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Facilitation of fisheries by natural predators depends on life history of shared prey

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Predators commonly share prey with human exploiters, intuitively suggesting that there is an inherent human–predator conflict through competition for prey. Here we studied the effects of fishing and predation mortality on biomass distributions and yields of shared prey using a size-structured model of competing populations, describing the life histories of Baltic Sea sprat and herring. Whereas both species responded in a similar fashion to increased fishing mortality, with decreasing juvenile and adult biomasses, we found that responses to predation mortality differed between species. Sprat only display weak compensatory responses with increasing predation mortality, while over a substantial range of mortalities there was a strong increase in adult (and total) herring biomass, i.e. overcompensation. The observed biomass overcompensation results from relaxed intraspecific competition as predation mortality increased, allowing for faster individual growth rates that in turn lead to a change in population composition (juvenile:adult biomass ratio). Our results suggest that the potential for biomass overcompensation is higher for species exhibiting substantial growth after maturation. Differences in size-selectivity of predators and fishing mortality resulted in a positive effect of predation mortality on fisheries yields, which can be explained by an overcompensatory response in adult herring biomass. Thus, somewhat counter intuitive, our results suggest that fishermen, depending on prey life history, may actually benefit from allowing for a higher abundance of predators, despite competing for shared prey.

Mortality is a major factor governing the structure and dynamics of ecological communities. The intuitive expectation is that mortality will decrease the abundance and biomass of a population as individuals are removed. Hence, there should be an inherent conflict between predator species targeting shared prey. Among surviving individuals, however, the effect of mortality in the population is commonly positive, leading to increased growth rates and fecundity as competition for resources is relaxed (Werner and Gilliam 1984, Craig et al. 2006). In size-structured populations, such individual-level responses to mortality can result in overcompensation in population fecundity and stage-specific biomass (de Roos and Persson 2002, Cameron and Benton 2004, Schröder et al. 2009, Ohlberger et al. 2011). Overcompensation arises as the relative composition (e.g. juvenile:adult biomass ratio) of populations changes with changing mortality which, in turn, relates to different responses in reproduction versus maturation rates following relaxed intraspecific competition (de Roos and Persson 2013). By specializing on different life-history stages of shared prey, predators may even help each other to persist by changing the prey size distribution (de Roos et al. 2008, Huss and Nilsson 2011). In addition to size- and food-dependent growth and reproduction, the strength of overcompensatory responses depends on the type of mortality imposed, i.e. size-independent or size-specific (de Roos et al. 2007). The extent to which the potential for biomass overcompensation varies among species is not known, although it has been speculated that differences in life-histories may explain variation in compensatory biomass responses to mortality (Walsh et al. 2011).

How predators coexist on shared resources has been the focus in ecological studies for decades (Hutchinson 1959). Not only do predator species share prey with other predators, but humans commonly exploit the prey species of these predators as well, making sustainable exploitation of the prey a challenging task. Accordingly, there has been an ongoing debate on how competition from natural predators affects human harvesting of consumer populations in the wild (May 1979, Yodzis 2001). For example, in marine food-webs, top-predators and fishermen potentially compete for shared prey fish. However, these two sources of mortality often differ in their size-selectivity; while mammal predators and fisheries often target larger prey (Law 2000), predation mortality from piscivorous fish is commonly negatively size-selective (Juanes et al. 2002).

Given a combination of harvesting and predation mortality with contrasting size-selectivities, human exploiters such as fishermen may in fact, contrary to popular belief (but see Yodzis 1994), benefit from allowing a higher biomass of predators with whom they share common prey (similar to emergent facilitation among natural predators, de Roos et al. 2008). A positive relationship between predation and prey biomass, leading to facilitation among predators, can result from increased prey growth rates, maturation and reproduction when predation relaxes competition among prey.

Most population models ignore fundamental characteristics of natural populations, such as variation in body size and the link between individual development and food availability (e.g. models in fisheries: Schnute and Richards 2001, Shepherd and Pope 2002). In light of the emerging theory regarding the effects of complex life-histories and food-dependent development on population and community dynamics (Miller and Rudolf 2011, de Roos and Persson 2013), studies on exploitation of natural populations should not ignore this complexity when aiming at understanding biologically relevant phenomena. Furthermore, most models on human exploitation of natural populations have historically been single prey and/or predator models (Quinn and Collie 2005, Marasco et al. 2007). Similarly, most models on the effects of size-selective predation mortality have focused on a single prey species (but see Hülsmann et al. 2005), ignoring effects of interspecific competition. Still, natural populations of pelagic fish species, exploited in marine fisheries worldwide, commonly exhibit strong interspecific competition (Garrison and Link 2000, Casini et al. 2006), like many other types of taxa. Hence, there is clear potential to increase our understanding about the interaction between human and natural predators by considering multiple prey species and individual-level processes such as size-and food-dependent growth and reproduction.

While the fisheries effects on large predatory fish stocks have been thoroughly documented, especially following the collapses of several important marine predatory fish stocks (Myers and Worm 2003), the effects on small pelagic fish are less well studied. Here, we contrast effects of fishing and predation mortality on biomass distributions and yield of two competing populations. These effects are studied using a size-structured model for two competing consumer populations exhibiting food-dependent growth, representing life histories of Baltic Sea sprat *Sprattus sprattus* and herring *Clupea harengus*, as in Huss et al. (2012). We hypothesize that opposing signs of size-selectivity will allow predators to facilitate fisheries by increasing adult prey fish biomass. We also evaluate the link between life-history type (i.e. growth potential, size at maturation, spawning characteristics) and potential for biomass overcompensation.

