equilibria (Figs 2 and 3). In the real world, transient dynamics like these that result from eruptions of prey populations can lead to surprising cascades of ecological interactions and complex but often mismatched management responses¹⁸.

Unlike prey-first recovery, our model suggests that both predator and prey recover directly to their unexploited equilibria in the case of predator-first recovery (that is, transient volatility is zero; Fig. 3), just over a longer time period. The increase in community return time occurs because the recovery of the predators increases prey mortality while they continue to be exploited.

The synchronous recovery strategy achieves a compromise between these two extremes, leading to considerably lower volatility than prey-first recovery (Fig. 3). Analytical approximations and numerical sensitivity analysis show that, irrespective of exploitation rates and species' productivity rates, predator-first recovery is always best at damping out transient dynamics, while

prey-first recovery always leads to the greatest community volatility (Supplementary Figs 1–4).

Thus, in ecological terms, restoration of exploited communities is generally predicted to be faster and more direct under synchronous recovery. On the social side, an analysis of foregone harvest yields suggests that synchronous recovery is no worse—and in several cases better—than the sequential recovery strategies (see Supplementary Fig. 5).

Our model therefore implies that both ecological and social goals tend to be best served via synchronous recovery efforts, yet empirical evidence from a comprehensive database of marine fisheries²⁴ shows that synchronous recoveries are not the rule. Rather, there are approximately equal numbers of synchronous and sequential recoveries in exploited marine ecosystems, with predator-first recoveries being less common than prey-first recoveries (Supplementary Tables 2 and 3 and Supplementary Figs 6–8). This analysis includes iconic examples, such as the Baltic, where predatory Baltic cod recovered (2011) only following their herring prey (2007); along the west coast of Vancouver Island, Canada, where Pacific cod recovered (2002) before their preferred Pacific herring prey (2008); and the Gulf of Maine, where predatory Atlantic cod and Acadian redfish, which are regular prey for Atlantic cod, both recovered in 2008 following decades of overdepletion (Supplementary Tables 2 and 3).

Discussion

Comparing theory to data. On the one hand, the disconnect between our theory and observed restoration patterns implies an opportunity for improvement in the more than half of empirical cases of sequential recovery, even in the context of multiple restoration goals such as long-term economic value, biological sustainability of multiple species, and short- and long-term harvest opportunities^{7,10,16,25,26}. On the other hand, these results are encouraging, because predator-first recovery—the slowest strategy according to our theory—is less common than prey-first recovery.

It is worth noting that the database we analysed did not include case studies with an explicit focus on spatial management measures such as protected areas, which might alter the frequency of synchronous and sequential recoveries compared with what we assessed. For example, marine protected areas may relax harvest pressure on all species in a community, or preferentially on a relatively sedentary predator while more mobile prey remain partially exposed to harvest outside the protected area²⁷. Furthermore, our empirical

Box 1 | Apex predator–multiple prey model with harvest.

We analyse a model of a generalist predator and its prey to evaluate the effectiveness of synchronous versus sequential community recovery in terms of rates and volatility of recovery to an unexploited community state. We extend a model^{25,45} that consists of a generalist predator (P , in number of individuals) consuming one explicitly modelled prey (X , the focal prey, in number of individuals) as well as a non-dynamical other-prey group (Y , in number of individuals). This focus on a three-node community module allows for tractability and is appropriate, as many food webs are characterized by few strong and many weak interactions³². As in Gordon–Schaefer fishery models, we assume that both the predator and focal prey experience logistic population growth such that:

$$\frac{dX}{dt} = r_X X \left(1 - \frac{X}{K_X}\right) - a_X P X - h_X X \quad (1)$$

$$\frac{dP}{dt} = P [c(a_X X + a_Y Y) - d_P] \left(1 - \frac{P}{K_P}\right) - h_P P \quad (2)$$

Here, r_X is the prey's intrinsic per-capita growth rate (units: yr^{-1}), K_X is the prey's logistic growth carrying capacity (units: number of individuals), d_P is the predator's per capita mortality rate (units: yr^{-1}) and K_P is the predator's carrying capacity (units: number of individuals) reflecting limiting factors other than prey availability, such as habitat¹⁴. The predator feeds on prey X and Y with linear type I functional responses at per-capita rates a_X and a_Y , respectively (units: number of individuals $^{-1} \times \text{yr}^{-1}$), the relative magnitude of which reflects its preference for the two prey, and converts these to predator biomass at rate c (units: prey per predator). The predator and focal prey are harvested at constant per-capita rates, h_P and h_X (units: yr^{-1}). Additional details on simulating recovery strategies are in the Methods, and analytical solutions appear in the Supplementary Information.

analysis focused exclusively on fish stocks without attention to the likely common situations where threatened/endangered species and carnivore protection have facilitated recoveries of predatory mammals and birds before their less charismatic prey (Table 1, and references therein, and Fig. 1).

The contrast between our theory and observed restoration patterns may also suggest a need to incorporate further complexities into the theory—such as stage structure or additional interactions between a greater number of species—to explain why synchronous and sequential recoveries are equally common in fisheries (see Supplementary Discussion for potential extensions). Perhaps the most important social consideration will be the relative economic value of predator versus prey species and the losses incurred by ceasing harvest on one or both¹⁹.

Implications for synchronous and sequential policy actions. Several policy mechanisms exist for shifting to synchronous recovery strategies (Table 1). One that has not been implemented often involves temporary and purposeful increases in exploitation of one species (that is, culling) to promote the recovery of another. In the context of fisheries, this approach could even involve purposefully overfishing abundant predators to transition sequential rebuilding of stocks to synchronous rebuilding (for example, via catch-quota balancing²⁸, under the rubric of a mixed-stock exception^{29,30}). This possibility has been raised recently in the California Current ecosystem, where lingcod and rockfishes benefited from US legislation provoking synchronous rebuilding. However, less desirable lingcod recovered faster than their rockfish prey because

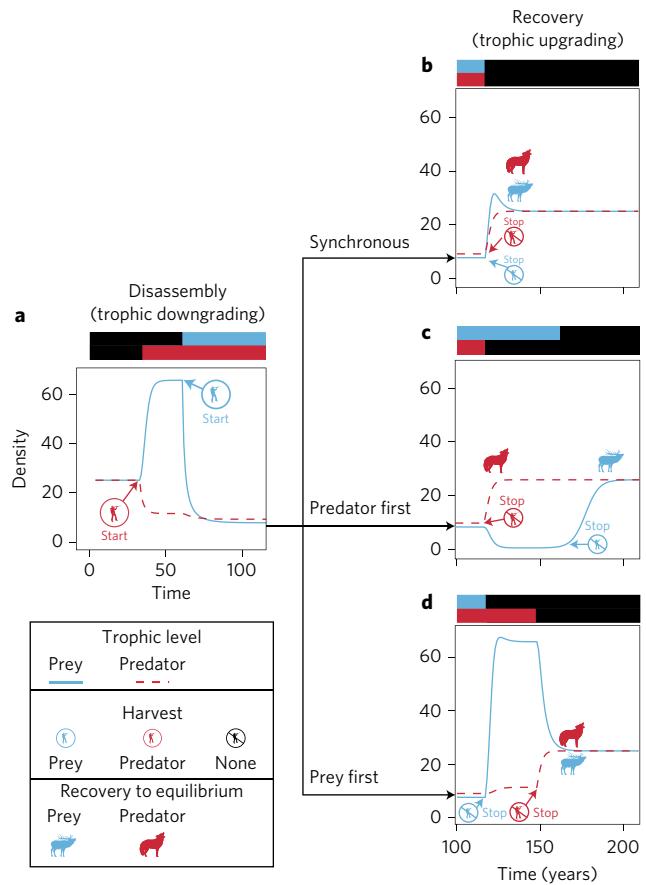


Figure 2 | Time series panels showing predator and prey densities during community disassembly and recovery. **a**, Community disassembly. **b–d**, Three community recovery scenarios: synchronous (**b**), predator first (**c**) and prey first (**d**). In the bars above each panel, black indicates no harvest over the corresponding time period (years), blue indicates prey harvest and red indicates predator harvest. Note that recovery time is defined as the time from when recovery begins—when exploitation is reduced to zero for at least one species—until it is completed, when harvest pressure is zero for both predator and prey and their densities (number of individuals per unit area) remain within 10% of their long-term equilibria. However, the analytical results show that relaxing this assumption to eliminate the time between cessation of predator harvest and cessation of prey harvest does not change the qualitative conclusions (see Supplementary Information for details). See Methods for parameter values.

of high natural productivity. Along with partners, The Nature Conservancy (www.pccouncil.org/wp-content/uploads/2015/11/I2_Sup_Att6_EFP_TNC_GearInnovations_Nov2015BB.pdf) is now exploring the possibility that a selective lingcod fishery may enhance rebuilding of rockfishes²⁷. Similar approaches have been proposed in terrestrial systems to limit predation on threatened prey while they are recovering³¹.

The exact tactics used to shift to synchronous recovery strategies would require careful study, as culling of predators can have unexpected consequences³². Other more passive restoration approaches with longer histories focus on umbrella species³³ or protected-area management. However, these tools may be inefficient if restoration objectives have a sharp focus on short-term gains of a particular subset of species (for example, ref. ³⁴) or if strategic interventions are necessary to accommodate differences in life histories within an ecosystem, even though they have the benefit of being able to affect recoveries at small spatial scales where necessary^{10,35}.

