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Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory

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Many marine ecosystems have undergone 'regime shifts', i.e. abrupt reorganizations across trophic levels. Establishing whether these constitute shifts between alternative stable states is of key importance for the prospects of ecosystem recovery and for management. We show how mechanisms underlying alternative stable states caused by predator–prey interactions can be revealed in field data, using analyses guided by theory on size-structured community dynamics. This is done by combining data on individual performance (such as growth and fecundity) with information on population size and prey availability. We use Atlantic cod (*Gadus morhua*) and their prey in the Baltic Sea as an example to discuss and distinguish two types of mechanisms, 'cultivation-depensation' and 'overcompensation', that can cause alternative stable states preventing the recovery of overexploited piscivorous fish populations. Importantly, the type of mechanism can be inferred already from changes in the predators' body growth in different life stages. Our approach can thus be readily applied to monitored stocks of piscivorous fish species, for which this information often can be assembled. Using this tool can help resolve the causes of catastrophic collapses in marine predatory–prey systems and guide fisheries managers on how to successfully restore collapsed piscivorous fish stocks.

1. Introduction

Regime shifts, representing abrupt ecosystem reorganizations across trophic levels, have occurred in marine systems worldwide [1,2]. Ecosystems have shifted to new states (or regimes) characterized by different species compositions, dominating interactions [3] and sometimes even ecosystem services [4]. If current and former regimes constitute alternative stable states [5,6], that is, are stabilized by feedbacks internal to the system, the system will not return to its former state when the external conditions do (as it does in the case of a phase shift, i.e. a shift in a single equilibrium state driven by external conditions [6]), but remain in the current regime (a case known as hysteresis [6]). The presence of alternative states stabilized by internal feedbacks has been suggested to explain the lack of recovery of overgrazed kelp beds [7], overgrown coral reefs [8] and overexploited top predatory fish [9,10]. Resolving whether observed marine regime shifts involve shifts between alternative stable states is especially crucial for management. For example, only reducing fishing intensity may be insufficient for an

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overexploited food web to recover in the presence of alternative stable states, as successful management strategies will depend on the mechanisms in the food web that stabilize the overexploited state.

There are methods to detect regime shifts [11–13] and alternative stable states [14]. Patterns in observation data from natural food webs, such as shifting relationships between a system state and a pressure variable or shifts in population abundance time series across trophic levels can indicate multiple regimes, but do not identify mechanisms stabilizing alternative stable states. Experimental approaches have therefore been developed [11,14] showing the presence of alternative stable states in laboratory and field experiments [14,15]. However, large marine systems are not possible to subject to controlled experiments (rendering no clear evidence for alternative stables states in these systems [14]). Identifying the presence and mechanisms of alternative stable states in marine food webs therefore requires novel approaches.

Here, we show how the mechanisms underlying alternative stable states in food webs can be resolved using field data, when the occurrence of these states is caused by predator–prey interactions. Theory on size-structured community dynamics [16] predicts how feedbacks between changes in individual performance and population dynamics can cause alternative stable states in predator–prey systems [17–22]. Therefore, it is possible to unveil the mechanisms underlying alternative stable food-web states by combining population and community-level information (population sizes and prey availability) with data on processes occurring at the level of individuals, such as growth and fecundity. Evidence in such field data for each link in the stabilizing feedbacks gives strong support for alternative stable states. Most importantly, it enables identification of the underlying mechanisms, which sets this approach apart from viewing population abundance data alone.

In our presentation of this approach, we focus on predator–prey interactions in exploited marine food webs. Overexploitation of fish-feeding fish species ('piscivores') can cause population collapses with cascading effects on lower trophic levels in the food web [23], characteristic of many marine regime shifts [24]. We describe two types of mechanisms by which interactions between piscivorous fish and their fish prey lead to alternative stable states, preventing the recovery of overexploited piscivorous fish. We derive predictions on individual- and population-level responses corresponding to each mechanism using theory on size-structured community dynamics and assemble these in a framework for structured data analysis to detect and distinguish mechanisms underlying alternative stable states in data from real food webs. Finally, we illustrate the approach on the Atlantic cod (*Gadus morhua*) in the Baltic Sea.

2. Species interactions causing alternative stable states in exploited food webs

Two different types of mechanisms have been identified by which stabilizing feedbacks between a piscivore fish population and their fish prey lead to alternative stable states with high and low piscivore population abundance, 'cultivation-depensation' and 'overcompensation' (table 1). Common for these are that, at high abundance, piscivores control the dynamics (and abundance) of the prey fish population, whereas at low abundance they do not. Instead, the prey controls piscivore population growth, preventing piscivore population recovery and hence also top-down control of the prey population. A prerequisite for these mechanisms to occur is consequently that interactions between piscivores and their fish prey are strong.

(a) Cultivation–depensation (mechanism 1)

In fish communities, species often both prey on and compete with each other, denoted as intra-guild predation [28]. Adult piscivores feed on prey fish, whereas juvenile piscivores and prey fish commonly compete for invertebrate prey. At high abundances, piscivores, by controlling their prey fish population through predation, 'cultivate' an environment with low competition for their offspring. By contrast, when piscivore abundance is low, piscivore population growth is controlled by competition with prey fish during their non-piscivorous life stage (i.e. depensation [18]; table 1). A variant of the cultivation–depensation mechanism is when the prey fish instead is a predator on early life stages of the piscivore (mechanism 1b, table 1). In this case, the piscivore population, when at low abundance, is controlled by predation by the prey fish after their release from top-down control [18].

