Impact of climate change on epibenthic predation as regulating mechanism on estuarine bivalve recruitment

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Chapter 1. General introduction

Intertidal areas occur along almost all coastlines worldwide. They are formed along tidal channels, in bays and lagoons, in estuaries, along coastal seas and inlets and are part of larger systems that include subtidal areas (Eisma 1998). These areas are interconnected as chains providing indispensable resting and fuelling stations for millions of wading birds on their migratory pathways (see for instance Piersma, 1994). In the temperate region, the Wadden Sea, with its extensive mudflats, is one of the most important stopover ground for birds along the East-Atlantic flyway, mostly because of its large size, but other areas along the European Atlantic coast have similar functions. These areas have an important role as nursery grounds for various fish and invertebrate epibenthic species (a.o. Zijlstra 1972). Because of the harsh environmental conditions, their species diversity is relatively low compared to adjacent marine and freshwater environments (Levin et al. 2001) but due to high productivity they can still support large populations (Pihl and Rosenberg, 1982, Gibson et al., 1993). Research in European estuarine coastal waters for more than five decades has recognized a dominant "epibenthic species complex" in soft-bottom communities comprising of mobile invertebrates, mainly the common shrimp Crangon crangon and the shore crab Carcinus maenas, various small gobiidae Pomatoschistus spp. and various juvenile flatfish species (plaice Pleuronectes platessa, flounder Platichthys flesus, sole Solea solea).

For both birds and epibenthic predators, the main food source consists of intertidal benthic fauna, whereby a main component is formed by bivalves. In general, birds can potentially only prey on those bivalves that have survived the youngest stages and have grown to an edible size. The availability of this food resource is to a large extent determined by annual recruitment of spat, in turn linked to survival of the bivalve youngest stages after a period of severe predation by a complex of epibenthic predators: shrimps (Pihl and Rosenberg 1984, Keus 1986, Van der Veer et al. 1998), shore crabs (Jensen and Jensen 1985, Sanchez-Salazar et al. 1987, Van der Veer et al. 1998), and flatfish (De Vlas 1979, Afman 1980, Pihl 1982, 1985, Aarnio and Bonsdorff 1997). However, these interactions are complicated by the occurrence of cannibalism of adult shrimps on juveniles (Pihl and Rosenberg 1984) and predation by gobies (Van Beek 1976, Del Norte-Campos and Temming 1994), shore crabs and flatfish upon adult shrimps (De Vlas 1979, Afman 1980). Therefore, there is an intricate web of interactions that will affect overall predation pressure on bivalve spat (Fig. 1). Since these interactions are size-dependent, overall predation pressure will depend on one hand, on the ability of the bivalve prey to outgrow the predation size spectrum and, on the other hand,

on predation intensity during the vulnerable stage which is a function of the predators consumption rate (functional responses) and its abundance (numerical responses) (Fig. 2). In this respect, both temperature and food conditions are crucial since they directly affect the size-structured interactions. Temperature dictates potential maximum growth rates and thus, the minimum time window for prey before they can escape predation by outgrowing predators, and food conditions ultimately determine if prey can achieve their growth potential. Furthermore, temperature also affects metabolic demands influencing predator's ingestion rates.

Processes such as climate change, here referring to an increase in average seawater temperatures, might affect these predator-prey interactions with consequences for population regulating mechanisms and the overall survival of bivalve spat. This requires insight in the functioning of the predator/ prey interactions in these estuarine systems.

Epibenthic predation as a regulating mechanism of bivalve recruitment

In temperate shallow soft-bottom marine systems, epibenthic predation is considered a major biotic factor structuring benthic communities (Pihl and Rosenberg 1984, Jensen and Jensen 1985). Decapod crustaceans are responsible for a large fraction of post-settlement mortality (Thorson 1966, Möller and Rosenberg 1983) and its impact is related to their generally high abundances, broad distribution in both intertidal and subtidal habitats, their high motility and their need to process large amounts of food (Gosselin and Qian, 1997).

In the Dutch Wadden Sea, crustacean predation seems to exert a strong top-down effect on bivalve population dynamics as suggested by correlations between year-class strength in bivalves and shrimp abundances (Beukema and Dekker 2005, Beukema et al. 1998) and by direct analysis of stomach contents in crustaceans (Van der Veer et al. 1998). However, the contribution of predation mortality to year-class strength and ultimate bivalve recruitment variability remains unclear. In flatfish which also present a pelagic larval phase followed by a demersal juvenile stage, it has been suggested that most of the interannual variability is determined in egg and larval phases and that density-dependent mortality, mainly by crustaceans, occurring during and shortly after settlement, has a dampening effect on this variability (Van der Veer et al. 1986, Van der Veer et al. 2000).

Although it is unclear when year-class strength in bivalves is exactly established (planktonic phase or after settlement onto the sea floor), crustacean predation seem to be an important post-settlement process. However, unlike crustacean predation upon just-settled flatfish (Van der Veer and Bergman 1987), in bivalves, there is limited evidence for a regulative action. In fact, the few data available suggests, in various bivalve species, a lack of reduction in inter-annual variability in the first year of life after settlement (Van der Veer et al. 1998). In addition, recent experimental work on the detailed functional response of *C. crangon* foraging upon small *M. balthica* showed a type II functional response, indicating that predation mortality by shrimps is not density-dependent (Andresen and Van der Meer 2010). However, in the field, other factors such as presence of alternative prey, interference with conspecifics or presence of other predators, all may affect the shape of the functional response and the overall bivalve mortality.