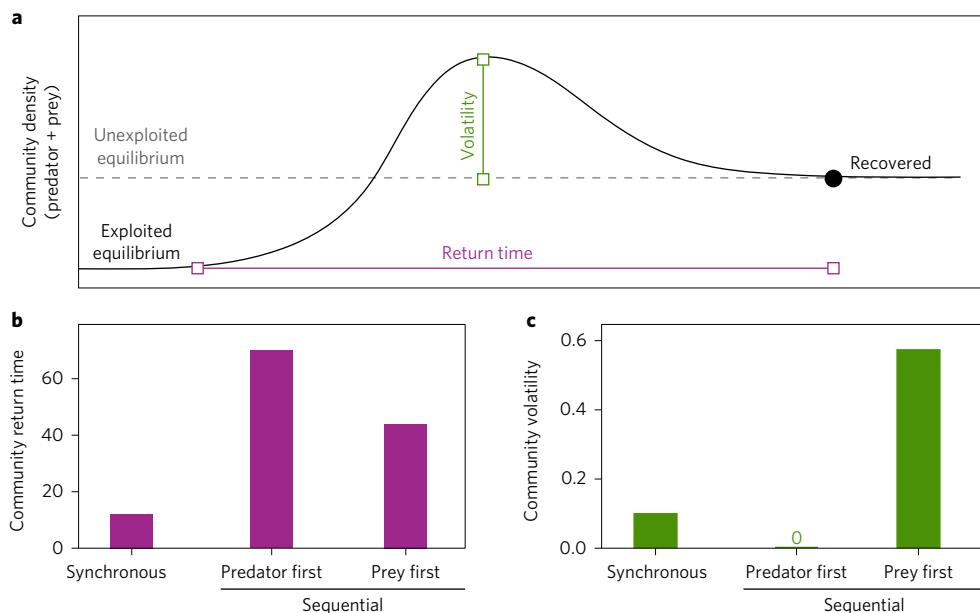


Figure 3 | Community return time and volatility for three recovery scenarios. **a**, Schematic illustrating the two recovery metrics, community return time and community volatility, used to analyse the effectiveness of alternative recovery strategies. **b,c**, Community return times (years) (**b**) and community volatilities (dimensionless) (**c**) for the baseline case under three recovery scenarios. See Methods for parameter values and definitions of recovery metrics. Note that these patterns are generally robust even if the lag time between recovery of the predator (prey) and cessation of exploitation of the other species is eliminated (see Supplementary Information).

Despite the availability of synchronous restoration approaches, it seems likely that many of the tools with the strongest legal underpinnings and in most widespread use result in sequential management actions that produce sequential recoveries (Table 1). Sequential recovery allows for continued exploitation of some species while harvest is discontinued for another. In addition, it is not necessarily concerned with coordinated management actions aimed at different species and potentially different sectors^{4,36}. While these social benefits are appealing in the near term, in the long term our findings indicate greater social and ecological benefits of synchronous recovery. Regardless of the exact intervention employed to achieve it, the critical component is to embrace systems-level thinking for restoration policy and practice.

Conclusions. Our study highlights how and why the sequence of restoration operations matters when one target of restoration

is eaten by another. We bridge community assembly and food web theories^{37–39} to improve restoration practice by demonstrating that synchronous recoveries of predators and prey are generally rapid and direct. In contrast, predator-first recoveries are slow and potentially risky because they can introduce a double jeopardy situation for prey, due to the combination of continued exploitation of prey populations and increased mortality from the recovering predator population.

These findings add emphasis to recent calls for coordinating management and restoration actions at the ecosystem level^{4,19,36}, while underscoring the central role of transient dynamics in making inferences about social-ecological systems^{18,40}. Moreover, we highlight the ready availability of key policies as opportunities to achieve restoration goals in ecosystems experiencing increasing exploitation demands as human populations continue to grow. In 1992, E.O. Wilson wrote, “The next century will, I believe, be

Table 1 | Relationship between policy or management actions and community recovery strategies.

Management approach	Terrestrial or aquatic system	Recovery strategy	Description	References
Protected area	Terrestrial, aquatic	Synchronous	Complete or partial protection of all species within a fixed area.	52–54
Mixed stock management	Aquatic	Synchronous	Single species management that regulates fisheries to account for and prevent low productivity or overexploited stocks from being overexploited.	22,55,56
Umbrella species management	Terrestrial	Synchronous	Single species management that focuses on a single species with a large home range to protect a broader community or ecosystem.	57,58
Threatened/endangered species actions	Terrestrial, aquatic	Sequential	Predator- or prey-first: single species focus reducing or eliminating exploitation of species that are at risk of extinction.	59–61
Carnivore protection	Terrestrial	Sequential	Predator-first: focus on the preservation of charismatic, higher-trophic-level species.	62,63
Pre-emptive single fishery closure	Aquatic	Sequential	Prey-first: allocation of lower-trophic-level species for dependent predators.	64,65

the era of restoration in ecology.” We are well into this era of restoration, but there remains an unambiguous need to advance theory and practice to meet its demands. Our work clearly shows how careful consideration of trophic-upgrade strategies provides a useful step towards the goal of reversing overexploitation at the top of the food chain.

Methods

The theory developed here is grounded in the notion that restoration relies on any actions that will re-establish a self-sustaining system, including all aspects of the environment required for constituent organisms^{6,9}. We define synchronous recovery of an exploited community as the simultaneous release of all trophic levels from harvest pressure, and sequential recovery as the release of predators from harvest before prey (predator-first recovery) or the release of prey from harvest before predators (prey-first recovery). Our primary interest is in the transient dynamics⁴⁰ expected following the implementation of a community recovery strategy. We develop this theory via both numerical simulation and analytical approximations (see Supplementary Information for details).

Using the model described in Box 1, we focus on how each of the recovery strategies affects the rates and volatility of recovery to an unexploited community state, as well as cumulative yields. For our simulations, community return time is the time from when recovery begins—when exploitation is reduced to zero for at least one species—until it is completed, when harvest pressure is zero for both predator and prey, and their densities remain within 10% of their long-term equilibria^{41,42}. Community volatility captures the magnitude by which the recovery strategies cause the summed predator and prey densities to exceed the unexploited community equilibrium. Specifically, we define it as the proportional difference between the maximum community density achieved during the transient period of recovery and the unexploited equilibrium⁴³. We define a recovery with lower community volatility as more direct because, in the limit, zero volatility indicates a monotonic return to equilibrium. As reductions in exploitation rates come at a cost of lost yields, we track the cumulative yields across all T years of the simulations ($\sum_{t=1}^T h_X X_t$, $\sum_{t=1}^T h_P P_t$ and $\sum_{t=1}^T h_X X_t + h_P P_t$) as well as yields per unit time t when exploitation is non-zero.

We first analyse a single baseline case that depresses the predator and prey population densities to levels resembling common sustainable exploitation goals (for example, target densities that are 30–40% of unexploited levels⁴⁴). In this baseline case, focal prey (X) productivity is higher than that of the predator (P), the exploitation rate of the focal prey ($h_X = 0.65$) exceeds that of the predator ($h_P = 0.325$), and the predator is a generalist such that the other-prey group (Y) constitutes the majority of the predator diet ($Y = 500$). This baseline other-prey density and the predator attack rates (identical for focal and alternative prey, $a_X = a_Y = 0.03$), predator conversion rate ($c = 0.05$), carrying capacities of the predator ($K_p = 25$) and focal prey ($K_X = 100$), intrinsic per-capita growth rate of the focal prey ($r_X = 1$) and death rate of the predator ($d_p = 0.25$) represent reasonable intermediate values that allow for coexistence of the predator and focal prey under a range of predator and prey productivity rates and harvest rates⁴⁵.

We also evaluate how variation in two major characteristics of the exploited predator-prey system influences inferences: (1) the intrinsic productivity rates of the predator and the prey, and (2) the legacy of exploitation in the community. We explore all combinations of prey intrinsic productivity rates ($r_X = [0.5, 1.5]$) and predator attack rates ($a_X = a_Y = [0.02, 0.05]$, reflecting the predator intrinsic productivity) that allow both predator and prey to coexist under a range of predator and prey harvest rates (see Supplementary Discussion and Supplementary Fig. 2 for parameter combinations that allow coexistence). Harvest rates span a range of values corresponding to three exploitation levels: underexploited, sustainably exploited and overexploited ($h_X = [0, 0.8]$ and $h_P = [0, 0.6]$). All other parameter values are identical to the baseline case.

In addition to conducting numerical simulations of synchronous and sequential community recovery, we determine the equilibrium solutions to the model (Box 1) analytically and assess community responses under the three recovery strategies based on those analytical solutions. We also examine the sensitivity of responses to changes in the per-capita rates with which predator and prey are harvested, increased intrinsic growth rate of the focal prey population (from $r_X = 1$ to $r_X = 5$) and increased availability of other prey (from $Y = 500$ to $Y = 1,000$), which effectively increases the intrinsic growth rate of the predator population. See the Supplementary Information for details.

To determine whether real-world community recoveries tend to be synchronous or sequential (predator first or prey first), we rely on a meta-analysis²⁴ of a global database of marine fisheries (RAM legacy stock assessment database⁴⁶). This meta-analysis provides a comprehensive source of recoveries of exploited species analysed and reported in a standardized format. We are unaware of a similarly comprehensive database of recoveries in exploited terrestrial communities.

To analyse the database, we use chi-squared tests to determine whether (1) synchronous community recovery case studies occur with equal frequency

to sequential community recovery case studies, and (2) synchronous, predator-first, and prey-first community recovery case studies occur with equal frequency (see Supplementary Information for details). We determine statistical significance via Monte Carlo simulation using `chisq.test` in R v3.0.3⁴⁷.

Data availability. The data from this study supporting our findings are available from the corresponding author on reasonable request.

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Author contributions

J.F.S., A.C.S., P.S.L. and M.N. designed the study. J.F.S., A.C.S., M.N. and S.M.H. collected and analysed all data. J.F.S., A.C.S., P.S.L., B.S.H. and M.N. jointly wrote the manuscript.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.

1 **Supplementary Information**

2 **Is this theory robust to different intrinsic productivity rates, exploitation histories,
3 and other considerations?**

4 Many factors might influence our theoretical expectations, the most important of which
5 relate to life history traits of the predator and prey^{1,2} and intensity of historical
6 exploitation levels^{3,4}. To assess potential effects of these factors, we evaluate which
7 recovery strategy produces the shortest return time and most direct recoveries given
8 different combinations of predator and prey productivity and three scenarios of historical
9 exploitation: under-exploitation, sustainable-exploitation, and over-exploitation¹, such
10 that exploited predator and prey densities prior to recovery were ~70%, ~30%, and ~20%
11 of unexploited values, respectively.

12 We calculate the percent reduction in community return time obtained from the
13 recovery strategy with the shortest value compared to that with the next shortest. Because
14 predator first recovery always minimizes community volatility to zero, we report the
15 volatility obtained from the recovery strategy with the second smallest value. This
16 quantity represents the percentage by which the maximum community density achieved
17 during the transient period of recovery exceeds the unexploited equilibrium community
18 density.