(b) Overcompensation (mechanism 2)

In the second type of mechanism, the stabilizing feedback results from how the prey fish population responds dynamically to the predation by piscivores. Predation depends on the body size of the predator, relative to that of its prey. Piscivores therefore rarely feed on all size classes in the prey fish population, but only part of the size range (often the smaller individuals). When piscivore abundance is high, predation releases intraspecific competition in the prey fish. Surviving prey fish individuals therefore grow faster and, due to their resulting larger size and higher condition, have a higher fecundity as adults. Their total reproductive output can then more than compensate for the biomass lost due to predation ('overcompensate') and the biomass production of prey fish vulnerable to predation increases following predation, leading to higher predator population growth (table 1). Correspondingly, at low piscivore abundance, predation has little effect on prey fish body growth and reproductive output. Intraspecific competition in the prey population is then high, reproductive output low and the amount of vulnerable prey fish individuals is lower. This lack of suitably sized prey fish individuals prevents the piscivore population from recovering, a mechanism first shown to induce alternative stable states by de Roos & Persson [19]. A variant of this mechanism is when the overcompensation in prey biomass does not occur through increased abundance of vulnerable prey individuals, but through their increased condition (weight in relation to body length; mechanism 2b, table 1). The high intraspecific competition in the prey fish population after a piscivore collapse then results in lean prey individuals, with low energetic content. If piscivores cannot compensate for such poor food quality by eating more food items (e.g. if limited by handling time), they are unable to grow and reproduce because their prey, although abundant, constitute 'junk food' (table 1), and the piscivore population will not rebuild.

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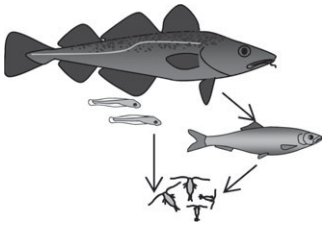
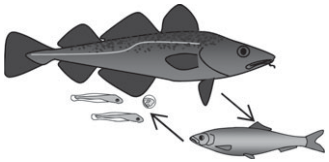
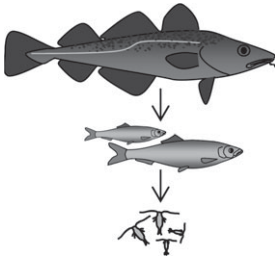
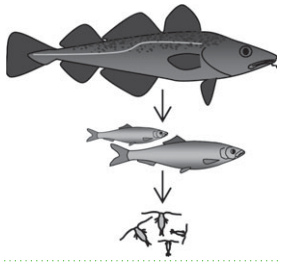
Table 1. Mechanisms that can cause alternative stable states with abundant versus non-recovering piscivore populations. The dominating feeding interactions under which each mechanism occurs are illustrated, showing different feeding stages of the piscivore (cod), their prey fish and zooplankton resources (arrows pointing in the direction of predation). The loop details the feedback stabilizing each of the alternative stable states (here shown for the high piscivore abundance state). Cod stocks for which the respective mechanism has been suggested to prevent recovery are listed. Numbers of the mechanisms are used as reference in the main text and in figure 1.

no.	mechanism	dominating interactions	stabilizing feedback loop (at high piscivore abundance)	references	cod stock non-recovery [suggested by]
1a	'Competitive *cultivation-depensation*' prey competing with early predator life stages		predation decreases abundance of prey fish → prey fish consumption of zooplankton decreases → abundance of zooplankton increases → predator population increases → predation decreases abundance of prey fish	[18]	Gulf of St Lawrence [25], Baltic Sea [9], Newfoundland [18] and Eastern Scotian Shelf [26]
1b	'Predatory *cultivation-depensation*' prey predating on early predator life stages		predation decreases abundance of prey fish → predation from prey on egg & larvae decreases → egg mortality in predator decreases → predator population increases → predation decreases abundance of prey fish	[18]	North Sea [10], Baltic Sea [27] and Gulf of St Lawrence [25]
2a	'Abundance *overcompensation*' predation-induced competitive release in prey		predation decreases abundance of vulnerable prey fish → competition within prey fish population decreases → abundance of vulnerable prey increases → more prey fish caught → predator population increases → predation decreases abundance of vulnerable prey fish	[19]	NW Atlantic [19] and Baltic Sea [21]
2b	'Condition *overcompensation*' predation-induced competitive release in prey		predation releases competition in prey fish → prey fish condition increases → more energy per prey fish caught → predator population increases → predation releases competition in prey fish		

