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Original Article

The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics

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Food-dependent growth and size-dependent interactions form cornerstones in the dynamics of fish populations. Using two freshwater examples, we illustrate the importance of considering both these cornerstones for understanding system dynamics. Moreover, a proper understanding of the dynamics requires mechanistic linkages between individual-, population-, and community-level processes based on mass conservation principles. In one example, we further find that quantitative predictions of individual-level energy flows are essential for understanding the community dynamics. This mechanistic approach to understanding system dynamics is generally not reflected in fisheries models as an overview shows that only half of them incorporate food-dependent growth, and none fully observe the principles of mass conservation. As a marine example we examine patterns in the Baltic Sea system and show that no relationship between cod growth and sprat biomass is present related to the low size resolution in prey fish. Linking individual cod performance to its resource base is complicated by the many prey types cod uses over its life cycle. We conclude that an ecological perspective including size- and food-dependent processes is vital for ecosystem-based fisheries management making necessary a proper description of the interactive trophic structure as a result of mechanistic linkages between individual, population, and community processes.

Keywords: Baltic Sea, energy budget models, fisheries models, food dependence, ontogenetic niche shifts, physiologically structured population models, size structure, trophic configuration.

Introduction

Text books in ecology generally assume that the dynamics of populations are the result of mortality and reproduction only (Begon *et al.*, 1996; Turchin, 2003). In this definition, one basic aspect of the individual's life history—ontogenetic growth or development—is ignored, although ontogenetic growth is indeed a vital process, preceding reproduction by ensuring the energy allocation for the production of biomass. Fish provide an obvious example of the importance of individual development as individuals commonly increase in body weight over several orders of magnitude while developing from egg to mature individual (Werner and Gilliam, 1984).

Moreover, the rate by which an individual fish grows is generally dependent on food availability, a fact long recognized and described by fish biologists (Beverton and Holt, 1957; Backiel, 1978). The pioneer paper by Hjort (1914) on the dynamics of fish populations also highlighted the changes and variability in individual growth of fish.

Fisheries management is mainly concerned with the biomass production of entire populations, which represent a collection of many individuals. Fisheries management approaches generally ignore the resource dependence of this production. Studies inspired by the dynamics of fish populations in freshwater lakes (cf. De Roos and Persson, 2001; Persson *et al.*, 2003, 2004), however, illustrate the

potential of gaining a thorough insight in community regulation and functioning from models that consistently link population output (biomass production) to individual energy acquisition (food-intake). With its focus on stock production and its basis in single-species and age-structured models, marine fisheries management has traditionally incorporated these insights only to a limited extent. Following the research experience from trophic cascades in lakes (Carpenter *et al.*, 1987; Carpenter and Kitchell, 1993), increasing evidence now shows that also in marine communities changes at the top of the foodweb influence overall ecosystem dynamics: examples include the Black Sea (Daskalov *et al.*, 2007), the North West Atlantic (Frank *et al.*, 2005), and the Baltic Sea (Österblom *et al.*, 2006; Möllmann *et al.*, 2008). Understanding such community-wide changes requires an ecosystem-based management perspective that strives after an integrated assessment, considers the functioning of the entire ecological community (FAO, 2003; Christensen and Walters, 2004), and mechanistically accounts for the linkages between the individual, the population, and the community level. Such a general understanding, however, has been lacking so far for two main reasons: first, available data have been under-valued and little-used (e.g. changes in population size distributions are not incorporated in the estimates of reproductive capacity or spawning-stock biomass), and second, there has been a lack of particular and essential information that allows for an appropriate description of the trophic configuration to be studied. Where the first issue is possible to solve by turning around and taking an ecological perspective, the second part calls for a reconsideration of what kind of information is essential for developing an understanding of the dynamics of systems that are heavily influenced by size-structured interactions.

To illustrate in more detail the points made above, we first discuss two examples from freshwater systems, which both show that to understand the community dynamics it is essential (i) to consider the size- and food-dependent interactions and (ii) to mechanistically link processes at different levels (individual, population, community) of organization. The second example additionally shows that a proper quantitative handling of individual-level processes by using rather detailed physiologically structured population models (Metz and Diekmann, 1986; De Roos and Persson, 2001) may be necessary to gain an understanding of the dynamics of the system as a whole. Next, we discuss how the models that are commonly used for fish stock assessments and predictions for stock production with a focus on multispecies models account for the basic concept of resource-dependent development and biomass production and contrast this with assumptions of the aforementioned physiologically structured population models. Finally, we focus on the Baltic Sea system as a marine example, where we first consider the extent to which the data that are usually available for marine fish stocks can or cannot provide a sufficient basis for a more thorough ecological understanding. We point out that insufficient time resolution and especially resolution of size frequency in the data on both predatory as well as prey fish tend to prevent establishing a proper link between resource (prey) availability and consumer (predator) performance. Furthermore, we discuss the basic problem of deriving a proper trophic description of the dynamic interactions between different trophic components. We also point out that the amount of information necessary to yield an understanding of the dynamics of a specific system may turn out not to be as overwhelming as expected at first glance. Although it will be a far more complex task to provide the necessary ingredients for drawing similar links among organizational levels in freshwater systems as for marine systems, we highlight the ecological aspects that require more research and deeper

investigations. A full consideration of food-dependent processes is essential for management purposes as food-dependent models yield different predictions about sustainable harvesting than do age-based models (De Roos and Persson, 2002; van Kooten *et al.*, 2010).

Linking individuals to populations and communities: experiences from freshwater lake systems

To examine how a (i) consideration of size and food dependence, (ii) linking of individual- and population-level processes, and (iii) correct quantitative predictions of individual-level mass flows can promote the understanding of fish communities, we will use two examples from freshwater systems. Our first example deals with a predator that feeds on a size-structured interspecific prey, whereas the other example considers a predator feeding on intraspecific prey (cannibalism) in which case the predator also shares the resource with its prey. In both examples, the community dynamics and structure over years have been characterized by high variations in both predator and prey population densities. For both examples, it also applies that a consideration of size and food dependence and a mechanistic linking of individual of population and community processes have been essential to unravel the mechanisms driving the dynamics of the systems.

Accounting for size and food dependence: the Takvatn system

Our first example considers changes in community structure over time as a result of the presence of alternative stable states. This empirical example relates to relatively recent theoretical developments that have shown that food-dependent development may give rise to stage/size-specific biomass overcompensation in response to mortality (i.e. increases in stage-specific biomass with increasing mortality), a phenomenon that cannot occur in unstructured or age-structured models (De Roos *et al.*, 2007; De Roos and Persson, 2013). Such overcompensatory biomass increases due to mortality have been experimentally demonstrated in many organisms, including fish (Schröder *et al.*, 2009; Ohlberger *et al.*, 2011). The presence of an overcompensatory biomass response to mortality leads to a 3-link (predator–consumer–resource) system that is prone to exhibit alternative stable community states. In the case when small juveniles in the consumer population are more efficient energetically than larger juveniles and adults, the consumer population will in the absence of predators suffer from strong resource limitation and very few smaller juvenile consumers will be present due to slow development of larger juveniles and a low reproduction rate among the adults. In contrast, if the predator is in the system and feeds selectively on small stages of the consumer (as is generally the case for piscivorous predators), its predation pressure will relax resource competition and lead to an increase in the biomass density and reproduction rate of adult consumers. This, in turn, leads to an increase in the biomass of the small stages of the consumer, although the predator is feeding on these small stages. Thus, the predator will through its predation activity cultivate its own prey leading to a situation where it may be able to sustain itself if present in the system but may not be able to invade the system (a scenario termed an Emergent Allee effect De Roos and Persson, 2002; De Roos and Persson, 2013). A state with both prey and predator present and a state with only a (stunted) prey population hence constitute the two alternative stable states of the community. Such a system is thereby also highly sensitive to harvesting-induced catastrophic predator collapses (De Roos and

Persson, 2002). In contrast, De Roos and Persson (2002; Figure 3) show that an age-based community description, in which the size-age relationship is constant and independent of changes in food availability does not allow for the overcompensatory biomass response and hence for the occurrence of the Emergent Allee effect.