Model description

We study the effects of exploitation of forage fish systems impacted by natural predation using a relatively parameter rich model. This model is in fact an extension of the simplest model present in the literature that accounts for size-dependent feeding and discrete consumer reproduction (Persson et al. 1998), which are both fundamental characteristics of most temperate forage fish systems. Using a modeling approach in which a detailed representation of individual-level processes is embedded allowed us to explicitly study how size-selective exploitation and predation influence biomass dynamics in a size-structured competition system. Using the Baltic Sea sprat-herring system as basis for our model, we could realistically derive the size-dependency of prey vulnerability to predation by Atlantic cod *Gadus morhua* (hereafter referred to as cod), as well as fishing mortality. Also, evidence suggests that both intra- and inter-specific competition for shared resources is essential to understand what governs the dynamics of sprat and herring (Casini et al. 2010, Lindegren et al. 2011, Huss et al. 2012), which makes this an ideal species pair to base our model on, and to address questions about exploitation in competition systems.

We have used the framework of physiologically structured population models (PSPMs), which is specifically suited to handle the dynamics and size-dependent interactions of size-structured populations (Metz and Diekmann 1986). Characteristic for PSPMs is their distinction between individual (i) and population (p) states and environmental (e) conditions. The i-state represents the state of the individuals in terms of a collection of physiological traits (i.e. size, age, energy reserves), the p-state is a frequency distribution over all the i-states and the e-condition describes the condition of the environment (i.e. resources). All size-dependent processes and interactions between species are defined at the level of individuals (i-state), whereas population composition and dynamics (p-state) emerge from these processes. Thus, we make no a priori assumptions about population level patterns. The model used was recently developed and parameterized by Huss et al. (2012), to which we refer for a detailed description (Ecol. Arch. E093-075-A1). Here we only provide a brief overview of the model design, detailing parameters and model formulations that are different from the model in Huss et al. (2012). For a complete list of model parameters see Supplementary material Appendix 1 Table A1.1, for the individual-level model formulation see Supplementary material Appendix 1 Table A1.2 and for equations describing the state variables see Supplementary material Appendix 1 Table A1.3. All fore mentioned (i.e. "A") tables are found in Supplementary material Appendix 1.

The model describes the interactions between two size-structured competing fish species and their zooplankton prey (subdivided into two populations to be able to vary the overlap in resource use). We assume that resource productivity is constant and hence independent of resource density (Supplementary material Appendix 1 Table A1.3). Resource densities decrease following consumption, which, in turn, decreases the amount of food available for other consumers. Consequently, we explicitly considered the feedback between individuals and their environment, leading to food-dependent individual growth as well as competition for resources. Our model represents a mixed continuous–discrete time system where growth, survival, consumption and resource production are continuous processes, taking place throughout the growing season

(see below), whereas reproduction occurs as a discrete process at the start of the growing season only (Supplementary material Appendix 1 Table A1.2, Eq. 21). The model formulation consists of a mathematical description of how individual growth, survival and reproduction depend on individual physiology and food densities (Supplementary material Appendix 1 Table A1.2). The physiological state of individuals is characterized by irreversible mass (x), which consists of bones and organs that cannot be starved away, and reversible mass (y), including tissues such as fat, muscle and gonads, which can be starved away when maintenance costs exceed energy intake. We have used, for most analyses, a simplified model structure where both species feed only on zooplankton throughout life history (in contrast to Huss et al. 2012). Two zooplankton resources are accounted for. The parameter R represents the degree by which consumers overlap in their use of these zooplankton resources (Fig. 1), which is defined such that $R = 0.5$ implies both species to spend half of their time on each zooplankton resource (i.e. there is 100% overlap in resource use). Still, we also studied herring biomass responses to predation and fishing mortality allowing for herring to feed both on zooplankton and zoobenthos at large body sizes. In this scenario, herring start to feed on benthos when they reach a body length of 15 cm. They thereafter gradually increase their time spent foraging on benthos according to a sigmoidal function and decrease their time spent foraging on zooplankton accordingly. For implementation of benthos feeding, see Supplementary material Appendix 1 Table A1.2, Eq. 3, 6, 9 and 13. However, benthivory had no qualitative effect on the results.

All functions related to foraging (attack rates, digestion capacity) depend on irreversible mass only, whereas energy expenditure for maintenance is modelled as a power function of total body weight (sum of reversible and irreversible mass) (for graphical illustrations, see Supplementary material Appendix 2 Fig. A2.1). The attack rate on zooplankton is modelled as a hump-shaped function of consumer irreversible mass. The feeding rate follows a Holling type II functional response and is a function of prey mass encounter and the capacity to digest prey (Supplementary material Appendix 1 Table A1.2, Eq. 12–13). Digestion time per unit mass ingested is assumed to decrease with consumer irreversible mass (Supplementary material Appendix 1 Table A1.2, Eq. 14) and prey mass encounter is the product of the consumer's attack rate, prey density and prey individual mass (Supplementary material Appendix 1 Table A1.2, Eq. 7–11). Thus, energy assimilation is assumed to depend on resource densities and size-dependent foraging capacity, leading to size- and food-dependent growth. Consumed prey is converted to energy (biomass) assuming a constant conversion factor. Assimilated energy is first used to cover maintenance costs (Supplementary material Appendix 1 Table A1.2, Eq. 17) and is only thereafter used for growth in irreversible and reversible mass (Supplementary material Appendix 1 Table A1.2, Eq. 18–19). The growing season is set to be 250 days, assuming that the remainder of the year is a period of stasis. For both species, reproduction takes place during a discrete time period in the beginning of the growing season.