19 Synchronous recovery consistently exhibits the fastest community return times; in
20 numerical simulations, synchronous recovery produces 70-90% faster community return
21 times than the other strategies (Supplementary Figs. 1-2). Higher exploitation levels
22 slightly diminish the relative benefit of synchronous recovery in terms of community
23 return time: synchronous recovery produces ~90% faster returns times in the under-

24 exploitation scenarios but ~70% faster returns times in the over-exploitation scenarios
25 (Supplementary Fig. 2). In any specific exploitation scenario, higher prey intrinsic
26 productivity rates reduces differences in community return time among recovery
27 strategies.

28 Predator first recovery damps out high-amplitude transient dynamics most under
29 all exploitation scenarios, causing this strategy to exhibit the most direct recoveries
30 (Supplementary Figs. 1-2). The second best strategy for producing small values of
31 community volatility is synchronous recovery, with values ranging from 0-32% and an
32 average of 8% (Supplementary Fig. 2). There was one exception to this pattern, where
33 predator first and synchronous recovery both had zero community volatility: $Y = 500$,
34 $a_X = a_Y = 0.03$, and $r_X = 0.8$. Community volatility was four-fold higher for the prey first
35 strategy than for the synchronous strategy in the underexploitation scenario, but fourteen-
36 fold higher in the overexploitation scenario (Supplementary Fig. 1). In any specific
37 exploitation scenario, higher prey intrinsic productivity rates reduces differences in
38 community volatility among recovery strategies.

39 Beyond species' productivity rates and exploitation histories, in real exploited
40 communities more species (that interact in many ways beyond predator-prey dynamics),
41 temporal variation in parameter values, environmental stochasticity, stage or spatial
42 structure within predator and prey populations, and the potential for hysteresis following
43 dis-assembly (especially due to predator-prey role reversals^{5,6}) may all interact to affect
44 expectations for recovery times and trajectories⁷⁻⁹. Our two-trophic level predator-prey
45 model assumes these factors are not necessary to understand broad patterns of ecosystem
46 recovery. Similarly, the social and economic costs associated with predator versus prey

47 harvest are nuanced, requiring incorporation of discount rates and consideration of the
48 optimal effort required to achieve pre-specified social goals^{10–12}. Certainly, exploring the
49 potential effects of additional complexities will be important extensions of the basic ideas
50 introduced here. Yet, even with their inclusion, the large differences in our transient
51 approximations of return time and volatility between synchronous and sequential
52 recovery strategies suggest the results should be general.

53

54 **Do analytical solutions of recovery correspond to numerical simulations?**

55 In addition to conducting numerical simulations of synchronous and sequential
56 community recovery, we determined the equilibrium solutions to the model (Box 1)
57 analytically using Mathematica v10. To make this analysis more tractable using
58 Mathematica, we reformulate equation 2 as follows:

$$59 \frac{dP}{dt} = P[c(a_x X + a_y Y) - sP - d_p] - h_p P \quad (S1)$$

60 In this formulation, s represents density-dependent losses due to food limitation or other
61 factors related to prey densities and is equivalent to

$$62 s = \frac{c(a_x X + a_y Y) - d_p}{K_p} \quad (S2)$$

63 We determine the equilibrium densities of the predator and focal prey that allow
64 for feasible fixed point coexistence in four situations, when: (i) both species are exploited
65 ($h_X > 0, h_P > 0$), (ii) only the prey is exploited ($h_X > 0, h_P = 0$), (iii) only the predator is
66 exploited ($h_X = 0, h_P > 0$), or (iv) neither species is exploited ($h_X = h_P = 0$) (Supplementary
67 Table 1). Situation (i) thus corresponds to a dis-assembled community at equilibrium that

68 could recover from exploitation via synchronous recovery (situation (iv)) or sequential
69 recovery (situation (ii) or (iii) followed by (iv)).

70 Because the three recovery scenarios are nested within these four situations, we
71 examine how the community responds to changes in the per capita rates with which
72 predator and prey are harvested. Specifically, we evaluate the characteristic return time to
73 the unexploited state following an instantaneous cessation of harvest ($-1/\text{Re}(\lambda_1)$), the
74 analytical first-order analog to true return time in the numerical simulations presented in
75 the main text¹³. In addition, we determine the community's reactivity (the maximum
76 possible growth rate of its transient response toward the unharvested state following a
77 cessation or reduction of harvest¹⁴ and its maximum amplification volume (the largest
78 relative change in species abundances that could occur during the transient phase of its
79 response¹⁴. Note that reactivity and maximum amplification volume relate closely to the
80 community volatility metric used in the main text, but differ in that they reflect a first-
81 order approximation to the community's response to a perturbation (i.e. the sudden
82 cessation or reduction of harvest) of any magnitude. Finally, all of the interpretations that
83 follow are predicated on the insight that a press perturbation from an exploited to an
84 unexploited state can be interpreted as the decay of a pulse perturbation from an exploited
85 state back to an unexploited state.

86 In general, our analytical results corroborated those obtained via numerical
87 simulations (Supplementary Fig. 3). As would be expected given our model, equilibrium
88 densities of both the prey (Supplementary Fig. 3a) and the predator (Supplementary Fig.
89 3b) decline linearly with increasing per capita harvest rates, with higher harvest rates on

90 the prey reducing the range of harvest rates on the predator that permit coexistence (cf.
91 blue and red lines in Supplementary Fig. 3b).

92 Analytical solutions confirm that synchronous recovery always exhibits the
93 shortest characteristic return times ($h_X = h_P = 0$, blue line intercept of y-axis in both
94 Supplementary Fig. 3c-d), but whether predator first reassembly ($h_P = 0$, blue line in
95 Supplementary Fig. 3c) or prey first reassembly ($h_X = 0$, blue line in Fig. Fig S5d) causes
96 the second shortest characteristic return time depends on the harvest rate of the species
97 still being exploited. These results account for characteristic return times from equilibria
98 reached when one or both species are harvested.

99 Predator first recovery exhibits the lowest reactivity levels for any feasible prey
100 harvest rate and declines with increasing prey harvest rate (Supplementary Fig. 3e),
101 whereas prey first recovery generates the largest reactivity levels at any feasible predator
102 harvest rate, and prey first reactivity increases with predator harvest rate (Supplementary
103 Fig. 3f). Synchronous recovery thus exhibits an intermediate level of reactivity (blue line
104 intercept of y-axis in both Supplementary Fig. 3e-f).

105 Amplification volumes are smallest for the predator first recovery at any feasible
106 prey harvest rate and decline with increasing prey harvest rate (Supplementary Fig. 3g).
107 In contrast, amplification volumes under the prey first scenario increase with predator
108 harvest rate and are either larger or smaller than synchronous recovery depending on the
109 predator's harvest rate (Supplementary Fig. 3h).

110 Our results may be understood more generally by considering the energy that is
111 taken out of the system via harvest: the more energy in the system, the faster the
112 characteristic return time and the larger the reactivity¹⁵. Because energy is already lost in

113 the transfer from prey to predator, harvesting some fraction of predators (i.e., at some
114 given per capita rate) will remove less overall energy from the system than the harvest of
115 the same fraction of prey. Thus, predator first recovery will always result in a less
116 reactive system. The effect of predator first recovery on the return time will depend on
117 the per capita rate at which the prey are harvested. If the prey's per capita harvest rate is
118 large (e.g., over-exploitation scenario) then a reduction (or cessation) in the harvesting of
119 the predator population can have a larger impact on recovery rate than when the prey's
120 per capita harvest rate is low.

121

122 **Are there drawbacks to synchronous versus sequential recovery?**

123 Synchronous and sequential recovery strategies will have different socioeconomic
124 implications due to different timing and durations of reduced harvest opportunities. We
125 compare the cumulative total, predator-only, and prey-only yields among the recovery
126 strategies assuming predators and prey hold equal value per unit biomass. We find that
127 the cumulative total yield and the cumulative yield of prey differ by 5% or less among the
128 recovery strategies (Supplementary Fig. 4). In contrast, predator first recovery produces a
129 cumulative yield of predators that is ~30% higher than cumulative predator yield under
130 the other two strategies (Supplementary Fig. 4). However, because the duration of
131 exploitation varies among the three recovery strategies (Fig. 2), predator yields per unit
132 time prior to cessation of harvest are equivalent among the three recovery strategies
133 (Supplementary Fig. 4). Furthermore, prey yield per unit time is lower for predator first
134 recovery than for the other two strategies (Supplementary Fig. 4). Thus, the drawbacks of

135 synchronous recovery in terms of foregone yields are less than or equal to those
136 associated with the other two strategies.

137

138 **How frequent is synchronous versus sequential community recovery in the real**
139 **world?**

140 We assessed a comprehensive database of marine fisheries³, focusing on exploited
141 communities in which time-series of generalist predators and their prey were available,
142 spanning time periods in which both were considered overexploited and had since
143 recovered. We define a dis-assembled community as one in which two or more species,
144 occupying different trophic levels and occurring in the same geographic region, had
145 overlapping periods of depletion. Following Neubauer et al.³, we classify a species
146 (stock) as depleted when its biomass, B , is less than half of its maximum sustainable
147 yield, B_{MSY} . Depletion periods are considered to overlap among species if $B < 0.5B_{MSY}$ for
148 both species for three or more consecutive years. We focus our analysis on the subset of
149 dis-assembled communities (hereafter, case studies) in which higher- and lower-trophic
150 level species have a documented predator-prey relationship (Supplementary Tables 2-3).

151 Within the case studies we define a recovered community as one in which the
152 biomass of both predator and prey meets or exceeds B_{MSY} , as inferred by Neubauer et al.³.
153 We designate a case study as an example of synchronous recovery if recoveries occur
154 within three years of one another, predator first recovery if the predator recovers four or
155 more years before the prey, and prey first recovery if the prey recovers four or more years
156 before the predator (Supplementary Table 2). Trophic levels for each species were
157 obtained from FishBase and are considered distinct if they differ by 0.5 or more units.

158 Note, however, that a trophic level distinction alone was insufficient for inclusion in our
159 analysis; we restrict our analysis to communities with documented predator-prey
160 relationships (Supplementary Table 3). Though this database precludes assessment of the
161 influence of management actions, climate, or other factors in the observed recovery
162 patterns, changes in exploitation rates were the primary factor under direct control of
163 managers in these systems.