A long-term whole-lake experiment in Lake Takvatn, northern Norway, provides experimental support for the presence of these two alternative stable states mediated via the mechanism described above. At the start of the experiment, the system was totally dominated by a stunted Arctic char (*Salvelinus alpinus*) population and the predator brown trout (*Salmo trutta*) was virtually absent from the system (Figure 1a; Persson et al., 2007). A heavy fishing on the Arctic char population for 5 years as a result of management decisions resulted in a decrease in the total yield of Arctic char and a recovery of the brown trout. This recovery has also been sustained for more than 20 years after that the removal of Arctic char took place providing strong support for the presence of alternative stable states in this system (Figure 1a).

Understanding the dynamics of this system relies on a consideration of (i) the linkages between individual, population, and community levels and (ii) food and size dependencies in interactions. The heavy reduction in the population size of Arctic char resulted in a substantial increase in the growth rate and maximum size of Arctic char (individual-level response, Figure 1c). This increased growth of Arctic char, which has been sustained after the termination of the heavy fishing, resulted in a drastic shift in the size distribution of Arctic char: the abundance of large Arctic char increased and, most importantly, also the abundance of the smallest size classes of Arctic char increased as a result of increased population fecundity (population-level response, Figure 1b). In turn, this increase in the abundance of small (<15 cm) Arctic char, on which brown trout feeds (measured as the encounter rate, see Supplementary material for calculations), had a positive effect on the performance (condition) of brown trout (individual-level response, Figure 1d). Finally, the increased performance of brown trout resulted in the recovery of the brown trout population exerting a strong thinning effect on small Arctic char (individual to community linkage) leading to the sustenance of the high growth rate of Arctic char (community to individual linkage; Figure 1). Recent analyses of the Takvatn system also shows that variation in the individual growth rate of Arctic char during the post thinning phase is largely explained by intraspecific density (Persson et al., 2013).

It is apparent from the above that the understanding of the dynamics of the Takvatn system relies heavily on a consideration of food-dependent growth and explicit linking of processes at different levels (i.e. Figure 1). The fact that the increased performance of brown trout was dependent on the abundance of small Arctic char further shows the necessity of considering the size dependence of interactions. This conclusion is also supported by analyses of the relationship between brown trout performance (body condition) and total Arctic char biomass that show no relationship or even a negative relationship between brown trout condition and Arctic char biomass (Persson et al., 2013). Data on total biomass of prey fish are thus clearly insufficient for linking prey availability to predator performance.

Quantitative predictions of individual-level mass flows: cannibalistic dynamics in Abborrtjärn 3

Although the above example illustrates how consideration of size and food dependence and linkages between different levels of organization are essential for understanding community dynamics,

the comparisons between model predictions and empirical data were qualitative rather than quantitative. In contrast, our second example dealing with the dynamics of a cannibalistic fish population of perch (*Perca fluviatilis*) in Lake Abborrtjärn, northern Sweden, will show that correct quantitative predictions of individual-level mass flows are in this case necessary to understand the dynamics.

To mechanistically link different levels of organization in the Takvatn system, the use of physiologically structured population models (Metz and Diekmann, 1986; De Roos et al., 2008), which predict population dynamics as the emergent result from processes taking place in the life history of individual organisms, has been essential. At the core of such population models is the description of the individual state dynamics by a dynamic energy budget (DEB) model (Persson et al., 1998; Claessen et al., 2000). This core DEB model implements a consistent cycle of energy flows and imposes strict mass conservation: energy assimilated from food intake is used for growth and maintenance (metabolism) of body mass or for reproduction, which are hence food-dependent. Alternatively, when reproduction only occurs annually it depends on body condition (Persson et al., 1998), making this biomass output dependent on previous energy input. Thus, a consistent link between energy input into the system, in terms of biomass intake, and energy output from the system, in terms of biomass production, is realized. This modelling philosophy has been implemented in detailed, continuously structured population models, as well as in their more simplified, stage-structured analogues, which contain a discretized separation of different life stages (De Roos et al., 2008; Van Leeuwen et al., 2008).

For the cannibalistic perch system, the intake rate of the individual is a result of the consumption of resources shared by cannibals and victims and consumption by cannibals of victims. The first relationship has generally been characterized by a hump-shaped attack rate function of the form shown in Figure 2a assuming a fixed size of the resource (a derivation of this function including the biological basis for it is given in Persson et al., 1998). In contrast, for the functional relationships between cannibals and victims, variation in both cannibal as well as victim size will have to be considered. In the fish ecology literature, the predation rate of piscivorous predators is generally viewed as being constrained by a lower prey–predator size ratio below which the piscivore cannot detect the prey fish and an upper prey–predator size ratio above which the prey fish escapes the piscivore (Lundvall et al., 1999; Claessen et al., 2000; Juanes, 2003). Within the range of predator and prey fish sizes where the predation rate is positive—the predation window—the predator's attack rate on differently sized victims for a specific predator length can be assumed to increase with victim size from zero at the lower size boundary to an optimum, to thereafter decrease again to zero at the upper size boundary (Claessen et al., 2000). Figure 2b shows a two-dimensional illustration with empirical data for perch inserted. Along the optimal cannibal–victim size ratio, it can be further assumed that the attack rate increases with cannibal size according to a power function yielding the three-dimensional graph shown in Figure 2c (for derivation of functional relationships including the biological basis for these, see Supplementary material). To complete the description of the DEB model for the cannibalistic perch system, additional functional relationships for metabolic rates, food conversion, and allocation of ingested energy to reproduction and somatic growth, respectively, have to be derived (e.g. Persson et al., 1998; Claessen et al., 2000).

Both experimental and modelling analyses have shown that the dynamics of the studied cannibalistic populations is characterized