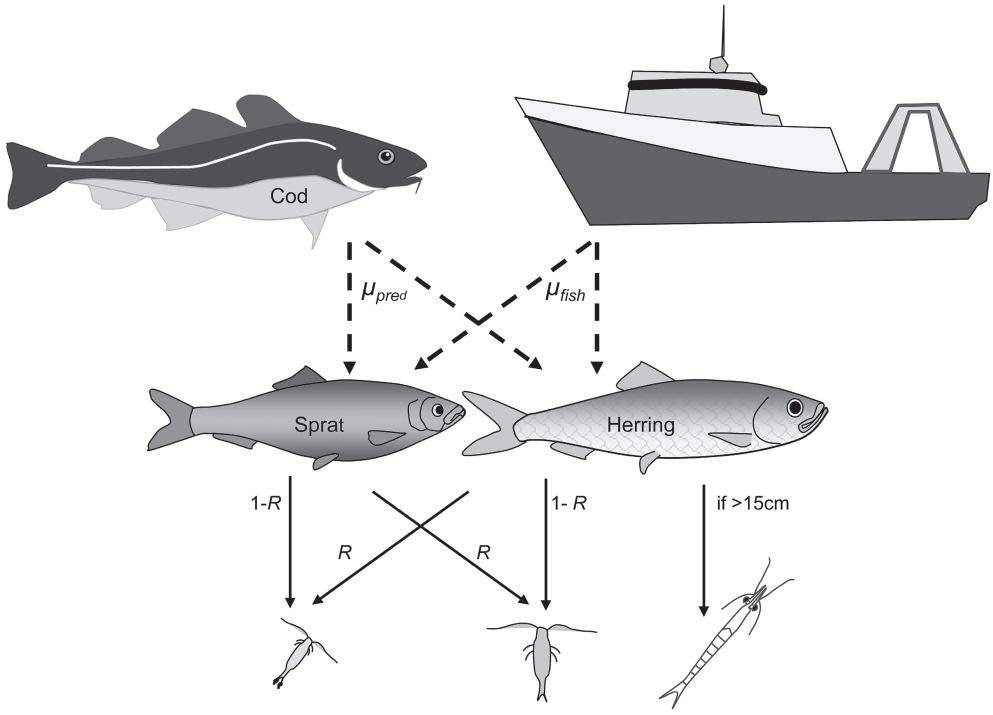

Figure 1. A schematic representation of feeding interactions, predation and fishing mortality. Our model analyses focus on the influence of variation in size-dependent predation mortality from cod (μ_{pred}) and size-dependent fishing mortality (μ_{fish}) on sprat (left) and herring (right). Both sprat and herring can feed on two zooplankton resources. In addition, herring can at large sizes feed on benthos. The value of the parameter R determines the degree of resource overlap between sprat and herring. Sprat and herring differ in the efficiency by which they can exploit the shared zooplankton resources, relating to different body size-scaling relations of the attack rate and handling time (Supplementary material Appendix 2 Fig. A2.1).

Mortality rates and fisheries yield

Several sources of mortality are implemented (Eq. 1–2, Supplementary material Appendix 1 Table A2: Eq. 22–24). All fish experience size-independent background mortality. Newborn individuals additionally experience a size-dependent mortality from time of hatching, decreasing sharply with body size. If the reversible mass decreases below a threshold value individuals will start to die from starvation. Two daily mortality rates are estimated specifically for the Baltic Sea sprat–herring system: cod predation and fishing mortality. The size-dependency of prey vulnerability to predation is modeled by a piecewise linear function (Eq. 1, Fig. 2, Table 1) based on estimates of mean number and length per age of Baltic Sea cod over the years 1974–2005 combined with a size-dependent cod attack rate function (Van Leeuwen et al. 2013, see Supplementary material Appendix 4 for details on prey vulnerability).

$$\mu_{pred}(L) = \begin{cases} \mu_p \dfrac{L\text{-P1}}{\text{P2-P1}} & \text{if P1} < L \leq P2 \\ \mu_p & \text{if P2} < L \leq P3 \\ \mu_p \dfrac{P4\text{-}L}{\text{P4-P3}} & \text{if P3} < L \leq P4 \end{cases} \quad (1)$$

Size-dependent fishing mortality reflects mechanical selection, assuming mixed-species trawl fisheries on sprat and herring. The fishing mortality (Eq. 2, Fig. 2, Table 1) is implemented as a sigmoidal function over body length (Ecol. Arch. E093-075-A1 for details on the sigmoidal function S_i), including mortality both among fish trapped in and escaping from (i.e. underwater discarding) trawl gears, parameterized according to Rahikainen et al. (2004).