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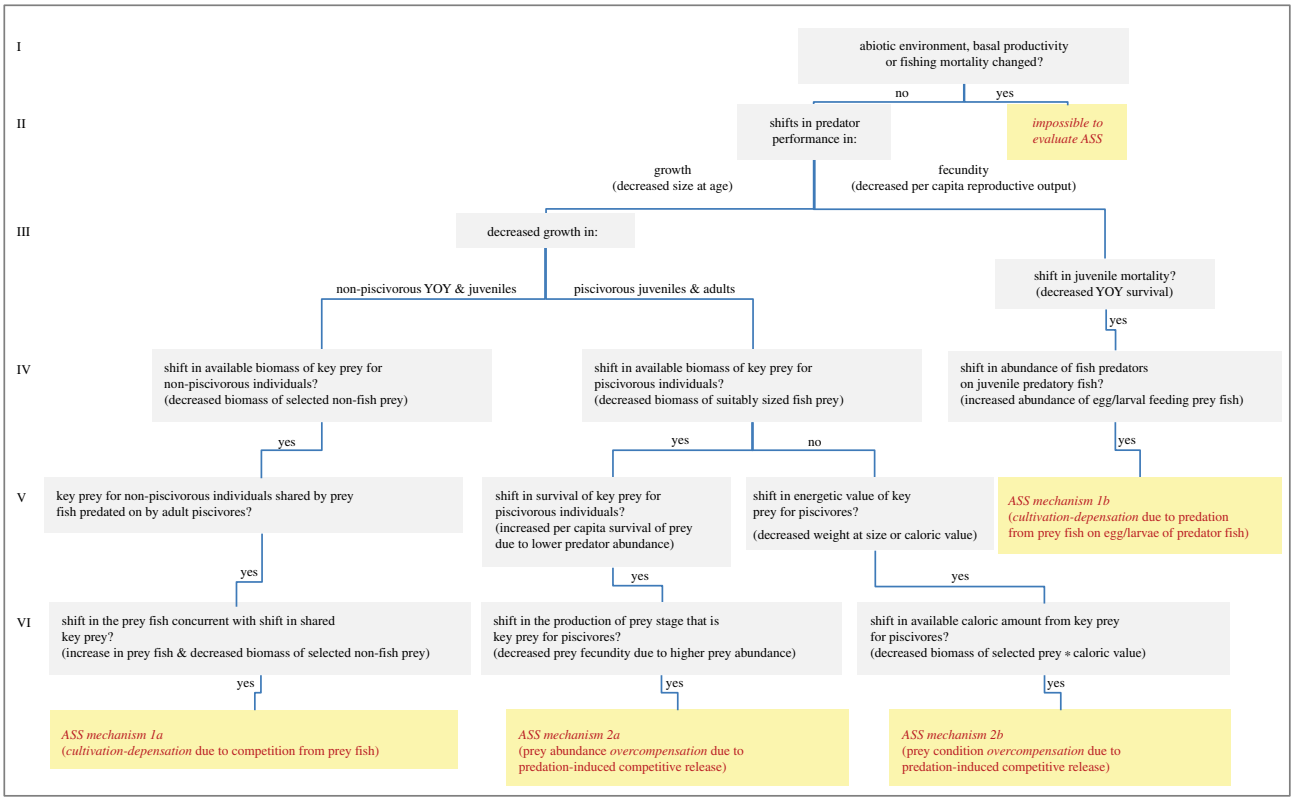

Figure 1. The framework for data analysis to distinguish among four mechanisms that can lead to alternative stable states in piscivorous fish populations. Parentheses describe expected changes when a system shifts to a state with low piscivore population size. The roman numbering on the left is used as reference in the text to denote the question level to which presented results pertain. ASS, alternative stable states; YOY, young of the year. See main text for further explanations. (Online version in colour.)

3. Resolving the mechanisms in real systems

Stabilizing predator–prey feedbacks have been suggested to explain the lack of recovery of a large number of Atlantic cod stocks (table 1), a species involved in many of the observed marine regime shifts [29]. The presence of predator–prey feedback mechanisms have commonly been proposed on the basis of population abundance data from these cod stocks and their prey [10,18,25–27]. However, clearer indications of these mechanisms can be found by analysing the individual performance of cod in their different life stages, as all these mechanisms underlying alternative stable states involve size- and life-stage-dependent responses (table 1).

Based on theoretical analyses of size-structured interacting predator and prey populations that account for individual-level processes (such as resource-dependent body growth and size-dependent feeding, metabolism and energy allocation) [19,22,30], piscivore individuals are expected to undergo different changes in their performance following a shift to low abundance depending on which mechanism keeps the piscivore population in the low abundance state. If prey fish are competing with early life stages of piscivores for zooplankton (mechanism 1a), these individuals are expected to grow slower due to resource limitation, whereas the performance of larger piscivorous individuals of the same population will not change [22,30]. If the piscivore population instead is regulated by a lack of suitably sized fish prey or by poor condition of suitably sized prey due to high intraspecific competition among fish prey (mechanism 2a and b, respectively), it is instead piscivorous individuals that will grow slowly, whereas growth of non-piscivorous individuals will not be impeded [19]. By contrast, predation from prey fish on piscivore eggs or larvae (mechanism 1b) is not expected to negatively impact body growth of either zooplankton-feeding or piscivorous individuals, but to reduce egg/larval survival [30].

To establish the presence of any of these mechanisms underlying alternative stable states, however, the changes in individual performance in the piscivore population need to be coupled to corresponding changes in each link in the stabilizing feedback loop formed by their interactions with the prey fish population (table 1). Figure 1 shows how these predictions can be assembled in a decision tree to guide a stepwise analysis of individual-level data from real piscivore populations and their prey to detect and distinguish the mechanisms causing alternative stable states. The first step is to identify whether the high piscivore abundance state and the low abundance state occur under similar environmental conditions (level I in figure 1), notably including intensity of exploitation. The second is to analyse whether the low piscivore abundance is due to decreased survival or individual growth (level II in figure 1), which distinguishes mechanism 1b from mechanisms 1a and 2. The third level analyses body growth of different feeding stages, before and during piscivory, to distinguish mechanism 1a from 2 (figure 1). Thereafter, concurrent changes in the essential prey for each of these feeding stages (mechanisms 1a, 2a and b) or predators on these life stages (mechanism 1b) are analysed (level IV in figure 1), and whether these are coupled to changes in abundance (mechanism 1a) or structure (mechanisms 2a and b) of the prey fish population (levels V and VI in figure 1).