In contrast to flatfish, there is also the suggestion that, in bivalves, the influence of controlling mechanisms may not be restricted to the pelagic phase but may operate until the end of the first year of bivalve life (Van der Veer et al. 1998) or even later, in northern latitudes, due to lower temperatures. Therefore, the relative importance of processes determining year-class strength might vary across species' geographical range and hence the discussion on bivalve recruitment patterns on a large scale may benefit from studies with a latitudinal perspective.

The study approach

The approach followed in this thesis is based on the observation that over a large distributional range, the same group of abundant benthic bivalve species as well as epibenthic predators are dominating (for bivalve species see Cardoso et al. 2006 and for the epibenthic predators, Pihl 1985) and the assumption that latitude is a good surrogate for mean water temperature conditions. Hence, we expect that the impact of temperature on bivalve recruitment can be mimicked by studying the same basic interactions along a wide geographical range.

The work presented in this thesis is based on three main components: [1] a review of species-specific physiological responses to temperature of both prey and predators, [2] field studies describing growth under natural conditions for the various groups, and [3] bioenergetic modelling to evaluate prevailing food conditions of both prey and predators.

Since food and temperature are the key factors affecting growth, a general framework describing growth in relation to environmental conditions (average food and/or temperature levels) in a consistent way and applicable to various species (predators and prey) is required. Such a theoretical embedding is provided by the Dynamic Energy Budget (DEB) theory developed by Kooijman (1988, 2010). The DEB theory builds on the premise that the mechanisms responsible for the

organization of metabolism are not species-specific (Sousa et al. 2010) and hence, a common model structure is employed whereby differences among species are reflected in different parameter values (Kooijman 2010). DEB models have already been successfully applied to study growth and reproduction in a wide range of marine organisms, from shellfish (Cardoso et al. 2006, Pouvreau et al. 2006, Troost et al. 2010) to fish (Van der Veer et al. 2001, Van der Veer et al. 2009, Pecquerie et al. 2009, Eichinger et al. 2010).

The schematic representation of the standard DEB model is given in figure 3 and a more detailed description of the main assumptions can be found in Kooijman et al. (2010).

Aims and outline of the thesis

With a focus on the potential impacts of climate change on the ecological functions of shallow-water systems, the aim of this thesis is to analyze the effect of temperature changes on a key predator-prey interaction, involving crustaceans as predator and bivalve spat as prey, but taking into consideration the multiple interactions that may occur within the epibenthic species complex.

Chapter 2 is the backbone of this thesis providing a review of the effect of predation on population regulation among (epi)benthic communities along both Atlantic coasts. The study combines experimental and field evidence for regulation in the coastal zone and discusses to what extent and under which conditions controlling and regulating mechanisms might be expected in relation to species distributional range and latitude. We surmise that instead of large geographic trends, control and regulation will most likely depend on local habitat, temperature conditions and species type involved in predator-prey interactions.

Chapter 3 analyses and compares the temperature tolerance range and temperature sensitivity of the various epibenthic predators and bivalve prey using experimental data reported in literature. Our results show that crustaceans have higher temperature sensitivity and tolerance range compared with their potential predators and with their bivalve prey. It is hypothesized that a temperature increase can potentially lead to an overall higher predation pressure in temperate systems; nevertheless, final conclusions still required an elucidation of food conditions in the field which was the addressed topic in the subsequent chapters.

In **Chapter 4**, the Dynamic Energy (DEB) theory is used to reconstruct the food conditions of four of the most common Northeast Atlantic coastal bivalve species (*Mya arenaria, Cerastoderma edule, Mytilus edulis* and *Macoma balthica*). By combining growth patterns in the field with prevailing temperatures, the relative assimilated energy is estimated for various areas along species distributional ranges. Results indicate food limitation over the range of locations examined with no clear trend or relationship with latitude.

Chapter 5 presents a first estimation or re-analysis of DEB parameters for some of the epibenthic fish and crustacean predators. Information on the thermal biology estimated in Chapter 3 is related to species bioenergetics revealed by the DEB parameters in an attempt to link physiological performance and response to temperature to the underlying mechanisms. Despite the uncertainties in some of the DEB parameters for various species, due to the lack of experimental data, differences in life-history strategies were clearly reflected in parameter differences between related species. Temperature tolerance and sensitivity seemed to be linked with the energetics of a species. In terms of growth, relatively high temperature optima, sensitivity and/or tolerance were related to lower relative assimilation rates as well as lower maintenance costs.

In **Chapter 6**, the topic of food limitation is reappraised, using juvenile plaice *Pleuronectes platessa* as a model species. In a combined approach of statistics and DEB modelling, food conditions in the Balgzand intertidal area were investigated using a long-term time series and considerations are done about the occurrence of intra- and/or interspecies competition in the area. The main findings seem to point out a reduction of growth in the course of the season possibly related to competition with epibenthic crustaceans and gobiidae and also highlighted that besides food quantity also food quality may play a role on overall growth performance.