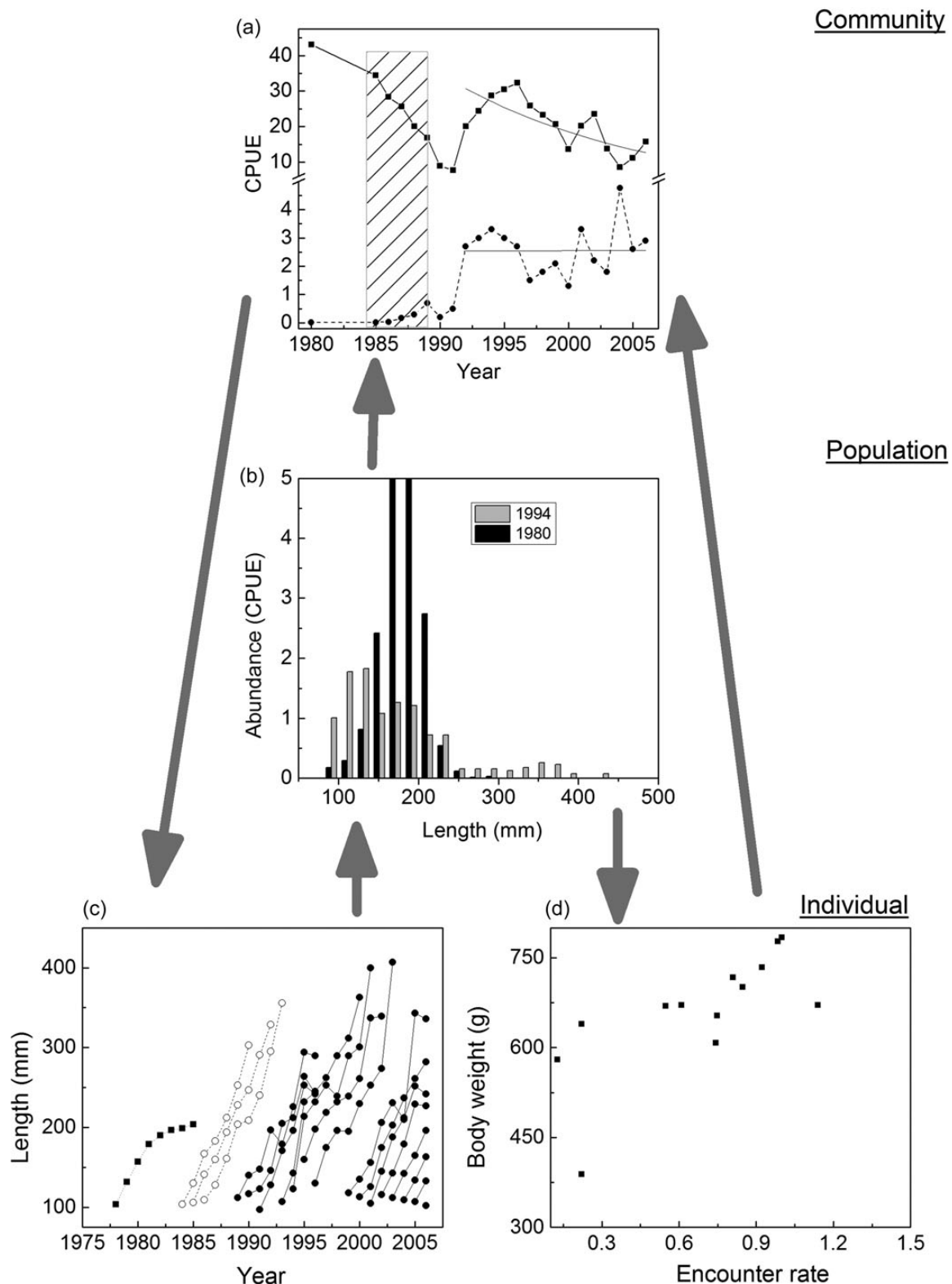


Figure 1. Different levels (individual, population, community) of organization in the Takvatn system including major linkages (grey arrows) between the different levels. (a) Changes in the abundance (cpue) of Arctic char (squares, solid line) and brown trout (circles, dashed line) in Lake Takvatn 1980–2006. Inserted thin solid curves starting in 1991 are trend lines. Hatched area represents the years with Arctic char thinning. (b) Abundance (capture per gillnet per 24 h, cpue) of difference size classes of Arctic char in Lake Takvatn before (1980, black histograms) and after (1994, grey histograms) the Arctic char thinning. (c) Individual growth rates of Arctic char before (filled squares, dotted line), during (open circles, dashed lines), and after the thinning (black circles, solid lines). (d) Relationship between the estimated encounter rate of a 400-mm brown trout with Arctic char and brown trout condition (g). See Supplementary material for estimation of encounter rate. Data from [Persson et al. \(2007\)](#).

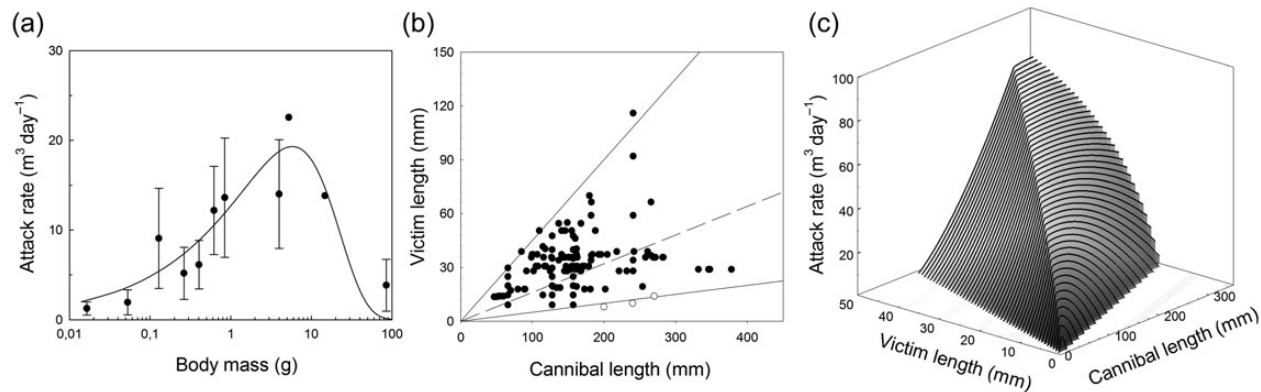


Figure 2. (a) Fitted relationship between the attack rate of perch on zooplankton and zooplankton resource density (*Daphnia* 1 mm). (b) Lower and upper size boundaries (solid lines) of the predation window for perch. The dotted line represents the optimum prey size for a specific predator size. Filled circles are empirical data points of observed prey sizes eaten by perch of different sizes based on field data or experiments. Open circles are results from experiments where perch did not attack the prey fish. (c) Three-dimensional plot of the attack rate ($\text{m}^3 \text{ d}^{-1}$) of cannibalistic perch as a function of cannibal and victim sizes. Parameter values were $\delta = 0.05$, $\epsilon = 0.16$, $\epsilon = 0.45$, $\beta = 0.4$, $\sigma = 0.6$. Data from De Roos and Persson (2013).