4. An example of the data analysis framework: cod in the Baltic Sea

To illustrate how the proposed framework can be used, we apply it to the case of Atlantic cod in the Baltic Sea. The stock

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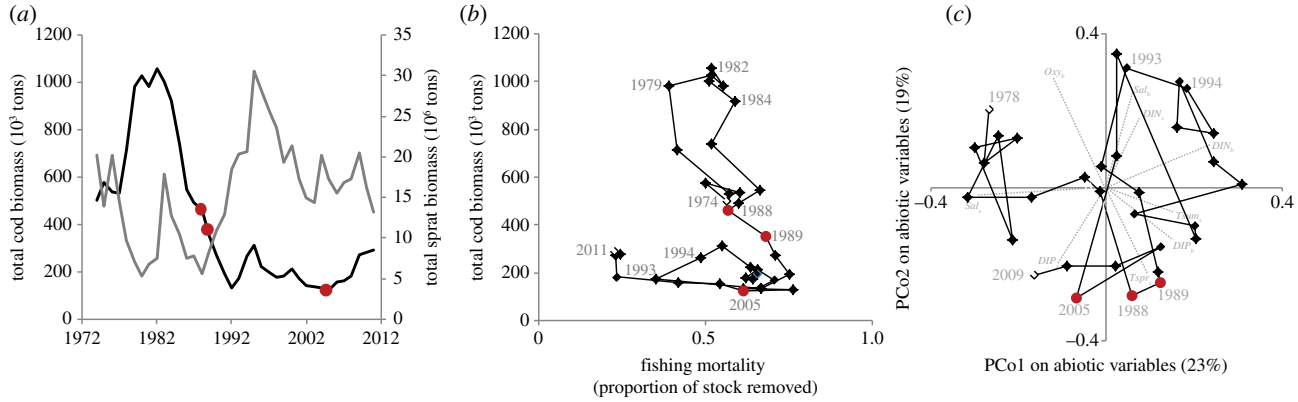

Figure 2. (*a*) Time trajectory of total population biomass of Eastern Baltic cod (black) and of sprat (grey) in the Baltic Sea, (*b*) fishing mortality (proportion of population annually removed by fishing) and total population biomass of Eastern Baltic cod (1974–2011) and (*c*) principal coordinates (PCo) of nine key abiotic variables in surface (*s*) and deep waters ('bottom', *b*) in the cod core distribution area (1978–2009; temperature in spring, *Tspr*, and summer, *Tsum*; oxygen concentration, *Oxy*; salinity, *Sal*; dissolved inorganic nitrogen, *DIN*, and phosphorous, *DIP*). Open symbols indicate the start and end year of each time series. Years of high versus low cod biomass under similar environmental conditions, used in analyses of changes in weight-at-age and weight-specific growth of cod, are highlighted by red circles. (Online version in colour.)

collapsed at the beginning of the 1990s due to overfishing and concurrent poor environmental conditions. Its subsequent lack of recovery during the late 1990s and early 2000s has been postulated to result from increased competition between sprat (*Sprattus sprattus*) and larval cod for zooplankton prey [3,9], resulting from decreased cod predation on sprat following the cod collapse (i.e. mechanism 1a in figure 1). This is based on a shift in the regulation of zooplankton dynamics, from bottom up in the period with cod domination (identified by Casini *et al*. [9] to end in 1992) to controlled by sprat predation from 1993 onwards [9]. Before attempting to untangle the support for any of the mechanisms causing alternative stable states in this system, we first consider whether the pre- and post-collapse cod biomasses may be alternative stable states (i.e. level I in figure 1). Cod biomass peaked in the early 1980s whereafter it decreased to about a fifth of its maximum biomasses, while sprat biomass showed an almost inverse pattern (figure 2*a*). Both high and low levels of cod stock biomasses have been observed for the same level of fishing mortalities (figure 2*b*), suggesting the occurrence of alternative states in cod population dynamics. For these to be indicative of alternative *stable* states (rather than a phase shift [6]), the external conditions (i.e. fishing and abiotic environment) need to be similar in the two states (level I in figure 1). The cod stock was subjected to fishing mortality of similar intensity in the 1980s as in mid-2000s, whereafter fishing mortality decreased and cod biomass subsequently increased (figure 2*b*). While the 1980s correspond to the 'high cod period' (for which abundance, biomass and body weight data on cod by age is only available from 1988 and 1989), 2005 therefore represents the last year of the 'low cod period', as the external conditions in terms of fishing mortality changed after this year. As for other relevant external conditions (level I in figure 1), a principal coordinate analysis of nine variables including temperature, salinity, nutrient and oxygen concentration (see the electronic supplementary material) shows that the abiotic environment was also similar in the late 1980s and in 2005 (figure 2*c*). Based on the similar fishing mortality and comparable abiotic conditions (figure 2*b*,*c*), the lower cod biomass in 2005 compared with in the late 1980s cannot be explained by different external conditions (level I in figure 1). We therefore proceed to analysing cod individual performance (level II in figure 1).