Chapter 7 expands the DEB analysis carried out with plaice in chapter 6 to other nursery grounds and to other flatfish species with contrasting elements in their life cycles, sole *Solea solea* and flounder *Platichthys flesus*. The comparison of observed growth with DEB- predicted maximum growth at prevailing local temperatures indicates a decreasing growth performance during the season for both plaice and flounder while for sole no clear change was observed. In addition, over the areas analyzed, a positive trend in growth performance with latitude was observed for flounder and, to a lesser extent, in plaice.

Chapter 8 addresses the applicability of the DEB approach to analyze growth conditions in multi-cohort species, epibenthic crustaceans and to a lesser extent gobies, for which growth is difficult to monitor due to prolonged settlement of brood. Despite the need for further fine-tuning in some model parameter sets, results seem to suggest a lack of food limitation in gobies while for crustaceans conclusions are hampered by growth variability in the field. The study also indicates that having accurate estimates of actual temperature conditions experienced in the field, especially in shallow tidal pools, is of importance for growth simulations.

Finally, **Chapter 9** contains a critical analysis of the assumptions and limitations of the approach followed in the present work and a general discussion of the main findings and their implications in a global warming context. The suggestion is made that rising seawater temperatures will affect predator-prey relationships and especially benefit crustaceans as predators with negative consequences for bivalve recruitment.

Chapter 2

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Population regulation of epibenthic species in coastal ecosystems, with implications for latitudinal patterns

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Abstract

The effect of predation on population regulation among (epi)benthic communities along the Atlantic coasts is reviewed. Population regulation requires density-dependent mortality at some phase in the life cycle, which can occur through predation under certain functional (Type III) and numerical feeding responses. Although the potential to induce regulation has been suggested for some epibenthic predators in the coastal zone, studies linking direct observations of predator–prey responses to observed regulation of the prey population are scarce. The identification of Type III functional response curves is mainly restricted to laboratory or cage studies, and the effect is confined to a limited range of prey densities. Numerical responses, especially predator aggregations, may be more common in the natural environment. The response type seems to be affected not only by habitat structure but also by water temperature. Prevailing temperature conditions can affect the functional response type possibly through changes in predator behavior. The effect of latitude on population regulation can be expected. Most likely there is a mosaic of predator–prey interactions that depend on local habitat, temperature conditions, multiple species interactions and predator and prey species types. We surmise that any latitudinal pattern in the overall recruitment variability along species distributional range is more likely to result from a trend in controlling rather than regulating factors.

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1. Introduction

Since Hjort (1914, 1926) advanced the hypothesis that year-class strength in fishes is controlled during the early life history when numbers are at a maximum, there

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appears to be a general agreement that recruitment of many marine organisms is largely established during the pelagic egg or larval period (e.g. Connell, 1985). Gulland (1965) suggested that coarse control during the period of egg and larval drift – whereby recruitment variability is generated – was followed by a second period of fine regulation – whereby variability is reduced – later on at the end of the larval stage or during the early juvenile stage. This concept has been recently supported in a review by Leggett and DeBlois (1994).

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Over the years, more information has become available indicating that the processes determining recruitment variability are not strictly species-specific or locally driven, but at least partly exhibit general and large-scale patterns. This view has been supported by the evidence of a link between the factors controlling recruitment and species- or group-specific early lifehistory patterns in fishes (Roff, 1982; Rothschild and DiNardo, 1987; Koslow, 1984), and by the synchrony in year-class strength often seen in adjacent fish populations over spatial scales of hundreds of kilometers (Rijnsdorp et al., 1992; Walsh, 1994; Myers et al., 1997; Fox et al., 2000). Miller et al. (1991) were among the first to build on this idea of general patterns in recruitment controls for Northwest Atlantic flatfishes. These authors examined factors generating recruitment variability in relation to the distributional range of species and early life-history patterns, leading to a series of explicit predictions about latitudinal variability in relation to various abiotic and biotic factors. However, their analyses did not include the pelagic stage during which recruitment may be controlled, but was restricted to the juvenile stage, during which regulating factors are considered to be more important (Leggett and DeBlois, 1994; Van der Veer and Leggett, 2005). Most studies focusing on overall recruitment variability have not distinguished between processes generating (controlling factors) and those reducing (regulating factors) variability (Leggett and Frank, 1997; Philippart et al., 1998; Brunel and Boucher, 2006) and therefore, do not provide a complete characterization of the recruitment process dynamics.

Van der Veer and Leggett (2005) have attempted to disentangle controlling and regulating factors focusing on flatfishes, a species group characterized by relatively low recruitment variability (Beverton, 1995). They concluded that the low recruitment variability of flatfishes is directly related to their life-history characteristics, and more specifically to their adoption of a spatially-size constrained, demersal juvenile stage. They elaborated the 'stage-duration' hypothesis that recruitment variability in flatfishes could be related to the duration of the pelagic early life stages - generating variability - versus the demersal stages - dampening variability, both in a relative and in an absolute sense. The importance of the demersal phase in dampening variability is stressed by the fact that in species with a demersal egg stage, density-dependent mortality was observed already during this early life stage (Taylor and Danila, 2005). Many other demersal species such as gobies, crustaceans, and to lesser extent predatory gadoids also concentrate in shallow coastal areas during their juvenile stages (Zijlstra, 1972; Pihl and Rosenberg, 1982). Therefore, if regulation occurs, it will most likely operate and be identified in these shallow areas (Zijlstra, 1972; Bergman et al., 1988). A side effect of the high concentration of juvenile fish and crustaceans in coastal areas is that their predation pressure might also affect and regulate recruitment of their main food items, particularly the macrozoobenthos (Van der Veer et al., 1998; Philippart et al., 2003).