$$\mu_{fish}(x) = \mu_f S_i\left(m, m_f, m_{f50}\right) \quad (2)$$

Fishing mortality increases from zero to one, starting (m_f) at 1g and with 50% of maximum fishing mortality (m_{f50}) at 3 g (Table 1, Fig. 2). While the mortality due to fishing affects all individuals that encounter the trawl, only the individuals retained in the trawl are included in the yield. We estimated this sigmoidal 'retention selectivity' (Fig. 2) from annual estimates of weight at age and fishing mortality at age for sprat and for herring in the Baltic Sea from ICES (2011) and the species-specific length–weight relationship (Supplementary material Appendix 1 Table A1.1, A2: Eq. 2). The yearly yield is calculated as the product of the size-independent fishing mortality (μ_f) and the retention selectivity (Eq. 3, Table 1).

$$Yield(x) = \mu_f S_i\left(m, m_y, m_{y50}\right) \quad (3)$$

The relative fishing yield increases from zero to one, starting at 5g (m_y) and with 50% of maximum fishing yield (m_{y50}) at 10 g and 20 g for sprat and herring, respectively (Table 1, Fig. 2).

Model analyses

Populations are divided into groups of identical individuals born within the same three days of the spawning period (i.e. cohorts). The dynamics of these cohorts were analysed using a numerical method for integration of PSPMs developed by de Roos et al. (1992). To study biomass responses to varying predation and fisheries mortality, we

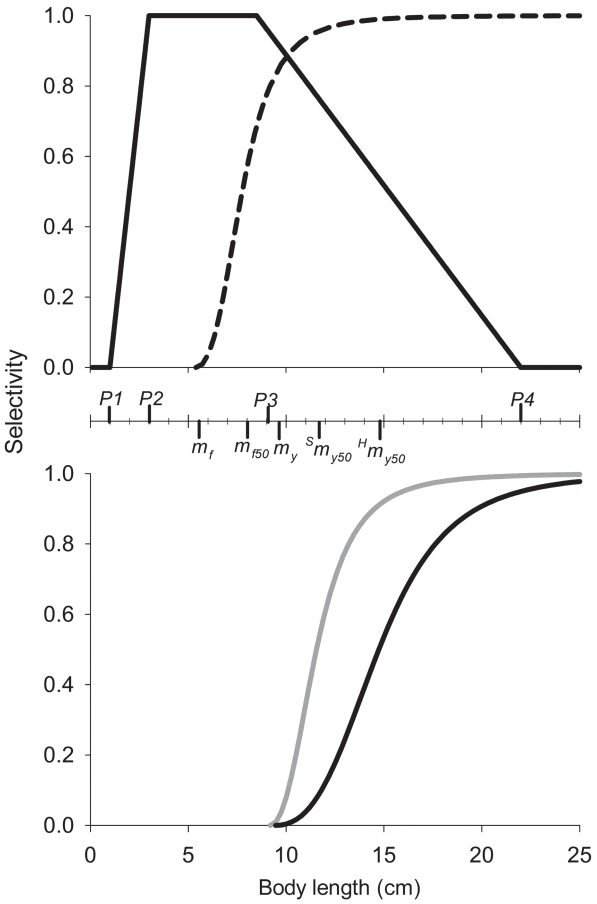

Figure 2. Top: selectivity curves for cod predation mortality (solid) and fishing mortality (dashed) as a function of consumer (herring or sprat) body size. Bottom: relative yield to fisheries of sprat (grey) and herring (black) as a function of body size. Parameter values are indicated in between the figure panels. All parameter definitions are given in Table 1. Superscripts S and H indicate sprat and herring, respectively.

Table 1. Model parameters for predation and fisheries mortality on herring and sprat. See Fig. 2 for selectivity and yield curves and location of these parameters.

	Value			
Symbol	*Herring*	*Sprat*	Unit	Interpretation
μ_p	variable	variable	day^{-1}	predation mortality constant
μ_f	variable	variable	day^{-1}	fishing mortality constant
m_f	1	1	g	size at start fishing
m_{f50}	3	3	g	size at 50% of max fishing
m_y	5	5	g	size at start fishing yield
m_{y50}	20	10	g	size at 50% of max fishing yield
P1	1	1	cm	min length for predation
P2	3	3	cm	length when max predation reached
P3	8.5	8.5	cm	length when max predation ends
P4	22	22	cm	max length for predation

identified the asymptotic population dynamics using bifurcation analysis where the level of mortality (mortality constants, μ_p and μ_f) was systematically increased or decreased in small steps. After every change in the bifurcation parameter, system dynamics were integrated over a period of 400 years (but only averages based on the last 240 years are reported). For details on the type of population dynamics observed in this study system, characterized by cohort cycles at low to intermediate mortality levels, we refer to Huss et al. (2012). For most analyses presented here, we have assumed 20% resource overlap between herring and sprat ($R = 0.1$) to ensure the presence of both species in the system for the range of mortalities studied. The results are, however, (qualitatively) valid for a range or R-values (runs carried out for $R < 0.25$), but coexistence is not possible for combinations of a high degree of resource overlap and fishing and/or predation mortality (results not shown, see also Huss et al. 2012 for details on coexistence as a function of diet overlap in absence of fishing and predation mortality).