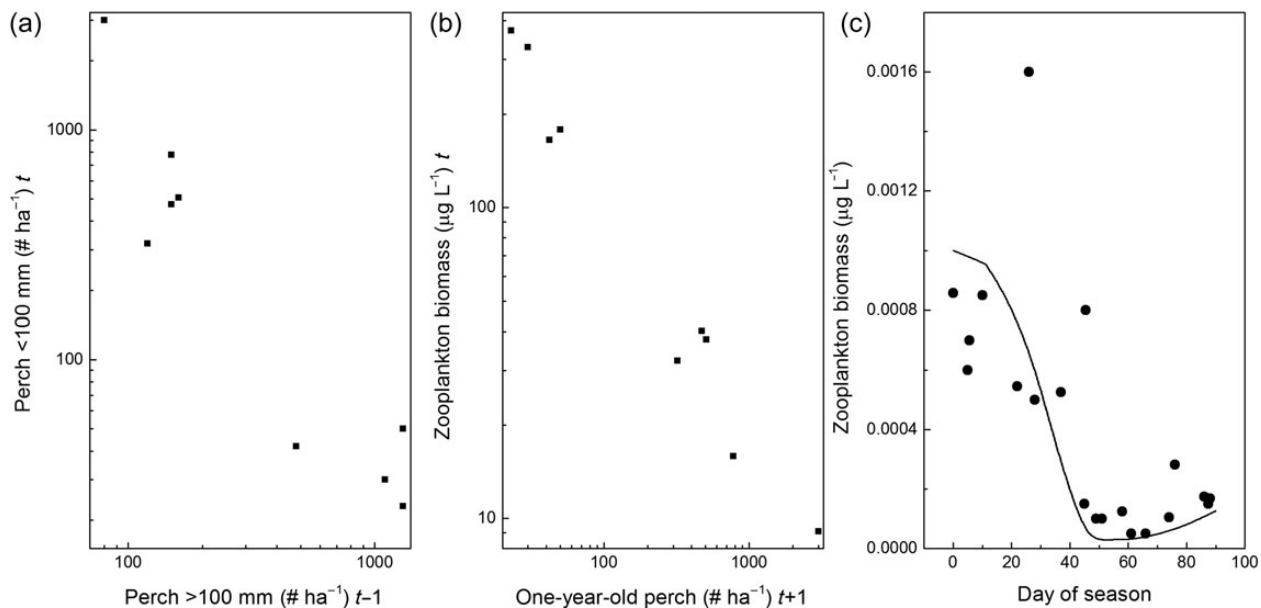


Figure 3. (a) Relationship between observed density of perch < 100 mm and the density of perch > 100 mm the previous year. (b) Relationship between zooplankton biomass (average of ≥ 3 samples for the period July – August) and the density of 1-year-old perch the following year. Densities of 1-year-old perch in year $t+1$ are taken as a measure of YOY perch densities in year t . (c) Predicted seasonal dynamics of the zooplankton resource during the giant phase (solid line). Superimposed on model predictions are the observed zooplankton biomasses in different years (filled circles). Data from Persson et al. (2003, 2004).

by high amplitude dynamics that can be separated into two phases (Claessen et al., 2000; Persson et al., 2000a, 2003, 2004). One (stunted) phase is characterized by high densities of cannibals imposing a high mortality on cannibalistic prey leading to low survival and low densities of 1-year-old perch the following year, a small asymptotic size of cannibals, and high biomasses of zooplankton. The other (giant) phase is characterized by low cannibal density leading to higher survival of cannibal prey and large number of 1-year-old perch the following year, a large asymptotic size of cannibalistic individuals, and low biomasses of zooplankton (Claessen et al., 2000; Persson et al., 2000a, 2003, 2004; Figure 3a and b).

Model predictions for young-of-the-year (YOY) perch mortality including the seasonal variation match well with the empirical

observations regarding YOY perch mortality in the different phases (Persson et al., 2004). Importantly, the lower mortality rate of YOY perch in the giant phase was not simply a result of the difference in cannibal density, but also due to a difference in the mean size of cannibals (which was higher in giant phase delaying the onset of cannibalism) and the increase in YOY perch size over the season. Detailed modelling of within season dynamics shows only a minor impact of perch consumption on zooplankton biomass in the stunted phase. In contrast, there is a strong impact of perch predation on the zooplankton resource during the giant phase (Figure 3c).

We next consider the question whether we can connect population level patterns (i.e. Figure 4a) to individual-level performance of

the predator (food intake and growth of cannibalistic perch). In contrast to the Takvatn example, we will ask whether we can quantitatively predict both the diet and the growth of individual perch taking all ecological feedbacks into consideration. For illustration, we choose a perch of a size of 189 mm and compare the predicted and observed diets during the stunted and giant phase (a more extensive discussion of this analysis is given in Persson *et al.*, 2004). The diet during the stunted phase was mainly dominated by macroinvertebrates while zooplankton feeding and cannibalism were only observed to a smaller extent (Figure 4a). Macroinvertebrates also constitute the main part of the diet during the first 30 d of the growth season in the giant phase. After this date, the perch switches to feed mainly as cannibals (Figure 4b). For all prey items, there is a high agreement between predicted and observed diets (Figure 4a and b). Furthermore, it is worth noting that the high cannibalistic mortality of YOY during the stunted phase is associated with a low incidence of cannibal prey in the diet of potential cannibals, whereas the lower cannibalistic mortality of YOY during the giant phase is associated with a high incidence of cannibal prey in the diet. However, paradoxical at first sight, this pattern makes perfect sense when considering the dependence on the victim size of energy return for cannibals: during the stunted phase, almost all YOY perch are cannibalized before each individual victim represents any significant energy package for the cannibal; in contrast, cannibalism during the giant

phase occurs over the whole growth season resulting in victim prey dominating the diet of cannibalistic perch from day 30 (early July) of the growth season.

Predicted and observed growth rates of perch differed substantially between the stunted and giant phases (Figure 4c and d). The difference in the growth rate between phases occurred for perch size >100 mm and is more or less entirely due to the consumption of cannibalistic prey. For both the stunted and the giant phase, predicted growth rates are also quantitatively in close agreement with observed growth rates (Persson *et al.*, 2003). This close match between predicted and observed growth rates of cannibalistic perch is essential to yield an appropriate estimate of population fecundity and thereby the overall cannibalistic population dynamics (i.e. the presence of the oscillation with two distinct phases depends on food dependence in both intake and reproduction). More specifically, the increased individual growth of cannibalistic individuals in the giant phase is essential to compensate for their small numbers and allows them to produce several strong YOY perch cohorts that in turn outcompete 1-year-old perch (previous year's YOY cohorts; Persson *et al.*, 2003). Without such a quantitatively correct prediction of individual growth rates—a result of a full handling of all rates—the model would not have predicted the sustained giant phase with its effect on overall foodweb structure of the system (Figure 3; Persson *et al.*, 2003).