164 To test whether the decisions we made in categorizing case studies influence the
165 outcomes of our analyses, we compare the results of the initial, moderately inclusive set
166 of assumptions to two alternative sets of assumptions (Supplementary Table 2), and to
167 removal of the most common species in the database, Atlantic cod (n=29). The first set of
168 assumptions is the most inclusive of case studies in the database, and designates distinct
169 trophic levels as a difference of 0.1 units or more, overlapping depletion periods as at
170 least 1 year overlap, and synchronous recovery as the depletion period of both the
171 predator and prey species ending in the same year. The second set of assumptions is the
172 least inclusive of case studies in the database, and includes predators and prey with a
173 trophic level difference greater than or equal to 1.0 with depletion periods overlapping by
174 5 years or more, and defines synchronous recovery as depletion periods that ended within
175 5 years of each other.

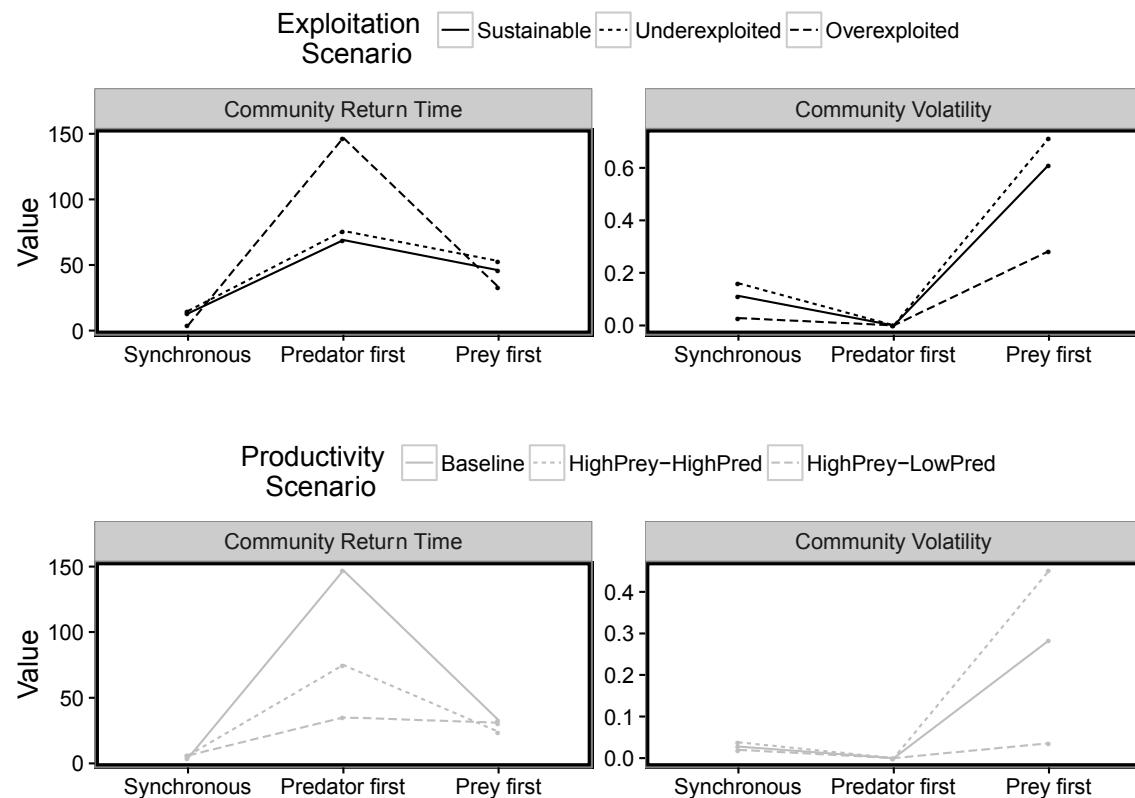
176 It is likely that some of the recoveries predicted by Neubauer et al.³ did not, in
177 fact, occur, especially for the most common species in the database, Atlantic cod (n=29).
178 Our analysis would be more likely to classify these case studies as synchronous when,
179 upon actual recovery of Atlantic cod, they would be more accurately assigned as
180 sequential recoveries (with Atlantic cod recovering after its species pair). Thus, our test

181 would conservatively favor the detection of synchronous recoveries. To determine the
182 influence of Atlantic cod on our results, we repeat the Chi-squared tests removing these
183 case studies.

184 Our assessment suggests that there are approximately equal numbers of
185 synchronous and sequential recoveries, with predator first recoveries being less common
186 than prey first recoveries ($N=32$ case studies; Supplementary Fig. 5). These patterns are
187 generally robust to different ways of categorizing the case studies as synchronous versus
188 sequential, and to the exclusion of the most common species from the database
189 (Supplementary Figs. 6-7). The most inclusive set of assumptions leads to the conclusion
190 that synchronous recovery is less common than sequential recovery (chi-square test,
191 $p=0.16$), while the least inclusive set leads to the opposite conclusion (chi-square test,
192 $p=0.0005$; Supplementary Fig. 6). However, neither of these alternative sets of
193 assumptions changes the qualitative inference that predator first recovery was least
194 common (both chi-square tests, $p<0.0005$; Supplementary Fig. 6). Finally, even with
195 removal of case studies that include Atlantic cod from the analysis the number of
196 occurrences of synchronous and sequential recoveries remains statistically
197 indistinguishable (chi-square test, $p=0.76$), and this change makes the number of
198 occurrences of synchronous, predator first, and prey first recoveries statistically
199 indistinguishable as well (chi-square test, $p=0.43$; Supplementary Fig. 7).

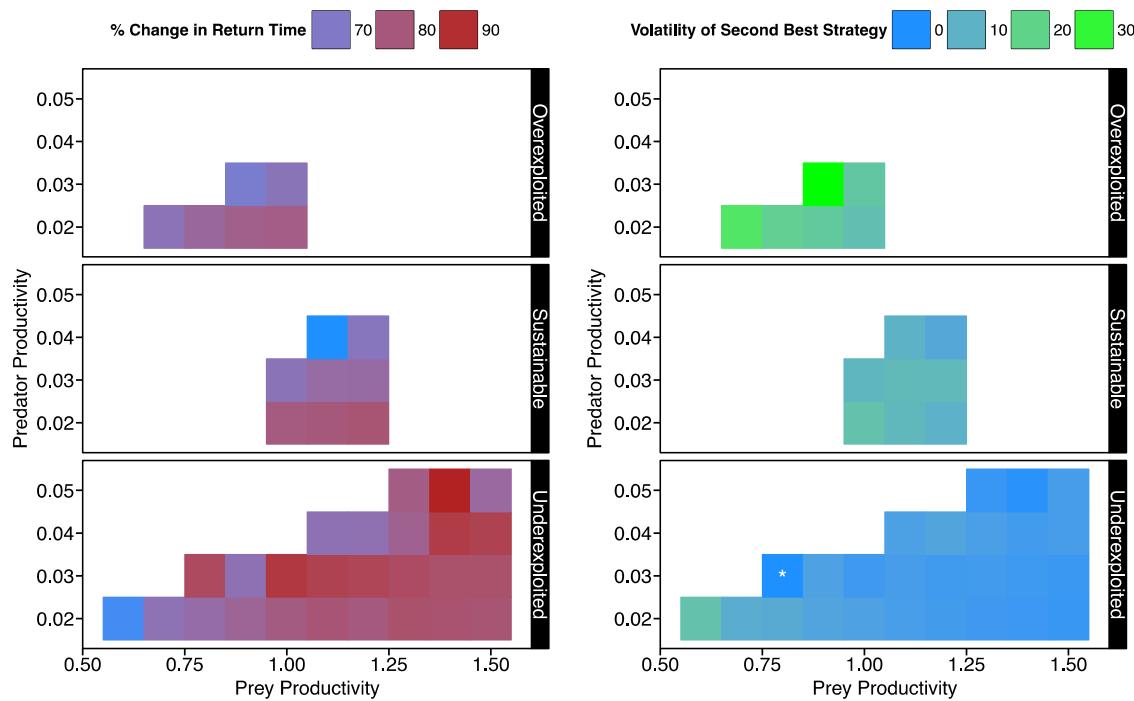
200 **Supplementary Figure 1.** Influence of alternative histories of exploitation (A,B) and
201 different predator and prey intrinsic productivity rates (C,D) on the effectiveness of three
202 recovery scenarios.