Because we lack egg production and egg survival information for cod, there is no direct data on cod fecundity (level II in figure 1) and we therefore have to restrict our analysis of cod performance to changes in body growth (level III in figure 1). As a consequence, we cannot draw any conclusions regarding the presence of mechanism 1b (predatory cultivation–depensation). To study body growth, we calculated weight-specific annual growth and body length corresponding to the average weight at age (see the electronic supplementary material). Because cod diet is body size-dependent, we categorized cod age groups into non-piscivores and piscivores based on their average length at age (electronic supplementary material, figure S1). At the end of their first growing season, young-of-the-year cod are too small to be fully piscivorous and they feed predominantly on benthic prey [31], while 1-year-old cod (and older) in quarter 4 are so large that they are likely to be piscivorous [32]. For both non-piscivorous and piscivorous cod, data suggest that growth has shifted between the late 1980s and 2005 (figure 3*a*–*c*). Mean weight of 0-year-olds at the end of their first year was higher in 2005 than in the late 1980s (figure 3*a*). By contrast, weight-specific growth of 1-year-olds was lower in 2005 than at the end of the 1980s (figure 3*b*). The growth of older piscivorous cod was also lowest in 2005, but has decreased continuously rather than shifted between the two periods (figure 3*c*). However, it must be noted that this comparison is of single years (due to lack of data and the need for similar environmental conditions) lacking variation because of the length-corrected sampling procedure (see the electronic supplementary material), preventing strong inferences. Growth seems to have increased among non-piscivorous individuals but decreased among, at least the younger, piscivorous cod individuals in the period with low cod biomass compared to when cod biomass was high. Thus, the growth changes observed in these data are not in line with mechanism 1a, competitive cultivation–depensation (level III in figure 1), which brings us to continue along the branch of mechanism 2 at level III (figure 1).

To support any of the proposed mechanisms underlying alternative stable states, changes in predatory fish individual performance (figure 3*a*–*c*) need to be linked to changes in their prey (level IV in figure 1). Because fish diet changes

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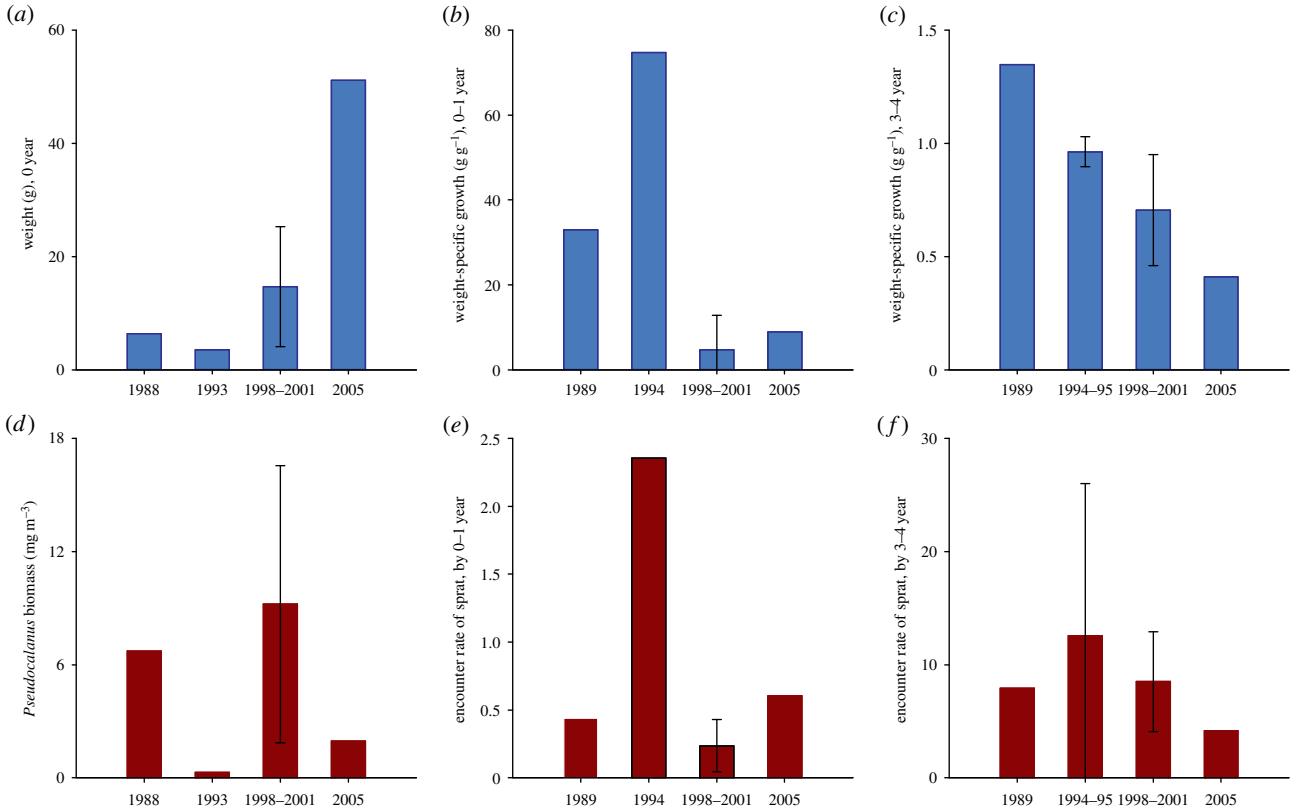

Figure 3. (*a*–*c*) Performance of cod at different life stages and (*d*–*f*) availability of their respective prey. Average weight of 0-year cod after first growing season (*a*), and annual weight-specific increase in weight of 1-year-old cod (*b*) and 4-year-old cod (*c*). Biomass concentration of key zooplankton prey (*Pseudocalanus* spp.) (*d*) and total encounter rate (ton yr^{-1}) with sprat prey for cod individuals with mean length of (*e*) 1-yr-olds and (*f*) 4-yr-olds (for annual length at age for these ages, see the electronic supplementary material, figure S1). Bars show standard deviations. (Online version in colour.)