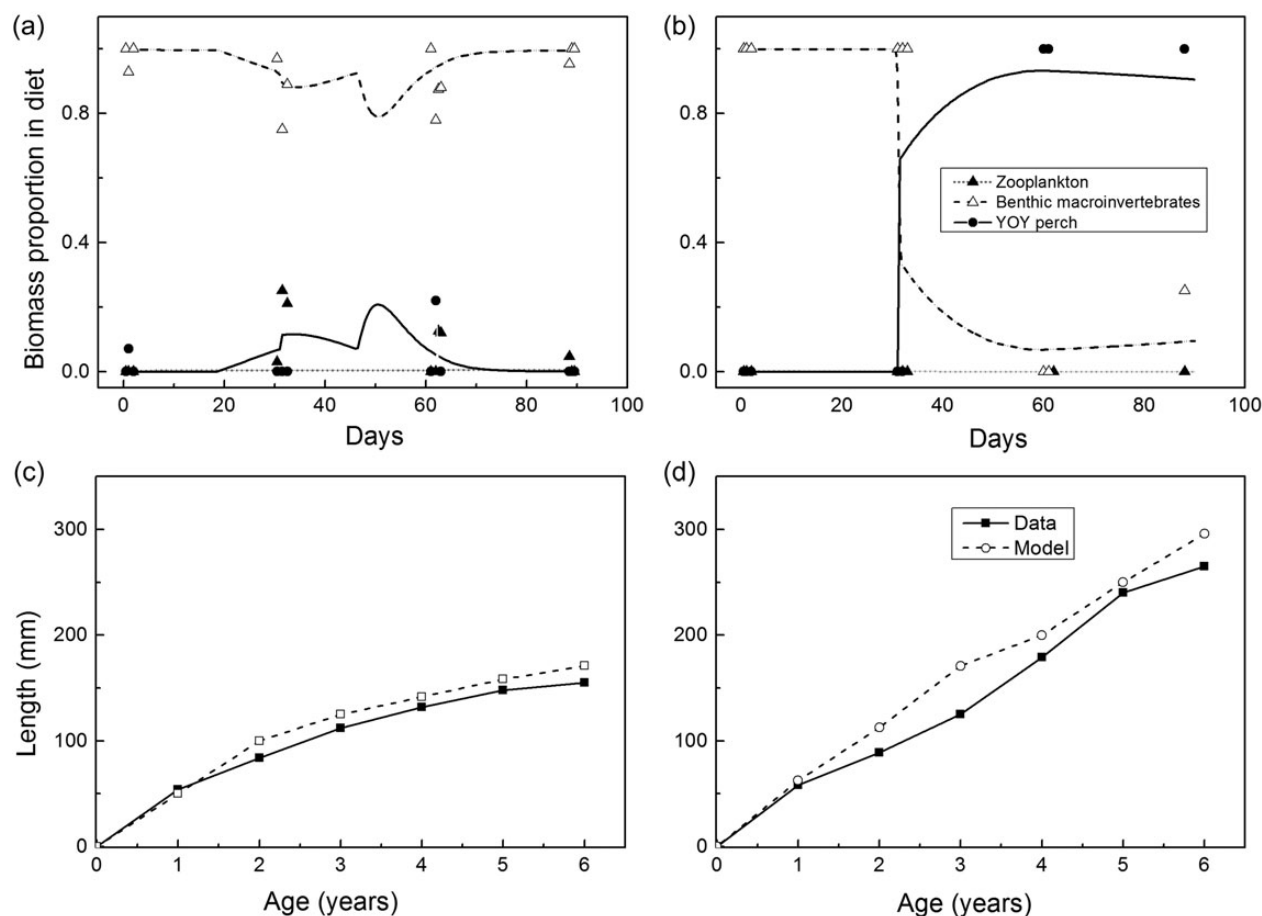


Figure 4. Predicted (lines) and observed (symbols) diets (biomass proportion) of perch over the season with an initial size in spring of 189 mm during the stunted (a) and giant phase (b) in Abborrtjärn 3. Observed data for the stunted phase include 1992, 1993, 1999, 2000, and that of the giant phase 1994–1997. Each data point represents the mean of >10 individuals. Model predictions and observed growth rates for perch during the stunted (c) and giant (d) phases. Data from Persson *et al.* (2003, 2004).

Conclusions

We have presented two examples, one of which focused on community structure and one of which focused on population dynamics. Both studies show that a sufficient size resolution in the description of prey fish and a consideration of food-dependent growth are essential to successfully establish links between processes and patterns and thereby allow for the prediction and understanding of population and community dynamics based on individual-level processes. In the Takvatn example, we furthermore showed that collapsing the description of a size-structured prey into a single point measure such as total biomass will generally lead to a failure in establishing the links between size-structured predators and size-structured prey at individual, population, and community levels. The detailed individual-level information that allows for a full accounting of individual-level mass flows and thereby quantitative predictions of piscivore performance, as exemplified by the perch system, is so far available for a restricted set of fish species constellations only (Persson and Brönmark, 2002; Persson *et al.*, 2004). Still, studies of these relatively few species constellations, which also include more complex trophic configurations (Persson, 2011), have helped us substantially in advancing our general conceptual understanding of the dynamics of freshwater fish populations and communities in general. These insights have also proven useful in the recent development of models for marine species such as herring and sprat and cod (Huss *et al.*, 2012; van Leeuwen *et al.*, 2013).

The Takvatn example also suggests that in some cases and for some type of questions only a relatively limited amount of information may be required to unravel the underlying processes that cause major changes in community structure in response to external perturbations such as harvesting. To identify the mechanisms driving dynamics in the Takvatn system, it was sufficient to have estimates of the relative size distribution (capture per unit effort) of predator and prey, individual growth rates/condition of predator and prey, and estimates of the encounter rate of brown trout with Arctic char (although additional information on the availability of the resource of Arctic char would have been preferable). This information is or could readily be extracted from monitoring data, but that is generally not done at present.

Although we have focused on the basic mechanisms underlying the dynamics of the two systems, both examples have major implications for management. In the Takvatn example, fishing on the prey (Arctic char) of the predator (brown trout) represents a management tool that can promote the recovery of the predator and also reduce the risk of predator collapse (Persson *et al.*, 2007). In cannibalistic systems, size selective harvesting of larger individuals in stable, non-oscillatory systems may induce the production of large “giant” individuals but at the same time induce oscillations as observed for the perch systems (van Kooten *et al.*, 2010).

To conclude, we argue that unless the size-specific interaction strengths between size-structured predator and size-structured prey are explicitly considered, attempts to understand whole-system dynamics will be futile. The extent to which a full quantitative accounting of all individual-level rates in the form of a more detailed DEB model is necessary to understand system dynamics (as was the case for the cannibalistic system) will likely differ between systems and also depend on the extent to which quantitative information is necessary for a particular management purpose. A relevant question to raise here is therefore to what extent existing fisheries management models, especially multispecies models, implement the modelling philosophy embedded in physiologically structured

population models with its explicit links between individual-, population-, and community-level processes.

Models for marine fish stocks: ecological considerations

In the current section, we review some commonly used fish stock assessment models with an explicit focus on multispecies models and discuss the question to what extent these models account for (i) size-dependent interactions, (ii) food-dependent somatic growth, and (iii) closed DEB of individuals, which elements were shown above to be crucial for understanding whole-system dynamics. We consequently consider whether these models account for a consistent energy flow in the ecosystem under assessment.

The most prominent objective of collecting fisheries data is to enable predictions of future stock production. Several multispecies models that are commonly used for making such predictions, or seen as front-runners in ecosystem-based approaches to fisheries, are listed in Table 1. In this table, we highlight seven model characteristics that are related to basic processes underlying ecosystem and community dynamics (which per definition pertains to a multispecies context). Specifically, the treatment of the link between intake of food and production of biomass is emphasized. In traditional approaches to model fish stock dynamics, the relationship between age, length, and weight is considered to be constant, which invokes the implicit assumption that individual body condition is also constant, and growth processes are not linked to food availability.

Probably the most used and most well-known multispecies assessment technique is MSVPA (multispecies virtual population analysis, Sparre, 1991). Both MSVPA and the SMS technique (stochastic multispecies model, Lewy and Vinther, 2004) are age-based methods that can account for multiple interacting species. These methods assume fish cohorts to follow a prescribed length–age relationship, which implies that growth is not linked to the availability of resources. Furthermore, the inclusion of predation interactions solely accounts for the (negative) mortality component caused by predation, while its positive effect, the biomass production of the predator population, is independent of the predation interaction and, hence, of prey availability. These models therefore do not capture any of the above listed three ingredients to enable a linkage between individual-level dynamics and population- and community-level dynamics. However, MSGVPA (Gislason, 1999) is an extended version of MSVPA that accounts for dynamic, food-dependent growth, though only for the predator and not for prey species. The stochastic foodweb model as described in Lindegren *et al.* (2009) is specifically designed in the context of an ecosystem-based management approach. Although this model accounts for a relatively extensive foodweb, population size distributions are ignored. With respect to the consistency of energy flows, it may be even more significant that the feeding links, being based on statistical correlations between total population biomasses, are not always reciprocal, meaning that predation mortality may be accounted for without a link to the concomitant food intake of the predator or *vice versa*.

Besides the food-dependence of growth, there is often an energetic inconsistency in the way reproduction or recruitment is accounted for in the models listed in Table 1. The Piscator model (van Nes *et al.*, 2002) goes a long way in accounting for food-dependent growth, but in this framework there is no connection between juvenile recruitment and the fecundity of the spawning

Table 1. Biological properties of some multispecies models used in the context of ecosystem based approaches to fisheries.