203



204

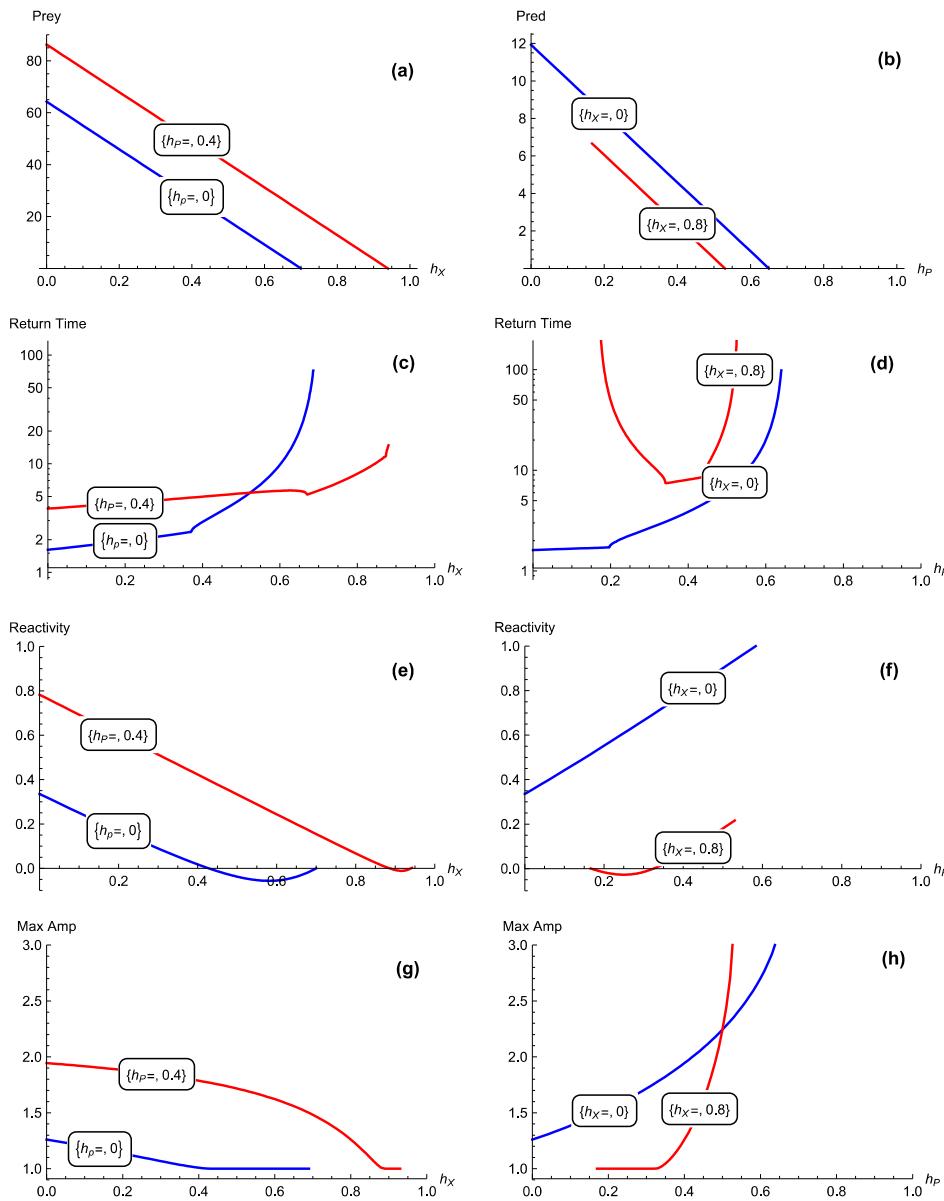
205 **Supplementary Figure 2.** Comparison of community (left) return times and (right)
 206 volatilities for a range of predator ($a_X=a_Y$) and prey (r_X) intrinsic productivity rates and
 207 across three exploitation scenarios. Community return times under synchronous recovery
 208 are compared to the next best strategy, while community volatilities are reported for the
 209 second best recovery strategy, as predator first recovery always produces zero volatility.
 210 Blank cells represent parameter combinations that cannot lead to coexistence of predator
 211 and prey at under-, sustainably- and over-exploited levels.



212

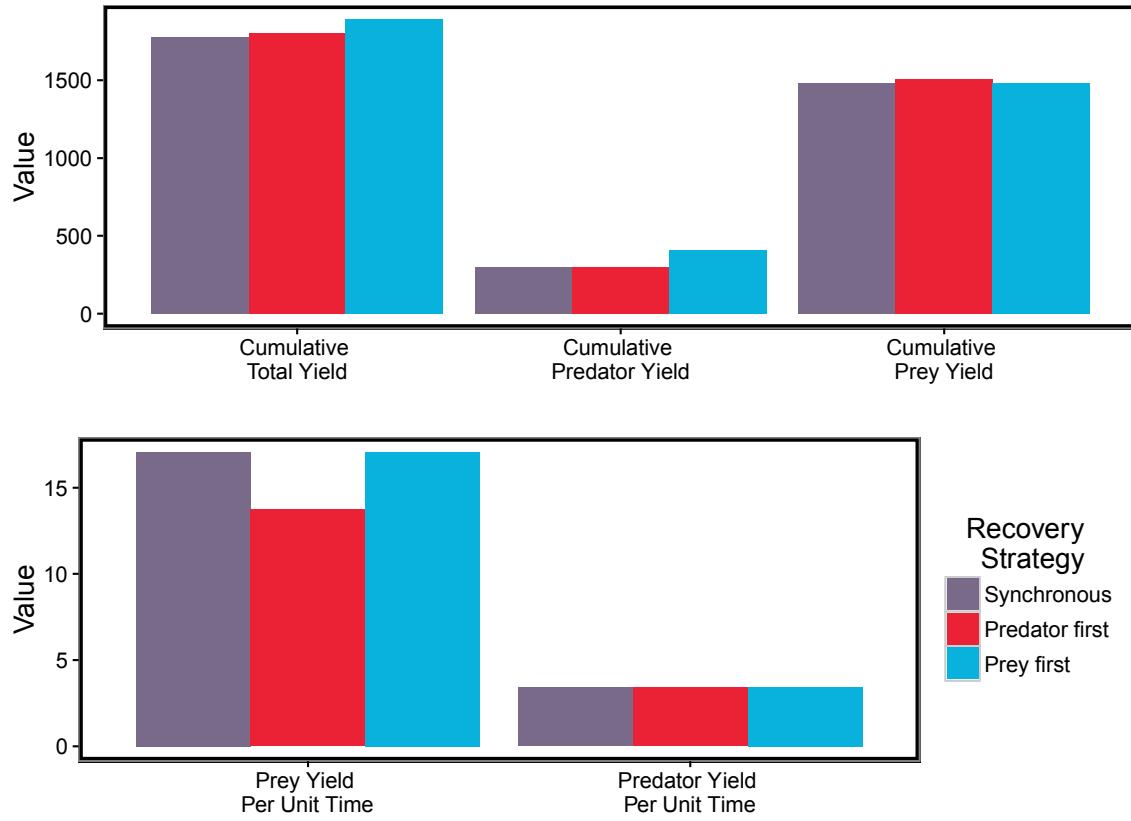
213 **Supplementary Figure 3.** Analytical solutions for the (a-b) equilibrium densities, (c-d)
 214 characteristic return times, (e-f) reactivities, and (g-h) maximum amplification volumes
 215 of the community as a function of per capita harvest rates on the prey and predator. Lines
 216 are drawn only within parameter ranges allowing feasible fixed-point coexistence. See
 217 Supplementary Information text for details, and *Methods* in the main text for other
 218 parameter values.

219



220

221 **Supplementary Figure 4.** Effect of three recovery scenarios under the baseline
222 parameter set on (top) cumulative yields and (bottom) yields per unit time.



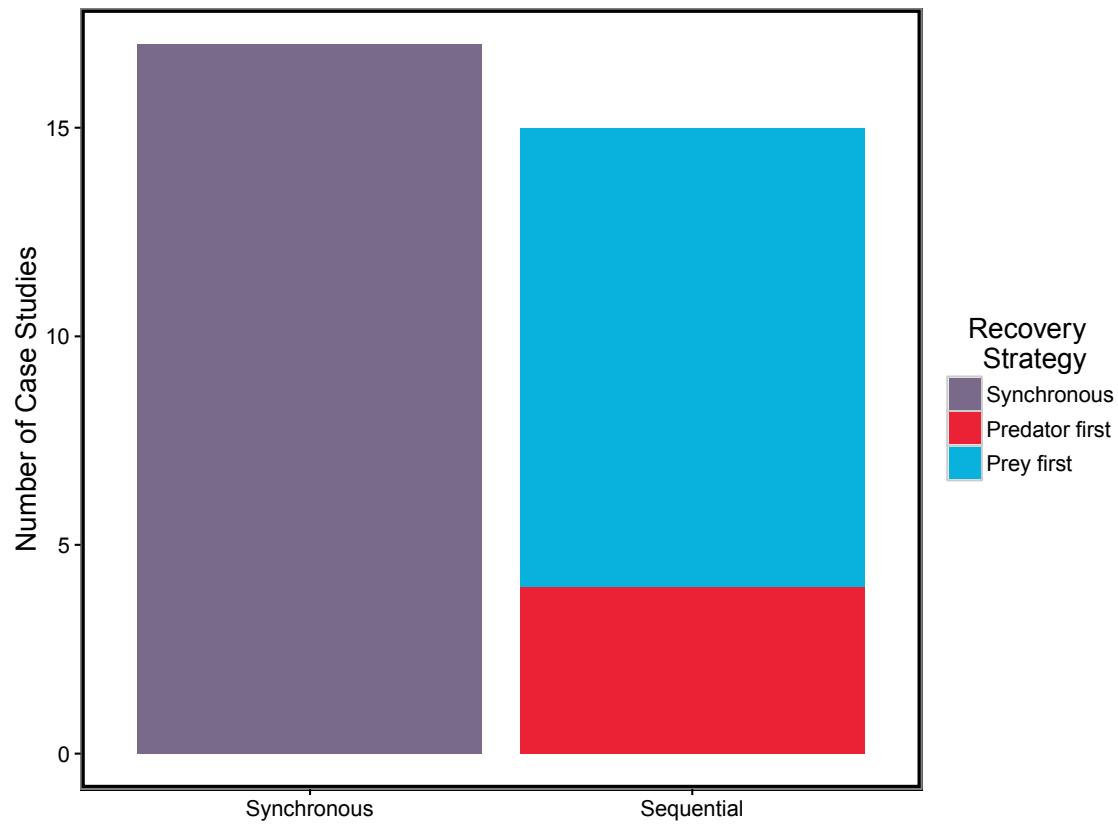
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225 **Supplementary Figure 5.** Frequency of synchronous vs sequential recoveries (chi-
226 square test: $p=0.87$) and synchronous ($N=17$), predator first ($N=4$), and prey first ($N=11$)
227 recoveries (chi-square test: $p=0.02$), identified in the RAM legacy database³.