with their body size, the size-dependent shifts in food items and prey size preferences need to be accounted for. Biomass of the key zooplankton prey for non-piscivorous young-of-the-year cod, *Pseudocalanus* spp., was lower in 1988 than in 2005 (figure 3*d*), showing a pattern opposite to observed changes in weight of young-of-the-year cod (figure 3*a*). When deriving prey availability for piscivorous cod, we used fish prey size preferences of differently sized cod individuals and their attack rates derived by van Leeuwen *et al.* [32] from cod stomach data. To obtain the total encounter rate with suitably sized fish prey for cod of different length, we multiplied these length-specific attack rates with sprat biomass at length (see the electronic supplementary material). Figure 3*e* shows that the shift in growth of piscivorous cod may partly be linked to prey availability, measured as the size-specific rate of encounter of sprat prey. However, there is little difference in encounter rate with sprat for cod between the late 1980s and 2005, and the dominating change is an increase in encounter rate in the intermediate period (figure 3*e*) when growth of 1-year-old piscivorous cod also peaked (figure 3*b*). For 4-year-old cod, encounter rate with sprat does also partly covary with the observed decline in cod growth (figure 3*c*,*f*). Both their growth and encounter rate were lowest in 2005, and the encounter rate is also lower in 2005 than in 1988. However, the variation around the estimated encounter rates is high (figure 3*e*,*f*), which may result from compiling size-dependent encounter rates for age classes across cohorts. While age information is necessary to estimate individual body growth, size-dependent encounter rates show resource availability, and can be used to indicate resource dynamics. Therefore, we additionally analysed the encounter rate with sprat for piscivorous cod directly for different size classes across years (figure 4). Size-specific rate of encounter of sprat prey has decreased for all sizes of cod since the period with high cod biomass (figure 4*a*; level IV in figure 1).

The encounter rate peaks a few years after the peak in cod biomass (cf. figures 4*a* and 2*a*; for encounter rate of e.g. 45 cm cod the highest correlation, $\rho = 0.45$, with cod biomass occurs at a lag of 3 years), suggesting a top-down effect of cod predation on the sprat population, necessary for all three mechanisms. However, we lack information on length-specific survival rate and fecundity of sprat, needed to investigate the extent and impact of cod predation. We therefore analysed the production of suitably sized sprat indirectly (i.e. move directly to level VI in figure 1), by contrasting the encounter rate with sprat prey for two sizes of cod. These two size classes of cod, 20 and 45 cm, were chosen such that they feed on almost completely different size ranges of fish (electronic supplementary material, figure S2). The rate of encounter of larger sprat, suitable for 45 cm cod, increased before the encounter rate with the smaller sprat sizes that are suitable prey for 20 cm cod (figure 4*b*; highest correlation, $\rho = 0.38$, occurs at a 2-year lag). This suggests that an increased encounter rate for large cod, and hence predation on large sprat, may have led to an increased production of small sprat (level VI in figure 1). This may occur if predation reduces intraspecific density-dependence among large sprat to such a degree that their individual growth or condition improves, and results in higher reproductive output, i.e. production of small sprat. Alternatively, the high encounter rate of large sprat represents a strong sprat cohort that may have been caused by some external conditions not accounted for, followed by their high reproductive output of small sprat. However, the encounter rate for 45 cm and for 20 cm cod cycled, out of phase, until the early

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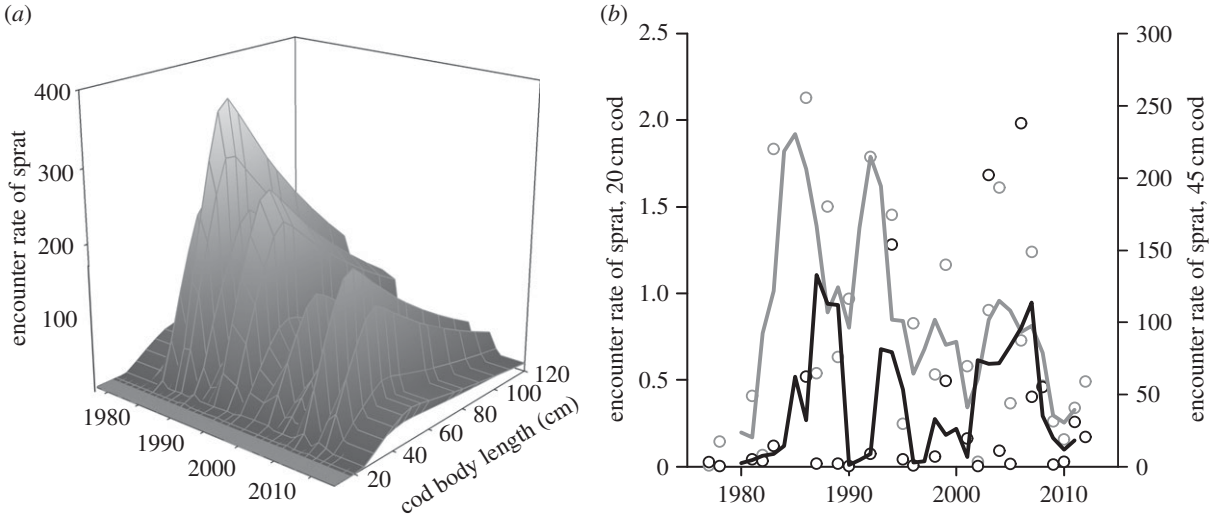

Figure 4. Encounter rate (ton yr^{-1}) of sprat for cod of different body length for (*a*) all sizes of cod across all years, and (*b*) for 20 cm cod (black) and 45 cm cod (grey) predating on different, largely non-overlapping, size-groups of sprat (lines are 3-year running averages, individual years as open symbols).