To better understand which traits are most important in causing an overcompensatory response in prey biomass, we performed simulations focusing on three life history traits that differ substantially between the two prey species: 1) differences along a gradient of determinate and indeterminate growth (capacity for growth at large body size) determined by digestion capacity, 2) size at maturation and 3) duration and timing of spawning. The consequences of these life history traits were studied using single-species analyses to distinguish which mechanisms in the two-species systems resulted from life history differences alone. To this end we set all parameters equal to their default value for sprat except for the parameters determining the life history trait of interest (d_1 and d_2; L_m; S_d and S_m, respectively), which we assigned their default values for herring (Table 2). This alternative parameterization, for example, allowed us to study the influence of growth potential leaving all other parameters unchanged. Subsequently, we studied the potential for overcompensation following increased predation mortality. We also studied biomass responses using bifurcation analyses of specific traits (d_2, L_m or S_m, Table 2) given a constant predation mortality value ($\mu_p = 0.01$ d^{-1}). To assess the role of growth after maturation, we varied the size scaling of digestion capacity (Supplementary material Appendix 1 Table A1.2, Eq. 14). Biomass responses to variation in spawning timing was studied by varying the date for maximum spawning (Supplementary material Appendix 1 Table A1.2, Eq. 21)

Table 2. Subset of life history parameters that were varied to study their role in biomass overcompensation.

	Value			
Symbol	Default	Alternative	Unit	Interpretation
S_d	90	76	days	duration of spawning period
S_m	45	38	day	date of spawning maximum
d_1	6.74	4.8	day g$^{-(1+d2)}$	allometric scalar (digestion)
d_2	−0.63	−0.74	–	allometric exponent (digestion)
L_m	9	14	cm	maturation length

Results

Both juvenile and adult sprat biomass generally decreased monotonically with increasing predation and fishing mortality (Fig. 3a–b). In contrast, the response in herring biomass was dependent on the type of mortality implemented (Fig. 3c–d). Whereas herring juvenile and adult biomass, similar as for sprat, in general decreased with increasing fishing mortality, adult herring biomass increased sharply following increasing predation mortality, reaching a peak at intermediate mortality rates (Fig. 3c). Herring biomass overcompensation also occurred without any niche overlap with sprat (results not shown). Consequently, the increase in adult herring biomass cannot be attributed to the removal of sprat individuals. Rather, herring biomass overcompensation relates to relaxed intraspecific competition following the removal of (mostly) juvenile herring by predators. Intraspecific competitive release is evident in that increased predation mortality had a positive effect on individual growth rates (irrespective of level of niche overlap). This was true for both species, although herring could reach much larger sizes at high levels of mortality than sprat (Supplementary material Appendix 3 Fig. A3.1).

Repeating, in a single-species setting, the bifurcation over predation mortality with different values for digestion capacity (d_1 and d_2), size at maturation (L_m) and spawning dates (S_d and S_m), revealed that only variation in digestion capacity (translating into varying growth potential after maturation) had a significant impact on the degree of biomass overcompensation (Fig. 4). However, note that in contrast to scenarios accounting for interspecific competition (Fig. 3a), overcompensation (albeit weak) is present also when using the default parameterization for sprat, if only intraspecific competition is accounted for. Clearly, the higher digestion capacity led to much stronger overcompensation in adult biomass following increased predation mortality than in the default setting with sprat-specific parameterization (Fig. 4). The positive response to predation mortality given a herring-specific digestion capacity relates to consumers reaching larger sizes (Supplementary material Appendix 3 Fig. A3.1–A3.2), because of their capacity for a higher rate of food intake at large body sizes when food densities are high. The importance of a high growth capacity for overcompensation under predation mortality was also evident as sprat population biomass increased as the allometric exponent for digestion (d_2) decreased, whereas only weak biomass responses to changes in timing of spawning (S_m) and size at maturation (L_m) were observed (results not shown).

Also fishing mortality led to competitive release and increased individual growth rates (Supplementary material Appendix 3 Fig. A3.1a). However, for intermediate mortalities (i.e. over the range at which overcompensation occurred with increasing predation mortality) the response was not as strong as for predation mortality (compare Supplementary material Appendix 3 Fig. A3.1b–c). Besides differences in mean biomass responses, high values of fishing mortality