228

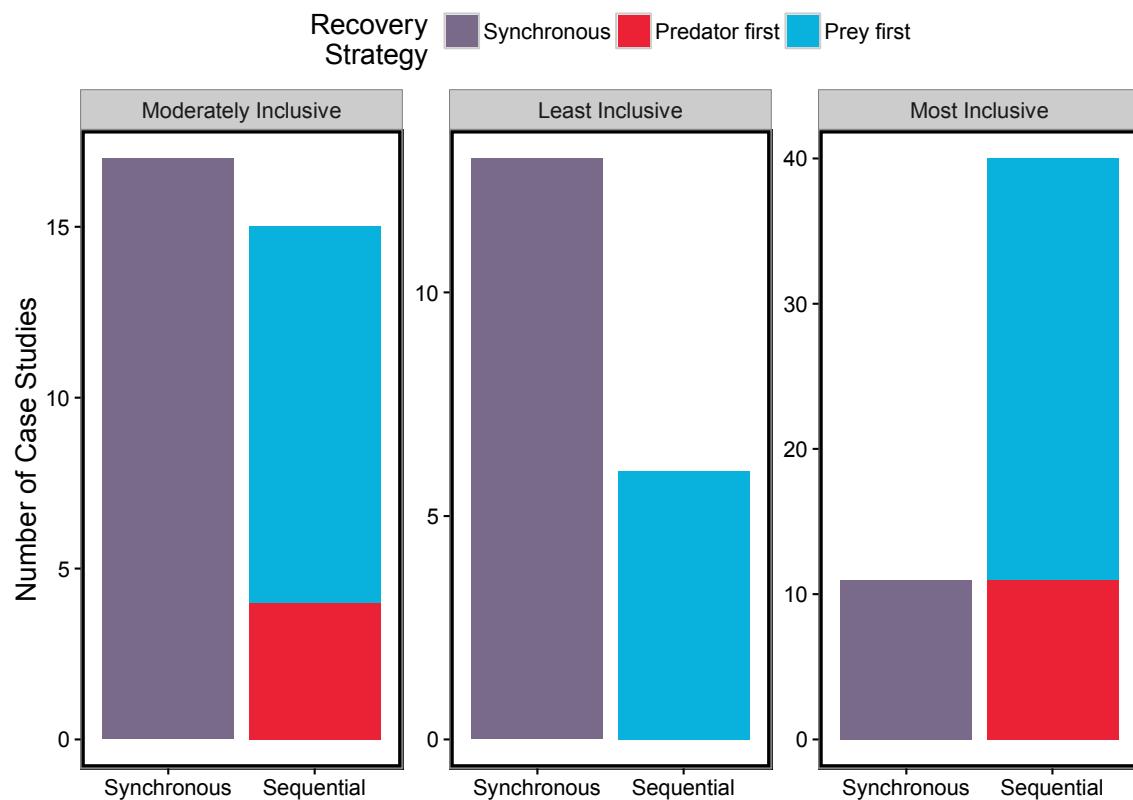
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230

231 **Supplementary Figure 6.** Frequency of synchronous vs sequential recoveries, and
232 synchronous, predator first, and prey first recoveries, identified in the RAM legacy
233 database³. Left, the moderately inclusive categorization, such that overlapping depletion
234 periods of predator and prey were defined as 3+ years, trophic level distinctions were
235 defined as ≥ 0.5 TL unit difference, and synchronous recoveries were identified as those
236 that occurred within 3 years of one another. Middle, the least inclusive categorization
237 (synchronous $N=13$, predator first $N=0$, prey first $N=6$), such that overlapping depletion
238 periods of predator and prey were defined as 5+ years, trophic level distinctions were
239 defined as ≥ 1 TL unit difference, and synchronous recoveries were identified as those
240 that occurred within 5 years of one another. Right, the most inclusive categorization
241 (synchronous $N=11$, predator first $N=10$, prey first $N=30$), such that overlapping
242 depletion periods of predator and prey were defined as 1+ years, trophic level distinctions
243 were defined as ≥ 0 TL unit difference, and synchronous recoveries were identified as
244 those that occurred in the same year.

245

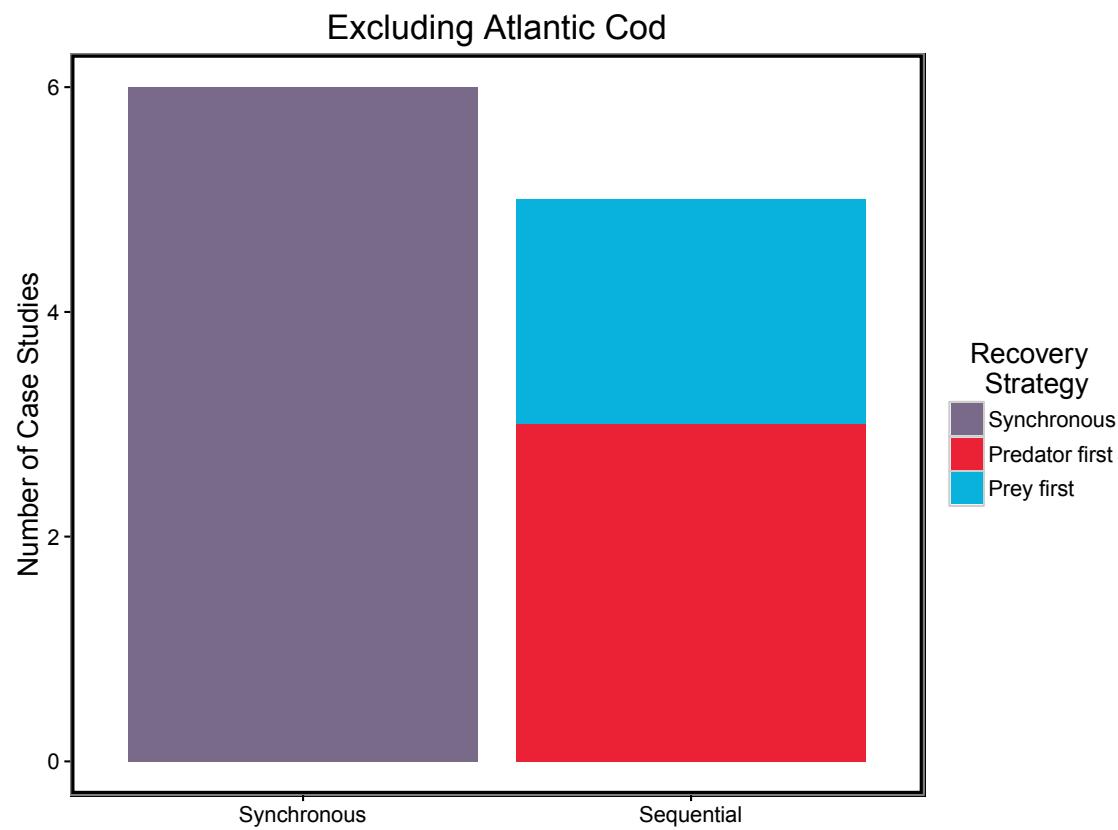


246

247 **Supplementary Figure 7.** Frequency of synchronous vs sequential recoveries, and
248 synchronous ($N=6$), predator first ($N=3$), and prey first ($N=2$) recoveries, identified in the
249 RAM legacy database³, after removing Atlantic cod from the case studies.

250

251



252

253 **Supplementary Table 1.** Steady state analytical solutions under exploited and three
 254 recovery scenarios.

Equilibrium	Prey	Predator
Exploited	$\frac{((-hX+r)s+a(d+hP-acY))K}{rs+a^2cK}$	$\frac{-r(d+hP-acY)+ac(-hX+r)K}{rs+a^2cK}$
Synchronous	$\frac{(rs+a(d-acY))K}{rs+a^2cK}$	$\frac{r(-d+ac(Y+K))}{rs+a^2cK}$
Prey-first	$\frac{(rs+a(d+hP-acY))K}{rs+a^2cK}$	$\frac{r(d+hP-ac(Y+K))}{rs+a^2cK}$
Predator-first	$\frac{((-hX+r)s+a(d-acY))K}{rs+a^2cK}$	$\frac{-dr+ac(-hXK+r(Y+K))}{rs+a^2cK}$

255
256

257
258**Supplementary Table 2.** Case studies extracted from Neubauer et al.³ for empirical analysis.

Region	Country	Predator	Prey	Predator Depletion period	Prey Depletion period	Depletion period overlap	Recovery strategy (moderate)	Recovery strategy (least)	Recovery strategy (most)
Baltic Area 30 (ICES)	Multinational	Atlantic cod	Herring	1966-1982	1979-1989	3	Predator first	Predator first	-
Baltic Area 31 (ICES)	Multinational	Atlantic cod	Herring	1987-2011	1994-2007	13	Prey first	Prey first	Synchronous
Baltic Areas 22 and 24	Multinational	Atlantic cod	Sprat	1986-2012	1986-1992	6	Prey first	Prey first	Prey first
Baltic Areas 25-32	Multinational	Atlantic cod	Herring	1987-2011	1996-2011	15	Synchronous	Synchronous	Synchronous
Baltic Areas 25-32	Multinational	Atlantic cod	Sprat	1966-1982	1979-1983	3	Synchronous	Predator first	-
Baltic Areas 25-32	Multinational	Atlantic cod	Sprat	1987-2011	1986-1992	5	Prey first	Prey first	Prey first
Faroe Plateau	Multinational	Atlantic cod	Haddock	1990-1995	1991-1996	4	-	Predator first	-
Faroe Plateau	Multinational	Atlantic cod	Haddock	2004-2012	2008-2011	3	-	Prey first	-
FO 3LN	Multinational	Greenland halibut	Redfish species	1995-2007	1992-2000	5	Prey first	Prey first	-
FO 3LNO	Multinational	Greenland halibut	American Plaice	1995-2007	1986-2008	12	Synchronous	Predator first	-
FO 3LNO	Multinational	Greenland halibut	Yellowtail Flounder	1995-2007	1976-1999	4	Prey first	Prey first	-
FO 3N	Multinational	Atlantic cod	American Plaice	1960-2008	1986-2008	22	Synchronous	Synchronous	-
FO 3NO	Multinational	Atlantic cod	Redfish species	1960-2008	1992-2000	8	Prey first	Prey first	-
FO 3NO	Multinational	Atlantic cod	Yellowtail Flounder	1960-2008	1976-1999	23	Prey first	Prey first	Prey first
FO 3NO	Multinational	Greenland halibut	Atlantic cod	1995-2007	1960-2008	12	-	Predator first	-
FO 5Y	USA	Atlantic Halibut	Haddock	1890-2008	1986-1998	12	-	Prey first	-
FO 5Y	USA	Atlantic Halibut	Witch Flounder	1890-2008	1994-2008	14	Synchronous	Synchronous	Synchronous
FO 5YZ	USA	Atlantic Halibut	American Plaice	1890-2008	1986-2008	22	Synchronous	Synchronous	-
FO 5Z	USA	Atlantic Halibut	Winter Flounder	1890-2008	1985-2007	22	Synchronous	Prey first	Synchronous
FO 5Zjm	Canada	Atlantic cod	Haddock	1993-2004	1970-2002	9	-	Prey first	-