Density-dependent mortality in shallow coastal areas has been demonstrated for several demersal fish species (Van der Veer, 1986; Sundby et al., 1989; Myers and Cadigan, 1993) and density-dependent mortality as a function of predation has been firmly established (Cushing, 1996). In most cases, the methods for detecting and testing density-dependence have been based on regressions (e.g. Beverton and Iles, 1992). However, these analyses without understanding the underlying processes are unsatisfactory (c.f. Bailey, 1994) and data on mechanisms of density-dependent mortality in marine species are rare (Hixon et al., 2002). Therefore, our aim is to identify density-dependent predation processes in (epi)benthic communities, either from field data or experimental manipulations, focusing on the Atlantic coasts because some of the main components of these communities are fairly consistently present over large areas. The benthic and epibenthic species complexes in these coastal areas are strongly linked through predator-prey relationships most of which are size-dependent (Kühl and Kuipers, 1983). The broad distributional and temperature ranges of species in these communities allow us to evaluate the hypothesis that density-dependent predation processes and hence, population regulation, may vary over a latitudinal gradient.

We first present a brief introduction of the various concepts used in predation regulation, followed by an overview of the experimental and field evidence for regulation in epibenthic and benthic species in the coastal zone. Next, we explore to what extent and under what conditions regulating mechanisms might be expected in relation to the distributional range of a species, and, finally, the impact of latitude is discussed.

2. Concepts

Population regulation requires density-dependent mortality factors to operate at some stage of the life cycle. Even if food limitation, diseases or parasites are proximate factors reducing survival value of individuals, these individuals are likely to be selected by predators and hence, in the absence of evidence for direct starvation-induced mortality, predation seems likely to be the most important mortality factor during the early life phase. At the population level, the magnitude of regulation through predation is determined by predation rate and the duration of the predation period. Predation rate is a function of the functional response of individuals (number of prey eaten per individual per day) and the number of predators.

Under laboratory conditions, the potential for regulation can be studied by analyzing the form of functional response curves under controlled situations. In the field, intra-annual regulation can be inferred from functional response curves often derived from stomachcontent analysis and numerical responses based on population surveys. Inter-annual regulation is often inferred from decreasing inter-annual variability in cohort abundance estimates between successive life stages (c.f. Van der Veer, 1986; Beverton, 1995).

From egg to adult stages, the characteristic population pattern is a decrease in numbers and an increase in individual size. Both theoretical considerations, such as the 'growth-mortality' hypothesis (Ware, 1975) and the 'bigger is better' hypothesis (for review see Litvak and Leggett, 1992), and field observations indicate that prey mortality decreases with increasing prey size. This is further confirmed by survival curves showing strongest decrease in numbers during the early life stage (Beverton and Iles, 1992), making the relatively early life stages most suitable for population regulation.

Regulation may occur through short-term, behavioral responses of predators – functional and aggregative responses – or through longer term, reproductive numerical responses to changes in prey density.

2.1. Functional responses

Three hypothetical types of response with increasing prey density can be distinguished depending on different combinations of searching and prey handling behavior, with all types reaching an asymptote at some level due to maximum gut capacity or handling time constraints (Fig. 1a). A Type I response (a linear rise to a plateau) reflects a constant searching time and no handling time, and leads to a situation where intake rate is proportional to prey density. When handling time is introduced, this interferes increasingly with the available time for searching as more individuals are consumed and a hyperbolic curve emerges (Type II response). A Type III response curve assumes that either the prey or the predator changes its behavior when prey density starts to increase, which results in an S-shaped rise to a plateau. In case of the predator, it might involve a learning process by



Fig. 1. Types of functional predator–prey response curves (after Bailey, 1994, based on Peterman and Gatto, 1978). a: Shape of different types of hypothetical response curves; b: Corresponding instantaneous mortality (d^{-1}) curves.

developing a 'search image' or a 'prey-switch' behavior (Murdoch, 1969) in response to increasing prey density relative to a more preferred prey whose density is lower. In terms of prey behavior, this type could result from a limited number of refuges or disturbance by crowding so that their availability for the predator increases. Typically, only the Type III response can induce regulation directly but only as long as the predation rate increases with prey density (Fig. 1b).

The classification of functional response curves was developed from laboratory experiments with single predator and prey species (Solomon, 1949; Holling, 1959, 1966). Although the theoretical curves may reflect the idealized behavior of how an individual responds to increasing prey levels, it is the aggregated response of a predator population that is important to prey mortality. In nature, prey may be aggregated and usually multispecies prey and predator assemblages will occur. This natural complexity is difficult to incorporate in experiments and models. Various predator species can interact with prey at (...) at different points along the prey density line (Fig. 2). Thus, the range of prey densities where an individual predator may regulate the prey population is quite limited, but it might extend as different predators become activated. In addition, predators do not operate

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Fig. 2. Illustration of the responses of various predators to different prey densities. Modified from Holling (1987).

in isolation, but have to compete with conspecifics over prey items thereby affecting the available foraging time. Incorporating this interference competition in functional response models have resulted in so-called 'generalized functional response models' (Van der Meer, 1997). However, it is unclear what the impact of interference competition is on a Type III functional response and whether interference competition affects the capacity for regulation. While interference competition is one type of predator-dependent response, other types may include cases where there is group hunting, or predator hotspots where a prey population is aggregated (Abrams and Ginzburg, 2000).