Ref	Type	Multispecies	Age	Body size	Food-dependent growth	Length – age relation	Predation effects	Reproduction/recruitment	Closed mass/energy budget
1	MSVPA	+	+	–	–	Fixed	Prey mortality only	Ricker	–
2	MSGVPA	+	+	+	Predator only	Food-dependent (in predator)	Prey mortality only	Ricker	–
3	SMS	+	+	+	–	Fixed	Prey mortality only	e.g. Ricker	–
4	Gadget	+	+	+	–	Dependent on feeding level	Prey mortality and predator feeding level ↑	Fecundity recruitment possible	No direct link between growth and actual food intake
5	Atlantis	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	Size- and condition-dependent spawning	No maintenance costs
6	EwE	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	Condition-dependent	No costs for reproduction
7	Stochastic foodweb model	+	–	–	–	–	Prey mortality and predator biomass ↑	Hydrographically driven	–
8	Piscator	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	No connection to spawning or spawner condition/abundance	No link between recruitment and spawners

(1) Sparre (1991); (2) Gislason (1999); (3) Lewy and Vinther (2004); (4) Begley and Howell (2004); (5) Fulton et al. (2004); (6) Walters et al. (2008); (7) Lindegren et al. (2009); (8) Van Nes et al. (2002).

population. The model frameworks of Gadget, Atlantis, and Ecopath with Ecosim (EwE) in principle link the reproductive output or juvenile recruitment to individual body-size or body-condition and population size distribution. Nevertheless, in these models, the energetic basis of at least one basic process is modelled in a manner that violates mass conservation principles (Table 1).

The formalism of stage-structured biomass models (*sensu* De Roos et al., 2008) shows similarities with the approach adopted in EwE (Walters et al., 2008; Table 1), in particular in terms of “user friendliness” and simplicity of equations. The two formalisms nevertheless differ in the way energy flows are modelled, especially with respect to maturation (biomass flow into subsequent life stages) and reproduction (biomass flow from adults to newborn individuals). In the EwE framework, maturation can in principle be represented as a food-dependent flow, but there is no published example exploiting that possibility in the context of a multispecies model and usually maturation is modelled as a constant process (Christensen and Walters, 2004). In addition, the EwE framework generally does not account for biomass costs of reproduction, which in essence allows for a spontaneous source of newborn biomass. The stage-structure biomass formulation, in contrast, models individual-level energetics with a closed DEB model, which makes maturation and reproduction rate dependent upon food intake and thus closes the loop of energy in- and outflow to the system (Table 1).

On the basis of the seven model characteristics highlighted in Table 1, we conclude that none of the models commonly used for fish stock assessment, management advice, or as a conceptual model considering ecosystem dynamics for an ecosystem-based approach to fisheries (e.g. Plagányi, 2007) bases itself on a completely closed mass/energy budget and that these models thus violate the basic law of conservation of mass/energy. Such a lack of a complete handling of mass balances is not a trivial problem as illustrated by the cannibalistic perch system where a quantitatively correct handling of mass flows was pivotal for understanding overall system dynamics.

Linking individuals to populations and communities: insights from monitoring data

Utilizing the Takvatn example, we test the hypothesis that a relatively limited amount of information can be sufficient to unravel the underlying processes that may cause major changes in community structure as a response to external perturbations such as harvesting. We use existing stock assessment data of two marine fish species, the predatory cod (*Gadus morhua*) and one of its main prey fish sprat (*Sprattus sprattus*) (the other being herring, *Clupea harengus*) in the Baltic Sea system, in combination with data available on zooplankton to look for relationships between resource or prey density and consumer (sprat and cod) growth performance. The question we address is whether the collected data are sufficient to obtain information about (i) size-specific interactions between individuals; (ii) food-dependent growth; and (iii) food-dependent reproduction.

Besides being the most abundant fish species, the populations of cod and sprat in the Baltic Sea are commercially important stocks and have been industrially fished with increasing intensity since the 1960s. Although since the 1970s stock assessments have been made and used for advice on fishing intensity, a steep decline and collapse of the cod stocks in the early 1990s could not be prevented nor reverted by the commonly adopted methods. The collapse of the

cod stock resulted in a shift visible at four trophic levels in the ecosystem (Casini *et al.*, 2008; Möllmann *et al.*, 2008). The occurrence of, and need to understand, such ecosystem-wide events calls forth an ecological perspective when considering the population dynamics of commercially important marine stocks.

Previous analyses of the Baltic cod and sprat populations showed the distinction between two periods, one with dominance of the predator cod (i.e. the period < 1994) and a second period with dominance of the zooplanktivore sprat (≥ 1994), which followed the overfishing of the cod stock (Casini *et al.*, 2008). Furthermore, in the second period, the abundance of sprat individuals (age 1+) is positively correlated with the biomass of the zooplankton resource base, a relation lacking in the first period (Casini *et al.*, 2008). A plot of the seasonal growth of individual sprat as a function of the resource (zooplankton) biomass shows the same outcome, with individual sprat growth being positively correlated with the resource availability only in the second period, in which the cod population is at a low biomass, (Figure 5b). In contrast, no relationship is present in the period with dominance of the top predator (Figure 5a).

The population data of sprat and its zooplankton prey thus provide evidence for energy-dependent growth in the period when the system is dominated by bottom-up control, whereas the relationship is absent in the period when top-down processes play a more important role. Since the first period is characterized by top-down control of the sprat population, the zooplankton densities would be predicted to be higher, relative to a bottom-up controlled situation. Comparison of the two panels in Figure 5, however, shows that there is a large overlap in the measured densities of zooplankton. Moreover, even the realized growth of sprat has comparable levels between the two periods, which contrasts with expectations under top-down vs. bottom-up scenarios.

The occurrence of these patterns (and their absence), both highlights the potential of the data, as well as shows its limitations. Logically, there must be a connection between individual growth and availability of resources. The representation of resource density by a single data point each year is apparently sufficient to reveal a

connection in the variation of individual growth and food availability for the zooplanktivore sprat, as long as the dynamics are regulated by bottom-up control. On the other hand, the same data resolution, in time, but specifically in terms of prey sizes, is insufficient to reveal the relation of body size growth in cod with availability of its food. To investigate the relationship between individual cod growth and the density of its major fish prey, we used the yearly total sprat biomass estimated in autumn. The growth data for cod are based on cohort estimates of yearly increments in average weight for cohorts with ages 3+ years old (> 30 cm). Acoustic data for sprat, including average weight-at-age for different cohorts contains data for ages 1-year old and older (> 8 cm). Sprat individuals in these cohorts all fall within the predation window of cod aged 3+ and because the relative component of alternative resources in the cod diet is unknown, we take the total sprat biomass as an indicator of available food for cod. The analysis shows that there is no relation between individual cod growth and the total biomass of its major prey species, in neither of the two periods (Figure 6). With respect to the energy dependence of biomass increase in cod cohorts, the population-level indicator of prey availability does therefore not confer the essential components for realized predator growth. This result is not *per se* surprising, when viewed in light of the patterns found between predator and prey fish in the Takvatn system (Figure 1), but again points to the need for prey fish data with a high size resolution.