Region	Country	Predator	Prey	Predator Depletion period	Prey Depletion period	Depletion period overlap	Recovery strategy (moderate)	Recovery strategy (least)	Recovery strategy (most)
Georges Bank	USA	Atlantic cod	Acadian redfish	1984-2008	1957-2008	24	Synchronous	Synchronous	Synchronous
Georges Bank	USA	Atlantic cod	Haddock	1984-2008	1968-2006	22	-	Prey first	-
Georges Bank	USA	Atlantic cod	White hake	1984-2008	1994-2008	14	-	Synchronous	-
Georges Bank	USA	Atlantic cod	Yellowtail Flounder	1984-2008	1974-2008	24	Synchronous	Synchronous	Synchronous
Gulf of Alaska	USA	Pacific cod	Arrowtooth flounder	1977-1983	1961-1981	4	-	Prey first	-
Gulf of Alaska	USA	Arrowtooth flounder	Pacific Ocean perch	1961-1981	1977-1998	4	Predator first	Predator first	-
Gulf of Alaska	USA	Pacific cod	Pacific Ocean perch	1977-1983	1977-1998	6	Predator first	Predator first	-
Gulf of Maine	USA	Atlantic cod	Northern shrimp	1983-2008	1998-2006	8	Synchronous	Prey first	Synchronous
Gulf of Maine	USA	Atlantic cod	Yellowtail Flounder	1983-2008	1985-2008	23	Synchronous	Synchronous	Synchronous
Iceland	Multinational	Atlantic cod	Capelin	1991-2012	2005-2007	2	-	Prey first	-
Iceland	Multinational	Atlantic cod	Haddock	1991-2012	1983-2012	21	-	Synchronous	-
Iceland	Multinational	Atlantic cod	Herring	1991-2012	1989-2011	20	Synchronous	Prey first	Synchronous
Iceland	Multinational	Haddock	Capelin	1983-2012	2005-2007	2	-	Prey first	-
Iceland	Multinational	Haddock	Capelin	1983-2012	1980-1984	1	-	Prey first	-
Irish Sea	Multinational	Atlantic cod	European Plaice	1978-2011	1995-2006	11	Prey first	Prey first	Prey first
Irish Sea	Multinational	Atlantic cod	European Plaice	1978-2011	1976-1988	10	Prey first	Prey first	Synchronous
Irish Sea (Northern)	Multinational	Atlantic cod	Herring	1978-2011	1978-2011	33	Synchronous	Synchronous	Synchronous
Kattegat	Multinational	Atlantic cod	common European sole	1982-2011	1984-1990	6	Prey first	Prey first	Prey first
North Sea	Multinational	Atlantic cod	Herring	1989-2011	1996-2002	6	Prey first	Prey first	Prey first
North Sea	Multinational	Atlantic cod	Norway pout	1989-2011	2003-2008	5	Synchronous	Prey first	Synchronous
North Sea	Multinational	Atlantic cod	Sandeel	1989-2011	2003-2008	5	Synchronous	Prey first	Synchronous
Northeast Arctic	Multinational	Atlantic cod	Haddock	1979-2009	1977-1993	14	-	Prey first	-

Region	Country	Predator	Prey	Predator Depletion period	Prey Depletion period	Depletion period overlap	Recovery strategy (moderate)	Recovery strategy (least)	Recovery strategy (most)
Northeast Arctic	Multinational	Greenland halibut	Atlantic cod	1975-2011	1979-2009	30	-	Prey first	-
Northeast Arctic	Multinational	Greenland halibut	Haddock	1975-2011	1977-1993	16	-	Prey first	-
Northeast Arctic	Multinational	Greenland halibut	Pollock	1975-2011	1984-1999	15	-	Prey first	-
Northeast Atlantic	Multinational	Hake	Whiting	1981-2011	1981-2002	21	-	Prey first	-
Northeast Atlantic North	Multinational	Hake	Whiting	1981-2011	2007-2008	1	-	Prey first	-
Prince Rupert District	Canada	Sablefish	Pacific herring	1997-2005	1966-2008	8	Synchronous	Predator first	-
Queen Charlotte Islands	Canada	Sablefish	Pacific herring	1997-2005	1986-2008	8	Synchronous	Predator first	-
Rhode Island	USA	Tautog	American lobster	1992-2008	1959-2008	16	-	Synchronous	-
West Coast of Vancouver Island	Canada	Pacific cod	Pacific herring	1994-2002	1995-2008	7	Predator first	Predator first	-

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261**Supplementary Table 3.** Documentation of predator-prey relationships analyzed for the case studies extracted from Neubauer et al.³.

Region	Predator	Prey	Predator-prey relationship	Predator diet citation
Gulf of Alaska	Arrowtooth flounder	Pacific Ocean perch	In the Gulf of Alaska, rockfishes comprise approximately 0.2% (frequency of occurrence) of adult diets, and are reported to be known potential predators of juvenile Pacific Ocean perch.	Knoth, B. A. and Foy, R.J. 2008. Temporal variability in the food habits of arrowtooth flounder (<i>Atheresthes stomias</i>) in the Western Gulf of Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-184,30 p. Rooper, C.N., Boldt, J.L., and Zimmerman, M. 2007. An assessment of juvenile Pacific Ocean perch (<i>Sebastodes alutus</i>) habitat use in a deepwater nursery. <i>Estuarine, Coastal and Shelf Science</i> 75:371-380.
Georges Bank	Atlantic cod	Acadian redfish	Redfish comprise 14% diet composition in cod stomachs near the Gulf of St. Lawrence (Kohler and Fitzgerald 1969), and while small redfish can make up <1% of cod diet by mass in the southern Gulf of St. Lawrence (Hanson and Chouinard 2002), cod over 50 cm near the Flemish Cap contained ~95% small	Hanson, J.M. and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. <i>Journal of Fish Biology</i> 60: 902–922. Kohler, A.C., and Fitzgerald, D.N. 1969. Comparisons of Food of Cod and Haddock in the Gulf of St. Lawrence and on the Nova Scotia Banks. <i>Journal Fisheries Research Board of Canada</i> 26(5): 1273-1287.

			redfish (Templeman 1965).	Templeman, W. 1965. Some instances of cod and haddock behavior and concentrations in the Newfoundland and Labrador areas in relation to food. ICNAF Special Publication 6: 449-461.
FO 3N	Atlantic cod	American Plaice	American Plaice are from 6% (Hanson and Chouinard 2002) to 27% (Waiwood and Majkowski 1984) composition in cod stomachs in the southern Gulf of St. Lawrence; 37% of cod over 100 cm in length contained some plaice (highest predation on small plaice; Powles 1958a).	Hanson, J.M. and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. Journal of Fish Biology 60: 902–922. Powles, P.M. 1958a. Life history and ecology of American plaice (<i>Hippoglossoides platessoides</i> F.) in the Magdalen Shallows. Journal Fisheries Research Board of Canada 22(2):565-598. Waiwood, K. and Majkowski, J. 1984. Food consumption and diet composition of cod, <i>Gadus morhua</i> , inhabiting the southwestern Gulf of St. Lawrence. Environmental Biology of Fishes Vol II 1:63-78.
Iceland	Atlantic cod	Capelin	Atlantic cod consume a mean of 27.1% (peak 40%) of capelin in their diet (by weight; primary fish prey) in	Jaworski, A. and Ragnarsson, S.A. 2006. Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES

			Iceland.	Journal of Marine Science 63: 1682-1694.
Kattegat	Atlantic cod	common European sole	Up to 4% (by weight) of cod diet in the North Sea is European sole (Daan 1973; Mackinson and Daskalov 2007).	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . Netherlands Journal of Sea Research 6 (4): 479–517. Mackinson, S. and Daskalov, G., 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Sci. Ser. Tech Rep., Cefas Lowestoft, 142: 196pp.
Irish Sea	Atlantic cod	European Plaice	European Plaice comprise from 2% (Mackinson and Daskalov 2007) to 20% (Daan 1973) of cod diet by weight in the North Sea.	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . Netherlands Journal of Sea Research 6 (4): 479–517. Mackinson, S. and Daskalov, G., 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Sci. Ser. Tech Rep., Cefas Lowestoft, 142: 196pp.

Faroe Plateau; George's Bank (FO 5Zjm); Iceland; NE Arctic	Atlantic cod	Haddock	Haddock of all sizes make up 25-40% of cod diet in North Sea (Daan 1973), and approximately 9% in the Gulf of St. Lawrence (Kohler and Fitzgerald 1969).	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . Netherlands Journal of Sea Research 6 (4): 479–517. Kohler, A.C., and Fitzgerald, D.N. 1969. Comparisons of Food of Cod and Haddock in the Gulf of St. Lawrence and on the Nova Scotia Banks. Journal Fisheries Research Board of Canada 26(5): 1273-128.
Baltic Area 30, 31 (ICES); Baltic Areas 25-32; Iceland; Northern Irish Sea; North Sea	Atlantic cod	Herring	Cod have from 2-15% herring in their diet in the North Sea (Daan 1973).	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . Netherlands Journal of Sea Research 6 (4): 479–517.
Gulf of Maine	Atlantic cod	Northern shrimp	Northern shrimp make up around 20% of cod diet, across size classes (Hanson and Chouinard 2002).	Hanson, J.M. and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. Journal of Fish Biology 60: 902–922.
North Sea	Atlantic cod	Norway pout	Norway pout comprise 6.7% of Atlantic cod diet in the North sea (Mackinson and	Mackinson, S. and Daskalov, G, 2007. An ecosystem model of the North Sea to support an ecosystem

			Daskalov 2007).	approach to fisheries management: description and parameterisation. Sci. Ser. Tech Rep., Cefas Lowestoft, 142: 196pp.
FO 3NO	Atlantic cod	Redfish species	Redfish (all sizes) comprise 14% diet composition in cod stomachs near the Gulf of St. Lawrence (Kohler and Fitzgerald 1969), and while small redfish can make up <1% of cod diet by mass in the southern Gulf of St. Lawrence (Hanson and Chouinard 2002), cod over 50 cm near the Flemish Cap contained ~95% small redfish (Templeman 1965).	Hanson, J.M. and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. <i>Journal of Fish Biology</i> 60: 902–922 Kohler, A.C., and Fitzgerald, D.N. 1969. Comparisons of Food of Cod and Haddock in the Gulf of St. Lawrence and on the Nova Scotia Banks. <i>Journal Fisheries Research Board of Canada</i> 26(5): 1273-1287. Templeman, W. 1965. Some instances of cod and haddock behavior and concentrations in the Newfoundland and Labrador areas in relation to food. <i>ICNAF Special Publication</i> 6: 449-461.
North Sea	Atlantic cod	Sandeel	Sandeel can make up from 5% (Mackinson and Daskalov 2007) to 10% of adult cod diet by weight (Daan 1973).	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . <i>Netherlands Journal of Sea Research</i> 6 (4): 479–517.