Interference competition is not only common among conspecifics but also if a prey is shared by several predators (Griffen, 2006; Griffen and Williamson, 2008). The effect of different interacting predator species on prey mortality is often not additive and therefore, cannot be predicted simply based on the responses of each predator separately (emergent multiple-predators effect; see Sih et al., 1998). Multiple trophic levels are also important to consider; for example, food density of a prey may change their risktaking behavior (Abrams and Ginzburg, 2000). Measurement of multi-species dependent functional responses seems critical to understanding predator– prey interactions (e.g. Essington and Hansson, 2004), but is logistically difficult to study in natural systems.

2.2. Numerical responses

The concept of 'numerical response' refers to the number of predators responding to prey density. Over short time scales, a numerical response may result quickly through aggregation to prey patches, while over longer time spans a response may be developed through reproductive output (involving birth, death, and growth rates) of the predators.

Short-term aggregation in response to prey density may result in Type II or Type III population response curves (Holling, 1959; Hunter, 1959; Hassell et al., 1977). The aggregated Type III response curve may provide a partial refuge for prey in low density patches acting as a stabilizing factor of the predator-prey interactions (Hassell, 1978; Mansour and Lipcius, 1991). Responses in reproductive output would assume food limitation of the predator as an underlying mechanism (i.e. bottom up control). A numerical response usually refers to a 'population response' on an inter-annual basis, however time scales over which a numerical response might occur can vary accordingly. In tidal areas, numerical responses may occur at the scale of the tidal cycle, but fast moving predators may exhibit even faster responses to local prey densities. The population dynamics of epibenthic species in coastal ecosystems often involves a sequence of different sizedependent predator-prey interactions each with a

restricted time frame. Hence, numerical response at an inter-annual time scale might be unlikely (Pihl and Rosenberg, 1982, 1984; Van der Veer et al., 1997).

2.3. Predator-prey system dynamics

In predator-prey interactions, activity levels of both predator and prey are important for the encounter rate and capture efficiency. Therefore, various interactions can be distinguished according to mobility of the various players.

One type of interaction refers to actively moving predators feeding on sessile prey such as bivalves. Predators range from the slowly moving star fishes feeding on mussels (Saier, 2001) to more active types such as crustaceans preving on bivalve spat (Van der Veer et al., 1998). The combination of a sessile (ambush) predator feeding on an active prey is less common, but the angler Lophius piscatorius luring prey fish to its self-made rod may serve as an example, although observations of similar ambush behaviors in coastal waters are limited. A common combination is active predators versus active prey, e.g. crustaceans preying on just-settled flatfish larvae (Van der Veer and Bergman, 1987). Finally, cannibalism must also be mentioned because it represents a form of self-regulation. Cannibalism is relatively common among a wide range of free-moving species, including piscivorous fish species and brachyuran crustaceans (Folkvord, 1997; Henderson and Corps, 1997; Moksnes et al., 1997; Moksnes, 2004).

Stomach-content analysis reveals that many of the common predators rely on a wide prey spectrum, which means that interactions between individual predator and

Table 1

	Observed	predator-prey	interactions	for North	Atlantic	coastal	species
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prey species may vary over short time and spatial scales between habitats or even in the same habitat. In addition, predators not only select for specific prey species but also for specific size ranges depending on their own size (Van der Veer et al., 1997; Claessen et al., 2002), which means that, during growth and development, both predator fields for a particular prey and the prey field for a particular predator change continuously. For instance, North Atlantic flatfish species pass through periods of vulnerability to different types of sizeselective predators, starting with coelenterates during their larval stage, crustaceans during the early juvenile stage, and fishes, birds, and seals later on in life (Van der Veer et al., 1997). Abundance-body size relationships indicate that generally predator abundance decreases with increasing size (Maxwell and Jennings, 2006).

3. The evidence for regulation

We have searched the literature for empirical evidence on population regulation factors for different types of predator-prey interactions, but information was limited to active predators feeding either on passive or active prey, as summarized in Table 1.

3.1. Functional response

Interactions between an active predator and a passive prey have been described in laboratory experiments for blue crab *Callinectes sapidus*, from the Atlantic west coast, feeding on various bivalve species (Eggleston, 1990a,b; Eggleston et al., 1992). A Type III response curve was found for *Macoma balthica* and also for *Mya arenaria* when buried in sand, but a Type II response

Predator type	Prey type	Study conditions	Reference	
Active	Passive			
Callinectes sapidus	Crassostrea virginica	Lab	Eggleston, 1990b	
	Mya arenaria	Lab	Eggleston et al., 1992	
	Macoma balthica	Lab	Eggleston et al., 1992	
Cancer irroratus	Placopecten magellanicus	Lab	Wong and Barbeau, 2005	
	Mytilus edulis	Lab	Wong and Barbeau, 2005	
Platichthys flesus	Macoma balthica	Lab	Mattila and Bonsdorff, 1998	
Active	Active			
Callinectes sapidus	Callinectes sapidus	Lab+field	Moksnes et al., 1997	
Carcinus maenas Carcinus maenas		Lab+field	Moksnes, 2004	
Crangon crangon	Pleuronectes platessa	Lab+field	Van der Veer and Bergman, 1987	
Crangon crangon	Pleuronectes platessa	Lab	Wennhage, 2002	
Crangon septemspinosa	Pseudopleuronectes americanus	Lab	Taylor and Collie, 2003	

For more information see text.