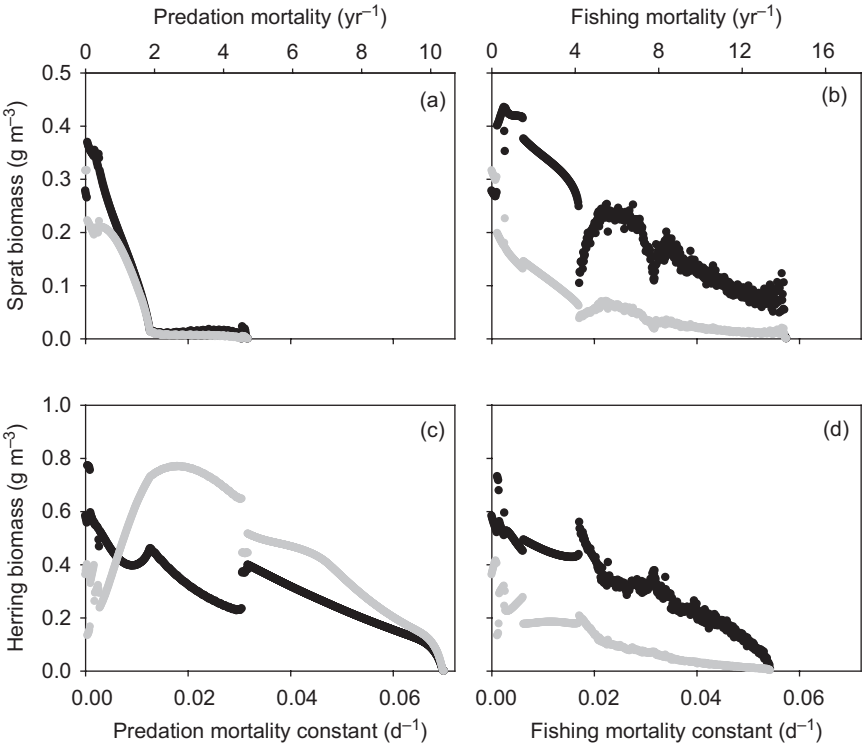

Figure 3. Variation in sprat (a, b) and herring (c, d) juvenile (black) and adult (grey) biomass (averaged over the last 60% of the integration period, for every mortality value) as a function of cod predation (a, c, assuming no fishing) and fishing (b, d, assuming no predation) mortality. Bottom x-axes indicate mortality constants and top x-axes the realized mortality (yearly) for a 14 cm individual. Note different scales on *y*-axes in top and bottom graphs.

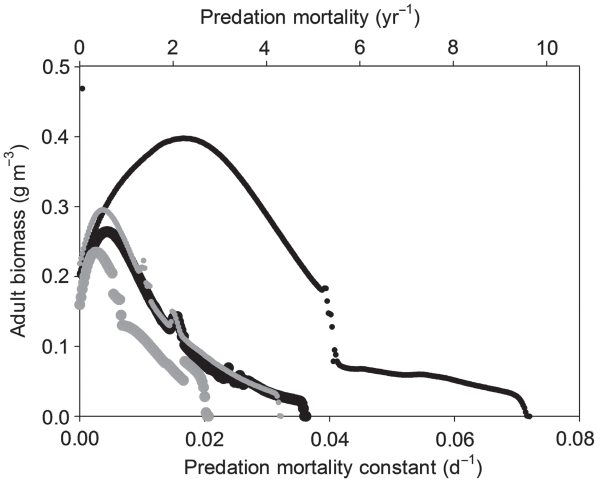

Figure 4. Variation in adult prey biomass as a function of cod predation mortality in single-species scenarios where the prey species has a parameterization identical to that of sprat (large black symbols), or an alternative parameterization for digestion capacity (small black symbols), maturation size (large grey symbols) and timing of spawning (small grey symbols) (assigned herring-specific values, Table 2). The bottom x-axis indicates mortality constants and top x-axis the realized mortality (yearly) for a 14 cm individual.

led to more irregular biomass dynamics than did predation mortality (i.e. Fig. 3 b, d: $\mu_f > 0.02$). Eventually, as predation and fishing mortality increased further, species were driven to extinction. Sprat went extinct at a lower level of predation mortality than herring. In the case of fishing mortality the extinction boundaries occurred at almost the same mortality level (Fig. 3). That sprat persistence is more limited by predation than fishing mortality results from sprat being exposed to predation mortality for most of their life cycle, whereas herring, at large sizes, are able to escape predation mortality (Fig. 2). The discontinuous "shifts" in the relationship between mortality and biomass at low mortalities (Fig. 3) correspond to transitions between cohort cycles with different periodicity (see Huss et al. 2012 for more details on the relationship between mortality and cycle period in the sprat-herring system). However, over the ranges of mortality for which the periodicity of the cohort cycles stays the same, the relationship between mortality and biomass is continuous. For the range of mortalities over which the relationship between adult herring biomass and mortality is hump-shaped, the system exhibits dynamics characterized by two-year cycles.

The relationship between predation mortality and annual yield generally followed the same pattern as that between predation mortality and population biomass. Consequently, as predation mortality increased from low to intermediate levels, so did fishermen's yield (Fig. 5). This was true for low, intermediate as well as high fishing mortality. However, the strongest positive biomass response to predation mortality was found at low fishing mortality (Fig. 5). Also, as for biomass, a strong positive response in yield to predation mortality was evident for herring but not sprat (Fig. 5: compare black and grey symbols). Again, the