				Mackinson, S. and Daskalov, G, 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Sci. Ser. Tech Rep., Cefas Lowestoft, 142: 196pp.
Baltic Areas 22 and 24; Baltic Areas 25-32	Atlantic cod	Sprat	Sprat in cod diet can reach 20% by weight in the North Sea (Daan 1973).	Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, <i>Gadus Morhua</i> . Netherlands Journal of Sea Research 6 (4): 479–517.
Georges Bank	Atlantic cod	White hake	White hake, all sizes, can make up 5% of cod over 60cm diet (Powles 1958b) or from 1-19% volume in stomachs of cod greater than 30cm in the Gulf of St. Lawrence.	Powles, P.M. 1958b. Studies of Reproduction and Feeding of Atlantic Cod (<i>Gadus callarias L.</i>) in the Southwestern Gulf of St. Lawrence. Journal Fisheries Research Board of Canada 15(6):1383-1402.
FO 3NO; George's Bank, Gulf of Maine	Atlantic cod	Yellowtail Flounder	Pleuronectidae comprise from approximately 3% of cod diet by mass (Kohler and Fitzgerald 1969), 6-32% of cod diet by volume (Powles 1958b), and up to 40% composition (Waiwood and	Powles, P.M. 1958b. Studies of Reproduction and Feeding of Atlantic Cod (<i>Gadus callarias L.</i>) in the Southwestern Gulf of St. Lawrence. Journal Fisheries Research Board of Canada 15(6):1383-1402.

			Majowski 1984) in the Gulf of St. Lawrence.	Kohler, A.C., and Fitzgerald, D.N. 1969. Comparisons of Food of Cod and Haddock in the Gulf of St. Lawrence and on the Nova Scotia Banks. Journal Fisheries Research Board of Canada 26(5): 1273-1287. Waiwood, K. and Majkowski, J. 1984. Food consumption and diet composition of cod, <i>Gadus morhua</i> , inhabiting the southwestern Gulf of St. Lawrence. Environmental Biology of Fishes Vol II 1:63-78.
FO 5YZ (Gulf of Maine and George's Bank)	Atlantic Halibut	American Plaice	American Plaice less than 35cm make up to 13.6% of cod diet on the Newfoundland-Labrador Shelf (Bundy <i>et al.</i> 2000).	Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310:1-157.
FO 5Y (Gulf of Maine)	Atlantic Halibut	Haddock	Haddock have been reported as a main fish prey item of Atlantic halibut through stomach content analyses (Nickerson 1978), and comprise about 1% of cod diet in the Grand Bank and Gulf of Maine areas (Kohler 1967).	Kohler, A.C. 1967. Size at Maturity, Spawning Season, and Food of Atlantic Halibut. Journal Fisheries Research Board of Canada 24(1): 53-66. Nickerson, J.T.R. 1978. The Atlantic halibut and its utilization. Marine Fisheries Review 40(7): 21-25; Cargnelli, L.M., Griesbach, S.J., and Morse, W.W. 1999. Essential Fish Habitat Source

				Document: Atlantic Halibut, <i>Hippoglossus hippoglossus</i> , Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-125: 1-17.
FO 5Z (George's Bank)	Atlantic Halibut	Winter Flounder	Flounder has been reported as a main fish prey item of Atlantic halibut through stomach content analyses (Nickerson 1978). They also make up from 4% ("flatfishes"; Kohler 1967) to 13.6% ("flounders" including winter flounder; Bundy <i>et al.</i> 2000) of cod diet on the Newfoundland-Labrador Shelf.	Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. <i>Can. Tech. Rep. Fish. Aquat. Sci.</i> 2310:1-157. Kohler, A.C. 1967. Size at Maturity, Spawning Season, and Food of Atlantic Halibut. <i>Journal Fisheries Research Board of Canada</i> 24(1): 53-66.
FO 5Y (Gulf of Maine)	Atlantic Halibut	Witch Flounder	Flounder has been reported as a main fish prey item of	Nickerson, J.T.R. 1978. The Atlantic halibut and its utilization. <i>Marine Fisheries Review</i> 40(7): 21-25; Cargnelli, L.M., Griesbach, S.J., and Morse, W.W. 1999. Essential Fish Habitat Source Document: Atlantic Halibut, <i>Hippoglossus hippoglossus</i> , Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-125: 1-17. Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model

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FO 3LNO	Greenland halibut	American Plaice	American Plaice make up less than 1% of Greenland halibut diet on the Newfoundland-Labrador Shelf, but are included as a prey item.	Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310:1-157.
FO 3NO; Northeast Arctic	Greenland halibut	Atlantic cod	Atlantic cod are approximately 4.5% of Greenland halibut diet in the	Hovde, S. C., Albert, O. T., and Nilssen, E. M. 2002. Spatial, seasonal and ontogenetic variation

			Northeast Arctic (Hovde <i>et al.</i> 2002).	in diet of Northeast Arctic Greenland halibut (<i>Reinhardtius hippoglossoides</i>). ICES Journal of Marine Science, 59: 421–437.
Northeast Arctic	Greenland halibut	Haddock	Haddock comprise approximately 0.4% of Greenland halibut diet in the Northeast Arctic (Hovde <i>et al.</i> 2002).	Hovde, S. C., Albert, O. T., and Nilssen, E. M. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (<i>Reinhardtius hippoglossoides</i>). ICES Journal of Marine Science, 59: 421–437.
Northeast Arctic	Greenland halibut	Pollock	Pollock are about 0.2% of Greenland halibut diet in the Northeast Arctic (Hovde <i>et al.</i> 2002).	Hovde, S. C., Albert, O. T., and Nilssen, E. M. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (<i>Reinhardtius hippoglossoides</i>). ICES Journal of Marine Science, 59: 421–437.
FO 3LNO	Greenland halibut	Redfish species	Redfish species of all sizes make up approximately 25% of Greenland halibut diet on the Newfoundland-Labrador Shelf (Bundy <i>et al.</i> 2000).	Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310:1-157.
FO 3LNO	Greenland halibut	Yellowtail Flounder	"Flounders" (including yellowtail flounder) of all sizes make up approximately	Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador

			0.3% of Greenland halibut diet on the Newfoundland-Labrador Shelf (Bundy <i>et al.</i> 2000).	Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310:1-157.
Iceland	Haddock	Capelin	Capelin make up to 15% of haddock diet by weight in Iceland (Jaworski and Ragnarsson 2006).	Jaworski, A. and Ragnarsson, S.A. 2006. Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES Journal of Marine Science 63: 1682-1694.
Northeast Atlantic	Hake	Whiting	Adult whiting comprise of less than 5% of hake diets near the Mediterranean Iberian coast (Cartes <i>et al.</i> 2004).	Cartes, JE., Rey, J., Lloris, D., and Gil de Sola, L. 2004. Influence of environmental variables on the feeding and diet of European hake (<i>Merluccius merluccius</i>) on the Mediterranean Iberian coast. J. Mar. Biol. Ass. U.K. 84: 831-835.
Gulf of Alaska	Pacific cod	Arrowtooth flounder	Adult Arrowtooth flounder comprise 1-3% of adult cod diet in the Gulf of Alaska (Aydin <i>et al.</i> 2007; Urban 2012).	Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., and Friday, N. 2007. A Comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems Through Food Web Modeling. NOAA Technical Memorandum NMFS-AFSC-178: 1-298
				Urban, D. 2012. Food habits of Pacific cod and walleye pollock in

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West Coast of Vancouver Island	Pacific cod	Pacific herring	Pacific herring occur in Pacific cod diets with 43% frequency on average, with peak occurrences of 75-100% at some times of the year off the West Cost of Vancouver Island (Ware and McFarlane 1986).	Ware, D.M. and McFarlane, J.A. 1986. Relative impact of Pacific hake, sablefish and Pacific cod on west coast of Vancouver Island herring stocks. International North Pacific Fisheries Commission Bulletin 47: 67-78.
Gulf of Alaska	Pacific cod	Pacific Ocean perch	Pacific cod are reported to be known potential predators of juvenile Pacific Ocean perch, with juveline POP comprising less than 1% of cod diet.	Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., and Friday, N. 2007. A Comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems Through Food Web Modeling. NOAA Technical Memorandum NMFS-AFSC-178: 1-298 Rooper, C.N., Boldt, J.L., and Zimmerman, M. 2007. An assessment of juvenile Pacific Ocean perch (<i>Sebastes alutus</i>) habitat use in a deepwater nursery. Estuarine, Coastal and Shelf Science 75:371-380.

Prince Rupert District; Queen Charlotte Islands	Sablefish	Pacific herring	Pacific herring have been reported as the most important fish prey off the southwest coast of Vancouver Island, found in up to 20% of stomachs (Tanasichuk 1997), and comprise of 6% of diet by weight off Vancouver Island's west coast (Ware and McFarlane 1986).	Tanasichuk, R.W. 1997. Diet of sablefish, <i>Anoplopoma fimbria</i> , from the southwest coast of Vancouver Island. NOAA Technical Report NMFS 130: 93-97. Ware, D.M. and McFarlane, J.A. 1986. Relative impact of Pacific hake, sablefish and Pacific cod on west coast of Vancouver Island herring stocks. International North Pacific Fisheries Commission Bulletin 47: 67-78.
Rhode Island	Tautog	American lobster	Tautog have been observed feeding on small American lobster, although not in significant diet proportions (16% average mortality in an experimental setting).	Richards, R.A. 1992. Habitat selection and predator avoidance - ontogenetic shifts in habitat use by the Jonah crab <i>Cancer borealis</i> (Stimpson). Journal of Experimental Marine Biology and Ecology 156: 187-197. Bigelow, H.B., and Schroeder, W.C. 1953. Fishes of the Gulf of Maine. Fishery Bulletin 53: 577 p. Steimle, F.W. and Shaheen, P.A. 1999. Tautog (<i>Tautoga onitis</i>) Life History and Habitat Requirements. NOAA Technical Memorandum NMFS-NE-118: 1-22.

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