1990s (figure 4*b*; highest correlation in 1977–1992, $\rho = 0.55$, occurs at a 2-year lag), with peaks of encounter rate of large sprat also following on those of smaller sprat. This suggests that the higher production of small sprat subsequently led to higher predation on small sprat, which reduced competition among them. Given that smaller sprat are competitively superior to larger sprat [33], their reduced abundance may also have released larger sprat from competition. This may have led to increased growth, and hence biomass, of larger sprat. This out-of-phase cycling of production of small and large sprat during the period with high cod biomass suggests top-down control of sprat by cod. Thus, cod predation may indirectly affect sprat population structure via competitive release and, hence, production of suitably sized sprat prey (i.e. mechanism 2a in figure 1). In line with this, the out-of-phase cycling between the availability of small and large sprat indicative of top-down control by cod ceased when cod biomass collapsed (figure 4*b*; highest correlation in 1994–2012, $\rho = 0.39$, occurs when there is no lag between encounter rate of 20 and 45 cm cod).

The application of the data analysis framework thus suggests that the high cod biomass in the 1980s and the low cod biomass in 2005 occurring under similar environmental conditions may have represented alternative stable states, caused by mechanism 2a; before the cod collapse, top-down control of sprat by cod led to high production of suitably sized sprat prey. In particular, predation by large cod seems to have increased production of sprat suitable for smaller cod, and vice versa (although we lack length-specific survival rates of sprat to confirm this). After the cod collapse and loss of top-down control, production of sprat of suitable sizes for large and for small piscivorous cod ceased to alternate and was halved for large cod (figure 4*b*), despite the higher total population biomass of sprat. This indicates that of the tested mechanisms (1a and 2a, as data was not available to test mechanism 1b), prey abundance overcompensation (2a in figure 1), may have been underlying the presence of alternative high and low cod biomass states.

5. Discussion

Establishing the presence of alternative stable states in systems in which a regime shift has occurred is of key importance for the prospects of system recovery and management. Available non-experimental methods (needed for large marine food-webs), relying solely on population abundance time series, can indicate shifts and multiple regimes in marine food webs [11]. We have shown how analyses of within-population observation data (i.e. from a lower ecosystem level) guided by theory on size-structured community dynamics [16] can be used to advance one step further: to distinguish possible causes of alternative stable states in real food webs.

Alternative stable states in marine food webs can be caused by feedbacks between size- and life-stage-dependent processes of individual predators and prey [16–22]. To resolve the relevant underlying mechanisms, it is necessary to accurately connect individual-level processes (i.e. energy acquisition and allocation, governing body growth and reproduction) to population dynamics through population and community-level feedbacks. Consequently, when assessing population biomass production, it is essential to consistently account for individual energy intake. The energy available for an individual depends on production of its prey and on feeding on this prey by other individuals. These explicit links can be analysed using physiologically structured population models [34,35], which mechanistically link size-dependent individual processes and interactions to emergent population and community dynamics through resource-dependent individual body growth and reproduction. Analyses of physiologically structured population models can yield testable predictions regarding the feedback mechanisms underlying alternative stable states due to predator–prey interactions. Our approach provides for structured analyses testing these predictions using observational data, which allows for an actual understanding of food-web dynamics (such as causes of alternative stable states), unlikely to be gained from population abundance data alone.

When systems have flipped to an alternative stable state, only restoring external pressures (like fishing) of the former state is insufficient for the system to revert to its former state. Successful management then relies on knowledge of the mechanisms underlying the regime shift. Lake Takvatn in Norway provides an example of a successful management approach to bring the ecosystem back to an alternative stable state. In this lake brown trout (*Salmo trutta*) shifted to very low abundance after overexploitation, and stocking of its

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prey Arctic charr (*Salvelinus alpinus*) did not increase trout biomass [36]. Subsequent trout stocking also did not lead to recovery, whereas reduction of the charr population successfully restored the state with abundant trout. The difference in success between the management strategies can be explained when the mechanism underlying the two states is known. In Takvatn, trout recovery was hampered by lack of Arctic charr of suitable sizes as prey. After the collapse of brown trout, charr density and intraspecific competition increased, resulting in lower production of small charr (i.e. prey abundance overcompensation, mechanism 2a in table 1) [36]. Harvesting prey (charr) then resolves the high prey density problem directly, while stocking of the predator trout only does so indirectly. Thus, elucidating the mechanisms underlying alternative stable states is crucial for successful management.