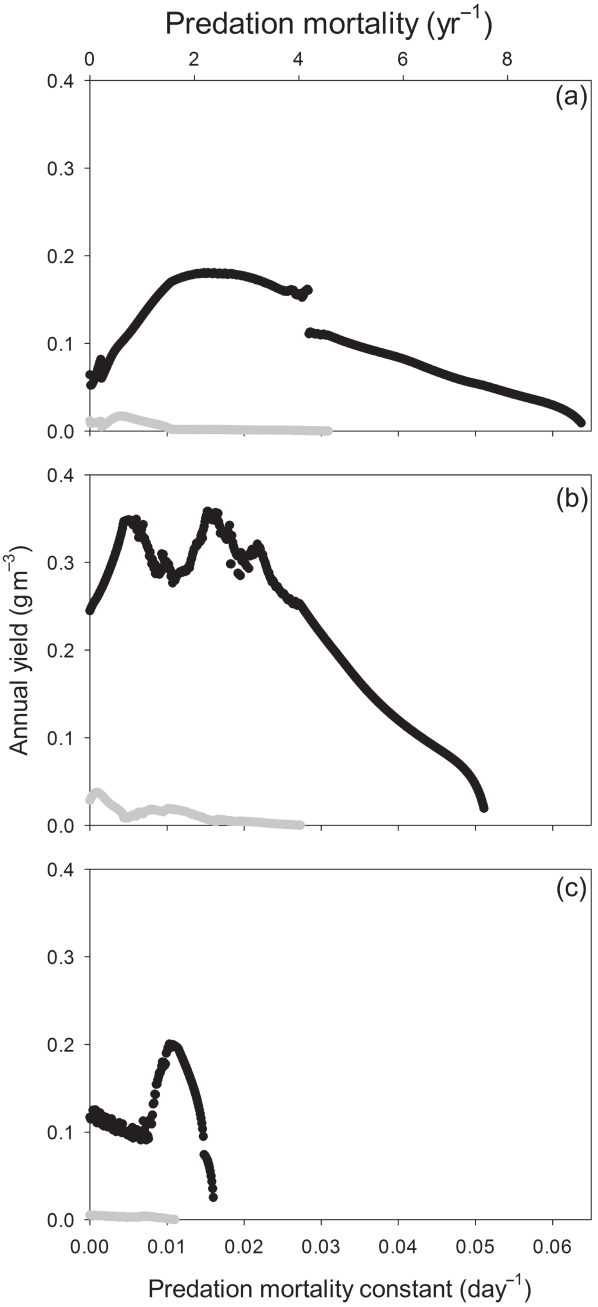

Figure 5. Annual yield (averaged over the last 60% of the integration period at every mortality value) for sprat (grey) and herring (black) as a function of predation mortality from cod for low (a, $\mu_f = 0.0025$), intermediate (b, $\mu_f = 0.01$) and high (c, $\mu_f = 0.04$) fishing mortality (corresponding to realized fishing mortalities of 0.62, 2.46 and 9.85 year^{-1}). The bottom x-axis indicates mortality constants and top x-axis the realized mortality (yearly) for a 14 cm individual.

positive response to predation mortality can be related to competitive release and faster growth rates (Supplementary material Appendix 3 Fig. A3.2), which in the case of herring even led to a higher standing stock biomass of large individuals, preferentially selected for by fishermen (Fig. 2, 3c, Supplementary material Appendix 3 Fig. A3.2). As fishing pressure increased, the level of predation mortality that results in extinction of one of the competitors decreased. None of the results obtained qualitatively changed when herring were allowed to feed on benthos, but the degree of overcompensation in adult herring biomass was somewhat stronger with benthos feeding (results are not shown for scenarios with benthos feeding).

Discussion

Here we have shown how biomass overcompensation in response to increased mortality depends on prey life-history type as well as on the size selectivity of mortality, and how overcompensation not only occurs within single prey species but also in a community of competitors. Compensation, but not overcompensation, between competing species has been shown to occur in a number of previous studies (Nee and May 1992). However, in contrast to these studies we here show how overcompensation in competition communities may arise from intraspecific competition, i.e. overcompensation within species rather than between species. Furthermore, we have shown how the potential for prey biomass to increase as mortality rises can overthrow the intuitive conflict between humans and predators competing for shared prey. In the case of cod and fishermen, facilitation of fisheries yields by predation results from the opposing signs of size-selectivity and increased prey growth rates following thinning. It should be noted that a combination of very high degree of resource overlap and mortality may lead to competitive exclusion. Thus, even if facilitation due to overcompensation is possible also at high interspecific resource overlap, coexistence may not be possible at high mortality. The degree to which prey species may exhibit a positive response to predation mortality, and thus facilitate fishermen, was shown to depend on their capacity for substantial growth after maturation.

The commonly held view in fisheries is that thinning out predators should increase fishermen's yield when they exploit prey species also selected for by those predators (Flaaten 1988). Similarly, it has been suggested that competition between fishermen and cod can accelerate the collapse of forage fish (Hjermann et al. 2004). However, similar to what has been shown for natural predators specializing on different life-history stages of shared prey (de Roos et al. 2008, Huss and Nilsson 2011), our results suggest that predators may help humans in exploiting shared prey to increase their yield via increasing prey growth rates and changing prey size distributions (Supplementary material Appendix 1 Fig. A1.1), when the size-specificity of predators and fisheries differs. For fishermen harvesting forage fish such as sprat and herring, allowing for higher predation rates from top-predatory fish preying on small prey individuals may substantially increase yields. Whereas increased fishing mortality leaves the juvenile to adult biomass ratio largely unchanged, cod predation mortality increased adult relative to juvenile biomass. This difference relates to that predators, but not fishermen, selectively target the competitively better prey life stage (juveniles, Supplementary material Appendix 2 Fig. A2.1) which experience more intense competition, leading to strong enough relaxation of intraspecific competition to more than

compensate for the loss of individuals due to the additional mortality. For planktivorous fish species, small individuals generally seem to be the competitively better life stage (Huss et al. 2012, de Roos and Persson 2013). For other species also the opposite competitive relationship between small and large individuals may be the case. Still, biomass overcompensation can occur whenever one of the stages has a foraging advantage over the other (de Roos and Persson 2013). In contrast to stage-structured models with a juvenile and adult stage (with no growth in body size within the adult stage, de Roos et al. 2007), overcompensation in our model is not only due to increased maturation or reproduction but also due to growth to larger body sizes with increasing mortality. Note that in the case of herring, shifting from low to intermediate levels of cod predation mortality actually led to a large increase in adult biomass (as in total herring biomass).