Besides the size- and time-resolution issue with respect to the data of the resource base of cod, it is problematic that the resource is represented as a single unit (sprat population biomass): cod is known to additionally forage upon herring, benthic macroinvertebrates, and zooplankton, but it is not known how important (in terms of energy dependence) these different prey are for cod of different sizes. The lack of this knowledge renders it impossible to use the data presented in Figure 6 for a derivation of empirical consumption rate of sprat by cod. The origin of this issue is impossible to solve by only collecting better data and can therefore be considered of a more basic nature than the issue of time and size resolution

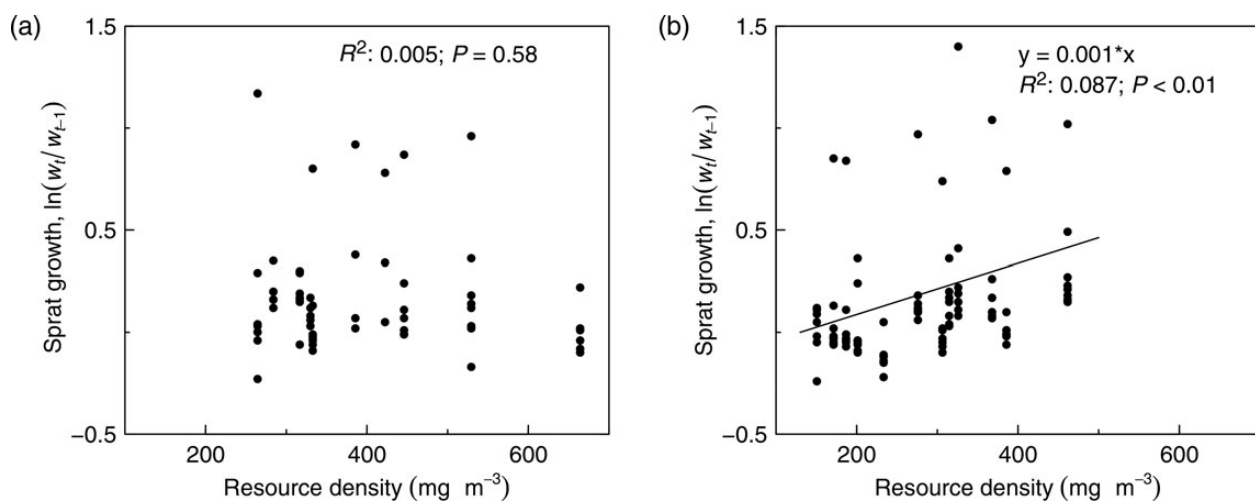


Figure 5. Annual increase in average weight in the Baltic sprat population (age 1+, 1978–2007) as a function of zooplankton density. (a) Sprat growth in the years where the sprat population is below the threshold level (1978–1994, as established in Casini *et al.*, 2009), sprat growth is derived from weight-at-age data from the acoustic survey in SD28 (carried out by Sweden and Latvia), Baltic Sea, resource density represents the summer density of zooplankton (sum of *Acartia*, *Pseudocalanus*, *Temora*, and *Cladocera* species; all unpublished data, Michele Casini, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Lysekil). (b) Sprat growth in the period 1994–2007, the period in which the sprat population density was above the threshold level and regulated by bottom-up control (Casini *et al.*, 2009).

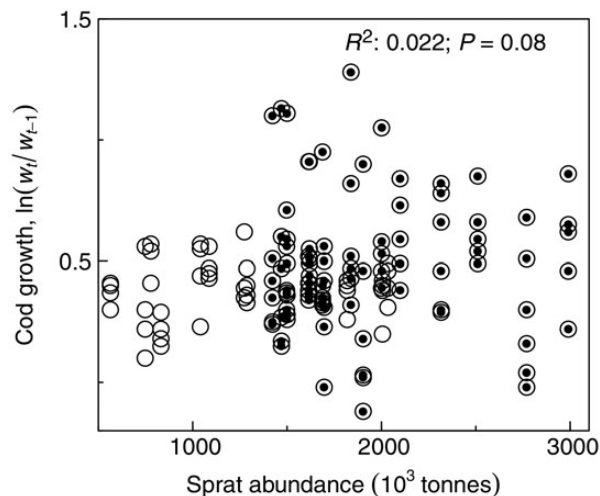


Figure 6. Annual increase in average weight in the Baltic Sea cod population (age 3+, 1982–2010) as a function of sprat total biomass (age 1+, all data from ICES, WGBFAS2011 – ACOM:10, Table 2.4.13; Table 7.7). Cod weight-at-age data in years < 1982 was left out because preceding this date a constant weight-at-age is assumed in the stock assessment data. The dots with a thick dot inserted indicate the data for the years the sprat population density was above the threshold level and regulated by bottom-up control (Casini *et al.*, 2009).

in the data. The measured effect shown in these data (average weight increase in age cohorts) is a result of several processes, taking place at the individual level. Yearly individual growth is the outcome of food intake and energy expenditure over the course of the preceding growth season. Furthermore, food intake in cod depends on the availability and densities of the different prey listed above; energy expenditure depends on activity, baseline metabolism, and allocation to reproductive tissue. To take just one measure (weight increase) as a representation of these many variables is taking a short-cut, preventing a clear view on those variables themselves. Inference of individual growth potential from such observations at the system level is virtually infeasible. At the same time, the inference of the essential community structure (trophic configuration) from individual-level observations (such as stomach data) can also be misleading. As illustrated by the cannibalistic perch example mortality by cannibalism may be substantial and to a large extent shape community dynamics (in the stunted phases of the dynamics), while the diet of the cannibals mainly consists of macroinvertebrate prey (cf. Figure 4a and b). Therefore, the diet of individuals can be analysed in the field, but it should be kept in mind that diets represent the output of the feeding process and can hence not serve as input to parameterize this process in a model that accounts for a mechanistic (bottom-up) system description. Furthermore, the mere occurrence of a feeding interaction (e.g. macrobenthos feeding by cannibalistic perch) does not imply that this interaction actually plays a major role in determining community dynamics (Persson *et al.*, 2007, 2013; Persson and De Roos, 2012).

Discussion

Overall, we have discussed three major interrelated issues: the problem of deducing an appropriate trophic configuration based on which to analyse a system; the necessity to mechanistically link individual, population, and community processes to obtain an understanding of whole-system dynamics; and the issue of

accounting for closed energy budgets and mass conservation and the extent to which this is done in contemporary multispecies fisheries models.

Trophic structure and niche shifts

Deducing an appropriate trophic configuration for the system to be studied is not a trivial task. As pointed out above, the use of observed diet data can be problematic, since the observed diet represents the result of interactions and cannot be taken directly to reflect the underlying processes. The individual diet, as it is observed, results as an output from size-dependent feeding interactions and encounter or availability of different prey and resources, which are the true input. Many observed feeding relationships may furthermore be unimportant in explaining community dynamics and structure (Persson and De Roos, 2012; Persson *et al.*, 2013), however, frequently occurring. It may even be so that a low incidence of prey fish in the diet of predators represents a high predation impact on the prey fish, or *vice versa*, as was the case in the cannibalistic perch system.