(which essentially represents the inverse of a densitydependent regulation) when buried in mud (Eggleston et al., 1992). The authors suggested that the mechanism behind the response in *M. balthica* was a reduction in successful encounter rates or an increase in emigration rates of crabs at low bivalve densities. Interspecies variability among prey species was thought to be related to habitat-specific burial depth and species-specific siphon size, whereby *M. arenaria* presents relatively larger siphons than *M. balthica*. For instance, deep burial depth appeared critical to the attainment of a partial or absolute prey refuge at low clam densities in mud or sand.

In another study of an active predator (*Cancer irroratus*) feeding on sessile prey (*Placopecten magellanicus* and *Mytilus edulis*), the availability of alternative prey species had an effect on the functional response of the predator (Wong and Barbeau, 2005). In the presence of mussels and at low scallop densities, rock crabs exhibited a Type II functional response on scallops, while no relationship between predation rate and prey density was found in the absence of mussels. Mechanisms underlying a differential response were suggested to be related to encounter rate and the probability of consumption upon capture.

Mattila and Bonsdorff (1998) investigated preyswitching behavior and functional responses of juvenile flounder *Platichthys flesus* in the laboratory, using the sessile bivalve *M. balthica* and the freemoving amphipod *Bathyporeia pilosa* as alternative prey. Under the experimental conditions tested, flounder exhibited a Type III response on both prey species individually while not showing prey-switching behavior.

More extensive information is available for the functional response of active predators feeding on active prey. In blue crab, strong cannibalism is observed in juveniles preying upon conspecific post-larvae (Moksnes et al., 1997). Habitat complexity affected the form of the functional response. In sand habitats, juvenile crabs displayed a Type II inverse densitydependent functional response resulting in very high mortality of post-larvae at low densities. In grassy habitats, the crabs displayed a weak Type III response, but this density-dependence disappeared at increasing predator density, possibly as a consequence of interference competition. Juvenile shore crab, Carcinus maenas, feeding on post-larvae displayed a Type III response in mesocosms with sand and mussels as 'natural' habitat (Moksnes, 2004). The cannibals' functional response appears to offer conspecific prey a refuge at low prey densities and high predator densities.

Another well studied case of an active predator preying on an active prey is the interaction between the brown shrimp Crangon crangon and newly-settled flatfish. Shrimps are important predators of flatfishes during and immediately after settlement but predation rate depends strongly on the size of both predator and the prey (Van der Veer and Bergman, 1987). This size-dependent predation is caused mainly by the superior escape capabilities of larger flatfish once contacted rather than differences in the ability of different sizes of shrimps to capture their prey (Gibson et al., 1995). Laboratory experiments have been performed on the eastern North Atlantic brown shrimp preying on plaice Pleuronectes platessa and flounder larvae (Van der Veer and Bergman, 1987; Wennhage, 2002) and on the western North Atlantic sand shrimp Crangon septemspinosa on juvenile winter flounder Pseudopleuronectes americanus (Taylor and Collie, 2003). Alternative prey was only offered in the experiments by Wennhage (2002). All three experiments suggested a Type III functional response curve, with the trajectory over which regulation could occur corresponding with the range of densities commonly observed under field conditions. In the sand shrimp, the change in predation rate with increasing prey density was attributed to the predators being exposed to increased prey-induced mechanical and chemical stimuli, alerting them of the presence of flatfish, and thus eliciting a feeding response, while 'learning' was considered to be of minimal importance (Taylor and Collie, 2003). In the experiments with brown shrimp, Wennhage (2002) argued that the high abundance of alternative prey in the field and the high prevalence of these prey items in shrimp stomachs suggest that prey switching might be the underlying process for the observed Type III response.

3.2. Numerical response

Information on the numerical response of active predators and active prey is limited. Evidence from mesocosm experiments and field studies indicate a numerical effect of juvenile crabs feeding cannibalistically on post-larvae based on a significant correlation between juvenile densities and losses of new settlers (Moksnes, 2004). Also a positive relationship between newly-settled plaice and brown shrimp abundance has been observed in field samples and in stomach-content analysis of the brown shrimp during the period of immigration of plaice larvae in the Dutch Wadden Sea (Van der Veer and Bergman, 1987). Brown shrimp, *C. crangon*, has also shown rapid aggregation after an episodic disturbance introduced in field experiments,

which resulted in increased prey availability (Eriksson et al., 2005).

3.3. Indirect evidence

Indirect evidence of intra-annual regulation is scarce. There are few studies combining observed mortality rates with stomach-content analysis of predators. However, for active predators feeding on active prey, there is evidence for within-cohort regulation of plaice during and after settlement in spring based on a positive relationship between plaice density and instantaneous mortality in field samples (Van der Veer, 1986). Stomach-content analysis suggests that this density-dependent mortality may be caused by crustacean predators, particularly brown shrimp (Van der Veer and Bergman, 1987).

Inter-annual variability in bivalve spat (passive prey) predation by crustaceans (active predator) has been studied in Swedish bays (Van der Veer et al., 1998). The absence of a reduction in among-year variability during the first year of life after settlement, between spring and autumn, suggested the absence of any regulation. For juvenile flatfishes, the decrease in among-year variability during and after settlement in the Wadden Sea indicated the presence of a period of regulation (Van der Veer, 1986; Van der Veer et al., 1991), while the suggestion of regulation by predators could be supported by stomach-content analysis (Van der Veer and Bergman, 1987).