Compensation and overcompensation in production rates in response to mortality is a well described phenomenon in populations that are limited by intraspecific competition (Werner and Gilliam 1984). Likewise, we know that community shifts can compensate for decreases in the abundance of one species. However, the notion that increased mortality on a population may lead to increased standing stock biomass, referred to as biomass overcompensation, and its implications for ecological communities, have only recently been acknowledged (de Roos and Persson 2013). Still, empirical evidence for stage-specific biomass overcompensation in response to mortality comes from a variety of systems and taxa, including blow flies, soil mites, fish and zooplankton populations (Nicholson 1957, Cameron and Benton 2004, Persson et al. 2007, Schröder et al. 2009, Huss and Nilsson 2011). As is systematically reviewed in de Roos and Persson (2013), biomass overcompensation can occur for a variety of parameter combinations and in many types of size-structured population models. The fact that the community context (i.e. acknowledging multiple competing species) was not crucial to explain the main conclusions derived from this study, could not be known beforehand. Our results, showing that overcompensation based on intraspecific mechanisms may indeed occur also in a community context further strengthen the generality of biomass overcompensation in ecological systems. A community approach also adds realism as many predators and fisheries (including cod and trawl fisheries in the Baltic Sea) target multiple prey species, enabling projecting the results to real-world systems.

Although the possibility for biomass overcompensation has been addressed using a variety of community modules (de Roos and Persson 2013), its dependence on consumer life history traits and presence of interspecific competitors has not been investigated. It has long been known that fishing changes the structure of fish populations and communities. Generally, as fishing mortality increases, population size is expected to decrease and individual growth rates to increase. Not only has it been shown that the response to fishing may depend on consumer life history (generally favouring small-bodied fast growing species, Jennings et al. 1999), but also that fishing, itself, may change life histories by creating strong artificial selection pressures (Jørgensen et al. 2007). However, the interaction between fishing, predation mortality and life-history type is not well known. Despite similarities (in life-history and ecological role), herring showed strong biomass overcompensation with increasing predation mortality, while sprat did not. Among the few life history traits subject to substantial interspecific differences in our model-system, only digestion capacity had any major influence on the degree of overcompensation. This is because a higher digestion capacity allows consumers to grow substantially after maturation, whereas consumers with a limited digestion capacity (i.e. sprat) have a lower growth potential at large size irrespective of resource availability (compare maximum body sizes in Supplementary material Appendix 2 and 3, Fig. A2.1 and A3.1). Thus, in a scenario with predation mortality, herring grow to much larger sizes, produce more offspring, and, as a result, can more than compensate for the loss of biomass due to mortality. Besides effects on vital rates of individual's and average population biomass responses, similar to van Kooten et al. (2007), we found that high rates of mortality targeting large individuals lead to unstable dynamics (see also Anderson et al. 2008). This relates to variation in the timing of reproduction events (i.e. age-at-maturation) and variation in the time at which individuals become vulnerable to fishing mortality. In contrast, negative size-dependent mortality, as caused by many piscivorous fish, generally has a stabilizing effect by preventing a strong competitive effect from recruits on older individuals (Murdoch and Oaten 1975, van Kooten et al. 2007, this study).

The possibility of overcompensation as a response to increased predation mortality has clear management implications. One reason is the association between stage-specific biomass overcompensation and alternative stable states in theoretical models (de Roos and Persson 2013), which have also been applied to the Baltic Sea (Van Leeuwen et al. 2008). Moreover, overcompensatory biomass responses have been shown to occur under experimental conditions (Schröder et al. 2009, Huss and Nilsson 2011), as well as in a whole lake system (Persson et al. 2007), revealing that this phenomenon is not just a theoretical construct. Our results add support to the potential role of size-selective mortality as a management tool. By allowing for depleted predatory fish stocks to recover, not only may fishermen gain from improved conditions of these fish stocks themselves, but also from the size-selective predation these predators exert, leading to relaxed competition, increased individual growth rates and fecundity and subsequent potential for positive biomass responses in both the biomass of exploited prey fish and their yields. Note, however, that the positive relationship between predation mortality and fisheries yield only applies if the prey population(s) show overcompensation in response to increased predation mortality. Here we have investigated a scenario in which fishermen and natural predators target different size ranges of shared prey. In the case that natural predators and fishermen target the same size range of prey (such as mammal predators on exploited meso-predatory fish, Gårdmark et al. 2012), facilitation based on opposing signs of size-selectivity is not to be expected. Analyzing (even) more complicated scenarios including the influence of dynamics of fisheries and predators on biomass responses

of shared prey was beyond the scope of this study (i.e. we assumed constant predation and fishing mortality rates and did not consider multiple independent fisheries), but could be interesting topics for future studies. Still, it is clear that overcompensation occurs also in fully dynamic predator–prey systems (de Roos and Persson 2013).

In conclusion, we have shown how predation mortality can lead to overcompensatory biomass responses in a guild of competing prey fish. For overcompensation to occur, however, a high growth capacity following maturation was crucial. Not only may the consequences of size-selective mortality and food-dependent growth lead to the counter-intuitive positive relation between mortality and biomass shown to occur for prey fish in our model system, but our results also imply that natural predators actually may facilitate humans' exploitation of shared prey.

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Supplementary material (available as Appendix oik-00839 at <www.oikosjournal.org/readers/appendix>). Appendix 1–4.