In view of the ecosystem changes happening worldwide in diverse systems, which are sometimes caused by anthropogenic impacts, we argue that despite its difficulties, building an understanding of trophic interconnections and foodweb structure is an essential component for an ecosystem-based assessment and management of fisheries. We propose that a number of steps can be taken to move forward, the first of which deals with the form of ontogenetic niche shifts that occur with increasing fish size. These shifts can be gradual and involve an addition of larger prey sizes where the smallest prey sizes stay more or less the same, or they may be discrete where smaller prey items are dropped from the diet when larger prey items are included (Werner and Gilliam, 1984; Schellekens *et al.*, 2010). Modelling of size-structured systems has shown that the shape of the ontogenetic niche shifts in predator life history and particularly whether the predator can mature on non-piscivorous resources has a major effect on community structure (Van de Wolfshaar *et al.*, 2006; Hin *et al.*, 2011; De Roos and Persson, 2013; van Leeuwen *et al.*, 2013). To unravel this ecological aspect of the life history of the predator species represents the first important step to reach an appropriate characterization of the trophic structure (cf. Huss *et al.*, 2013). Second, the extent to which top-down effects can occur when top predators experience multiple (zooplanktivory–benthivory–piscivory) niche shifts during life may depend heavily on the discreteness of their ontogenetic niche shifts (Van de Wolfshaar *et al.*, 2006; van Leeuwen *et al.*, 2013). Existing theory and empirical studies here suggest that it may be possible to use observed individual-level growth trajectories in combination with size-distributed densities of interacting fish populations (preferably also resource levels) to track dynamically important interactions, because patterns in these data can distinguish between different trophic configurations (Persson *et al.*, 2003, 2007; Van de Wolfshaar *et al.*, 2006; De Roos and Persson, 2013; van Leeuwen *et al.*, 2013). For example, for the Baltic Sea system, three major mechanisms have been proposed to potentially explain the changes in the fish community: an Emergent Allee effect as in the Takvatn system, mixed competition/predation interactions (or cultivation/depensation) between predatory fish and prey fish and predation on early life stages of the top predator cod by prey fish (van Leeuwen *et al.*, 2013). Modelling studies show that these three scenarios yield vastly different individual growth curves of the top predator and also different size distributions of predator and prey fish (De Roos and Persson, 2013). The attempt

to resolve which of these three processes contributes most to explaining the dynamics of the Baltic system should thus be based on empirical analyses of patterns at the population (e.g. size distributions) and individual (cf. individual growth rates of predator and prey) levels.

Individual to population to community

Our analysis of the perch–zooplankton interactions in Abborrtjärn 3 and partly also the sprat–zooplankton interactions in the Baltic Sea suggests that a relationship (although poor) between resource level and individual planktivorous consumer performance can be present even when resource availability is represented by a single point estimate in terms of total resource biomass (for the strength of the interaction the size of the consumer must still be taken into consideration). This may be a result of the limited size variation in the resource and the average size of resource compared with the consumer being relatively small. In contrast, fish predator–prey interactions are characterized by major changes in size of both prey fish and predator fish, and in this case, a condensed biomass estimate in terms of total biomass will inevitably fail in allowing an establishment of a relationship between prey availability and individual performance. Even worse, the Takvatn example shows that there may actually be a negative relationship between total prey fish biomass and predator performance. To appropriately characterize these interactions, it is therefore basic to incorporate size-dependent interactions between predator and prey.

One of the major advantages of the physiologically structured population models that we used in our freshwater examples is that they allow for a more critical testing of model predictions, involving both population-level information such as population size distributions and individual-level information such as individual growth curves that are shaped by ecological feedbacks (Figures 1, 3, and 4). It is worthy to note that fisheries sampling programs often include information at both these levels of organization. Although the data collection procedure may be limiting, data on population abundances and size distributions as well as growth curves are often present, but generally not used efficiently in an integrated way to investigate population and community dynamics. The dynamics of the Takvatn system that we discussed extensively in the text above illustrate the kind of analyses that can be carried out with an actually limited amount of information (Figure 1). At the same time, it is obvious that more complete analyses of the dynamics of this system could have been done if information had also been available on (zooplankton and macroinvertebrate) resource levels and the seasonal abundance of the smallest size classes of Arctic char (<80 mm). Having access to and efficiently using time-series data on predatory fish and prey with a high intraspecific size resolution, individual growth curves and resource levels will undoubtedly form the basis for a true ecosystem-based management approach that takes into account relevant ecological feedbacks.

The two freshwater examples we have used undoubtedly represent rather simple systems in terms of the number of fish species involved. Still, the framework we propose has been used to understand the dynamics of, for example, the multispecies fish community of Lake Victoria (Downing *et al.*, 2013). This suggests that the dynamics of species-rich fish systems may be possible to assess with a relatively limited amount of information. The changes in the ecological system in Lake Victoria are still driven by the dynamics of one dominant top predator, the Nile perch (Goudswaard *et al.*, 2008). To obtain robust tools for both assessment and management of systems with many top predatory fish species undergoing

multiple ontogenetic niche shifts represent a major challenge for future research.

Accounting for energy budgets and mass conservation

For fish, as for all living organisms, growth and reproduction (i.e. the production of biomass) come at an energy cost. Availability of this energy depends on food intake. To ignore food-dependent development in projections of (population) biomass production equals implicitly assuming a “free” energy source to the system. Essentially, whether or not to enforce strict mass conservation boils down to a modelling philosophy decision between on the one hand a specification of whole-system dynamics in terms of the underlying, mechanistic processes at the individual level or, alternatively, a mimicking of these dynamics by combining observed, but not necessarily causal, relations into a phenomenological system description. However detailed, the latter will by its nature be less likely to correctly extrapolate system dynamics to novel environmental conditions. We have particularly considered the incorporation of food-dependent growth and a coupling between energy intake and reproductive output (including a cost for reproduction) in existing models used for fish stock assessments and stock predictions. The overview given in Table 1 shows that none of these models are based on a fully consistent incorporation of the individual-level processes and energy conservation. Ignoring the food-dependent basis of both development and reproductive output completely could be justified when there would be no or only limited effects of doing this. Our two examples from freshwater systems show that food-dependent growth and reproduction are both vital processes affecting population and community dynamics. The extent to which a complete handling of mass balances as for the perch system is important will likely differ between systems and also depend on the questions addressed, but should be increasingly important when questions related to harvesting yields are decided. Quantitative predictions may also become more important when effects of environmental variation such as temperature variation are included because changes in temperature, for example, affects both individual-level processes (intake and metabolism) and community-level processes (e.g. resource productivity) where the dynamical outcome depends on the relative scaling of these processes (Vasseur and McCann, 2005).

A possible reason for the lack of a consistent link between energy intake and allocation to reproductive output and recruitment in several fisheries models may be a disagreement about the role, the extent and the mechanisms of larval mortality (e.g. Hjort’s 1914 “critical larval period” concept; Elliott, 1989; Jenkins *et al.*, 1991; Houde, 1994, 1997; Persson *et al.*, 2000b) which partly explains the commonly observed high, unexplained variation in stock–recruitment curves. These factors may have led fisheries scientists to conclude that there is little meaning in making reproductive output depend on the energetic state of the reproducing individuals and instead assume it to be stochastic or dependent on environmental factors only. One problem here is that recruitment of a cohort generally refers to a cohort at an age (or size) when major density-dependent interactions have already taken place. Considering the major change in size that a fish individual undergoes during its first growing season, an understanding of the community dynamics may critically depend on a sufficient resolution in size and thereby also time resolution, which current stock–recruitment models do not capture.

As discussed here, the approaches to management of fisheries and fish stocks has so far neglected essential ecology of fish and

fish population dynamics. The ecosystem-based management approach to fisheries management is supposed to take into account the ecological consequences of fisheries for entire ecosystems. We have shown that an understanding of population dynamics, which is based on mechanistic descriptions of individual-level processes, can reveal the way and processes by which populations are regulated. Changes in stock size distributions and variation in individual body sizes of age cohorts represent invaluable data of commercial fish stocks in this regard, which was already clearly recognized since the days of Hjort (1914). Creating a connection between such data and the underlying ecological foundation of that variation is the necessary and vital next step towards an understanding of the ecosystem wide impacts regarding system structure and dynamics as a result from imposing fishing pressure and other perturbations. Doing this is the way forward in pursuit of a true ecosystem-based approach to fisheries.

Supplementary material

Supplementary material includes the ecological background to and derivation of the functions used for calculating encounter rate for brown trout with Arctic char and cannibalistic perch with perch victims.

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