In large exploited systems, where controlled experiments are practically impossible, our approach of combining individual- and population-level analyses makes it possible to demonstrate these mechanisms in observational data from multiple ecosystem levels (interacting species, populations and individuals). Specifically, by combining predator population biomass with predator body growth (size at age information) in different ontogenetic stages, particularly for life stages feeding on fish prey versus other types of prey, and subsequently with availability of their respective prey species (table 1) it was possible to disentangle the underlying mechanisms. The Baltic Sea example showed that it is especially important to account for both life-stage-specific and size-dependent feeding preferences. Although total sprat biomass increased following the collapse of cod, the availability of suitably sized sprat for cod to feed on did not. On the contrary, the size-dependent rate of encounter of sprat prey decreased for all available sizes of cod. Changes in suitably sized fish prey and other resources concurrent with changes in predator performance (and hence predator population sizes) provide strong support for the feedbacks leading to alternative stable states, but already predator growth (and fecundity) patterns alone can be used to infer the underlying mechanisms (table 1).

In the low cod biomass period in the Baltic Sea (mid-2000s), growth of piscivorous individuals was lower than in the period with high cod biomass (late 1980s), whereas the weight of young-of-the-year cod (primarily feeding on non-fish prey [31]) was higher. These patterns alone suggest that low cod biomass may be caused by a lack of suitably sized fish prey, due to prey overcompensation (mechanism 2, table 1) rather than lack of non-fish prey (mechanism 1a, table 1). That suitably sized sprat may be lacking is also supported by the decreased size-dependent rate of encounter of sprat prey suitable for 3- to 4-year-old cod. However, it should be noted that this inference is based on very few data points, for two reasons. First, age-resolved data with individual weights of cod was not available for the full period of cod population estimates. Second, because we focus on evidence of alternative stable states, we restricted this analysis to periods with similar environmental conditions, in terms of abiotic factors and fishing mortality, which occur only in very few years (1988–1989 and 2005). This does not mean that in other periods the mechanisms that may cause alternative stable states with high and low cod biomass are no longer acting; it only means that they cannot be disentangled from concurrent changes in the cod's abiotic environment and exposure to fishing. For example, rate of encounter of suitably sized sprat prey peaked a few years after the peak in cod population biomass, and peaks in availability of larger sprat prey were followed by those of smaller sprat, which suggests top-down control by cod affecting sprat population size structure and dynamics. The cessation of this cycling in the period previously identified as a sprat-dominated period (from 1993 [9]), with low cod biomass, further indicates that the mechanism of prey abundance overcompensation (mechanism 2a) may have been hampering cod population growth throughout this period. Thus, while these cannot be claimed to be strictly alternative stable states since the environment has changed considerably (figure 2*c*), the size-structured predator–prey interactions still seem important for predator recovery.

We have focused on alternative stable states arising from strong interactions between predatory fish and their fish prey. If these are weakened, e.g. if the predatory population is instead regulated by other prey species, in life stages not included here (table 1), these mechanisms stabilizing alternative states are predicted to not occur [32]. Considering the high diversity of many marine food webs, with their multiple interacting predators and prey, may suggest that strong predator–prey interactions are unlikely to occur. It is, however, common for omnivorous species to predominantly forage and depend on a particular prey type during different life-history stages. The diet of many fish species shift from zooplankton to fish prey throughout ontogeny (these species are 'ontogenetic specialists'). In such cases, strong predator–prey interactions do likely occur. Alternatively, predatory fish may indeed feed simultaneously (in the same life stage) on multiple types of prey. If reproduction in the predator population is regulated by the availability of only one of these prey, alternative stable states may still occur due to prey abundance overcompensation [21]. However, theory on mechanisms that may lead to alternative stable states in systems with predators feeding simultaneously on multiple size-structured prey species that interact with each other is still lacking [16]. However, changes in predator growth in particular feeding stages indicate both prey availability (independent of the number of prey species fed upon) and type of predator–prey mechanism that may be underlying alternative stable states with high and low predator biomass. Corroborating the presence of that mechanism also requires data on availability of prey, and hence knowledge of which prey species and prey sizes that are important for predator performance and population growth. As long as the predator is an ontogenetic specialist, or as long as the multiple prey species fed on by a generalist predator are not regulated by mutual size-dependent interactions, the analysis framework can be used to identify mechanisms underlying alternative stable states due to predator–prey interactions.

The applicability of this analysis framework may seem to rely heavily on the availability of detailed data on growth, survival and fecundity of piscivores in different ontogenetic stages, and on size-resolved data on densities of their respective prey species. The latter can be scarce for many exploited piscivore species, in particular in terms of lower trophic level prey resources. Indeed, any knowledge of the relative importance of different prey species for piscivore performance may be lacking. By contrast, data on body growth in piscivore populations should be easily assembled, as detailed information on exploited piscivorous fish species in terms of age, weight and length, is often gathered for the purpose of fish stock assessment and fisheries advice (although younger life stages may

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be under sampled). Body growth curves and size-dependent diet switches can together be used to infer the type of mechanism (1a, 1b or 2a/b in table 1) that may hamper piscivore population growth and stabilize such food-web states.

Our approach builds on information from growth and diet data, data from lower trophic levels and community theory accounting for size-dependent interactions in more complex communities. Using this approach to corroborate each mechanistic link underlying alternative stable states in predator–prey systems may only be possible in data-rich systems. However, the necessary data to infer the type of mechanism causing such regime shifts should be available for monitored stocks of piscivorous fish species. Thus, this is a tool that can be applied to data that is already available. The analysis framework presented here helps to resolve the causes of sudden shifts and catastrophic collapses in marine predatory–prey systems. Moreover, this approach provides insights into the mechanisms stabilizing potential overexploited regimes. Unless we start using the data and methods that are available and base fisheries management strategies on ecological understanding of food-web dynamics, any attempt to restore collapsed piscivore stocks risk being a shot in the dark.

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