4. Effect of temperature on regulation

The effect of temperature on the functional response has been studied in the blue crab preying on the eastern oyster *Crassostrea virginica* and in *Crangon* spp. preying upon just-settled flatfishes. In the blue crab preying on the eastern oyster, the functional response changed from a Type II curve at 13-14 °C into a Type III curve at 19-20 °C, and back into Type II curve at 26-27 °C (Eggleston, 1990b). The positive correlation between persistence time in unsuccessful encounters (the time from the initial active encounter of the crab with the prey until rejection) and attack success (proportion of active encounters resulting in consumption) as a function of temperature and oyster density provides evidence for a behavioral mechanism (Eggleston, 1990b).

For shrimp preying upon just-settled flatfishes, Type III curves have been found for *C. crangon* in experiments with water temperatures varying between 12.6–15.6 °C (Wennhage, 2002) and 15–18 °C (Van der Veer and Bergman, 1987). Taylor and Collie (2003) investigated the effect of temperature (10 °C and 16 °C) for *C. septemspinosa* under laboratory conditions. The Type



Fig. 3. Relationship between weekly mean temperature (°C) and predation of newly-settled plaice *Pleuronectes platessa* [expressed as instantaneous mortality rate M (d^{-1})] by the brown shrimp *Crangon crangon* at Balgzand in 1980. Data after Van der Veer and Bergman (1987).

III response found at 10 °C shifted to a Type II response at 16 °C, which could be explained by the observation that the attack rate at low prey densities increased at higher temperatures (Taylor and Collie, 2003).

Little information is available on the effect of water temperature on numerical responses under field conditions, with the exception of *C. crangon* in the Dutch Wadden Sea. Shrimp predation on just-settled 0-group plaice during the period of March–May was densitydependent and showed, on a weekly basis, a relationship to water temperature over a range of 3.5 to 10 °C (Van der Veer and Bergman, 1987) (Fig. 3). This finding suggests that shrimps were capable of generating regulation at least over a range of relatively low temperatures.

5. Discussion

5.1. Regulation through predation

In shallow temperate marine systems, predation by epibenthic species, particularly crustaceans, is considered the major biotic factor structuring benthic communities (Pihl and Rosenberg, 1984; Jensen and Jensen, 1985). The general stability of some epibenthic populations, such as the brown shrimp, also points to potential regulation of these predator populations themselves (Siegel et al., 2005; Henderson et al., 2006). Likewise, there is good evidence for the occurrence of densitydependent mortality (Beverton and Iles, 1992; Myers and Cadigan, 1993) and population regulation of flatfishes (Van der Veer and Bergman, 1987). Available information suggests predation-induced mortality to be the most important factor in cases where population regulation is occurring (Van der Veer and Bergman, 1987; Moksnes, 2004). For some of the epibenthic

predators in the coastal zone, their potential to regulate prey by predation-induced mortality is supported by the presence of a Type III functional response, but most evidence has been obtained under laboratory conditions. The presence of a Type III response is particularly evident among crustaceans. Among the Crangonidae, the potential to induce regulation appears to be a general feature; C. crangon, C. affinis and C. septemspinosa all prey on flatfish larvae (Van der Veer and Bergman, 1987; Seikai et al., 1993; Taylor and Collie, 2003), and Type III functional response curves have been found under some conditions for two of these species. In brachyuran crabs, cannibalism appears to act as a self-regulating mechanism (c.f. Moksnes et al., 1997; Moksnes, 2004) as has been observed in sea bass Dicentrarchus labrax (Henderson and Corps, 1997). Evidence for numerical responses under field conditions is relatively scarce but again, the few examples include the crustaceans (Van der Veer and Bergman, 1987; Moksnes, 2004). Field observations are complicated by the differences in feeding rhythms among species and the sometimes large scale (up to kilometers) of their tidal migrations relative to where they feed, while long digestion times make it difficult to relate stomach contents to local predation rates. For instance, flatfish exhibit tidal migration on and off the tidal flats to feed, whereby feeding is restricted to a period of a few hours only (Kuipers, 1977). Thus, unbiased observations of functional responses are hard to obtain.

Although field evidence for regulation through predation in temperate Atlantic coastal habitats is sparse, there are intriguing studies supporting the concept in other ecosystems, sometimes demonstrating complex interactions. For example, covariation in settlement site quality and settlement density in coral reef fish can obscure patterns in density-dependence on larger scales (Shima and Osenberg, 2003). Structural complexity of habitat can change the shape of the functional response by providing refuges that result in lower predation (Luppi et al., 2001) or altering predator foraging success through modifications in prey detection (Johnson, 2006). Predator density influenced the shape of the individual functional response in juvenile rockfishes, (Sebastes spp.) becoming an accelerating response at high predator densities (Johnson, 2006). The structural complexity of habitat has also been shown to interact with density of kelp perch, Brachyistius frenatus, as prey in determining density-dependent mortality, by acting through both functional and numerical responses of the predatory kelp bass, Paralabrax clathratus (Anderson, 2001). Densitydependent mortality was also demonstrated in juvenile damselfish Chromis cyanea, but only in the presence of two suites of predators which acted synergistically, as a result of an aggregative response of one of the piscivorous predators (Hixon and Carr, 1997). These studies show that functional responses may vary across habitats and factors such as alternative prey, presence of competitors and their own predators are important conditions that might affect response type in the field.

In studies of predation, there is another key issue of scaling up from laboratory and local-scale studies to population-level responses because the dominance of different processes changes at different scales (Fauchald and Erikstad, 2002; Anderson, 2006). Furthermore, discovery of regulation in marine populations is challenged by their open-system nature relative to the logistically-driven scale of most studies (Hixon et al., 2002).

In this review, predation by top predators such as seabirds on epibenthic prey and mammals on various fish species is not considered although its impact can be substantial (Reijnders, 1984; Leopold et al., 1998). In case of seabirds, numerical responses appear to be a common phenomenon since there is a good amount of evidence for predator swarming on prey patches (Mehlum et al., 1999; Fauchald and Erikstad, 2002).

5.2. Effect of temperature on the overall predation response

Temperature is one of the most important environmental factors in nature governing metabolism through its effects on rates of biochemical reactions (Gillooly et al., 2001). Since metabolism sets the demands for feeding, increasing temperatures, within the species optimal temperature range, will cause higher ingestion rates. Linking the effect of temperature at the individual level to the population level, we may assume that temperature is a crucial factor determining predation response and hence, the potential for regulation.

The available evidence – although limited and restricted to crustaceans (shrimps and crabs) – indicates that the capacity of these predators to regulate their prey populations through functional feeding responses depends to some extent on temperature conditions. However, the regulatory potential does not show a clear general trend with temperature and the available evidence suggests that the variations are speciesspecific. In this respect, cannibalistic interactions may provide some indications on the temperature effect on the regulation potential.

Studies suggest that behavioral mechanisms may be among the factors underlying temperature effects in predator response. Barbeau and Scheibling (1994) and Barbeau et al. (1994) tried to elucidate the effects of temperature on various components of predation by sea stars and crabs on scallop prey. Both laboratory and field experiments indicated that water temperature had a strong effect on predator behavior (searching time, movement velocity, handling time) that led to overall higher predation rates at higher temperatures. Increased sea star predation rate with temperature was associated with a decreased effectiveness of the escape response of the prey. The sea star ability to capture scallop prey appeared to increase more with temperature than did the scallop escape ability which highlights differences in temperature sensitivity of predator and prey with consequences on overall predation.

Temperature can also have an indirect effect on sizestructured predator-prey systems because differential growth potentials of both predator and prey (c.f. Claessen et al., 2002) affect the window of predation before the prey outgrows its predator (c.f. Chambers and Trippel, 1997; Van der Veer et al., 1997). However, growth is also closely linked to the prevailing food conditions, which ultimately determine to what extent the growth potential is realized. For most of the epibenthic species, there is a lack of information concerning food conditions. Available information for juvenile flatfish in the Wadden Sea suggests that, during spring and early summer, feeding conditions seem to be optimal and hence, growth appears to be largely determined by prevailing water temperature conditions (Van der Veer, 1986; Van der Veer et al., 1991; Van der Veer and Witte, 1993). However, during summer growth rates became lower than predicted based on temperature conditions and unlimited food thus, suggesting food limitation (Nash et al., 1994; Teal et al., 2008); in some cases of poor feeding grounds, food limitation might occur even during peak settlement (Berghahn et al., 1995).

Temperature may have other indirect effects on predation caused by shifting distributions of predators and prey leading to varying levels of overlap (e.g. Ciannelli and Bailey, 2005). Higher temperatures may also influence oxygen levels in sediments, which may affect the burrowing depth of prey and their availability to predators.

We expect that under field conditions, differences in relative sizes of prey and predator and differences in temperature would change the asymptote of the functional response curve if digestion or handling times are affected. This, along with the factors mentioned above, means that under field conditions, there is no such thing as a single functional response between a predator and a prey, but rather a continuously changing mosaic of interactions. The aggregate of these interactions ultimately determines the potential for regulation of a prey by a predator. Therefore, it remains questionable whether variation in temperature conditions will affect the impact of predation and regulation over the distributional range of a prey species.

5.3. Implications for latitudinal patterns in population regulation

Latitude is a surrogate for other primary environmental gradients such as temperature, seasonality and insolation which interact and are cross-correlated (Willig et al., 2003). Typically, moving from the tropics towards the poles, the seasonal variation in daylength and insolation increases resulting in colder air temperatures and greater seasonality at higher latitudes. Water temperatures in shallow coastal systems, although buffered by the higher heat capacity of water, largely follow the air temperature patterns, being modified by currents. The inverse relationship between mean water temperature and latitude in shallow coastal areas indicates that an impact of latitude on population regulation would most likely reflect the effect of temperature. Although the lack of basic information on the effect of temperature on predator behavior for most epibenthic species makes any discussion rather speculative, some generalizations may be offered. For ectotherms, whose metabolism is strongly dependent on temperature conditions, the inverse trend of temperature with latitude implies that in absolute terms predation pressure (ingestion rates) should decrease with latitude. Intuitively, with higher predation pressure the potential for regulation should be stronger. In addition, due to the progressively pronounced seasonality with increasing latitude, the time window for population regulation concentrates and narrows. On the Swedish coast, for instance, more than 50% of the annual epibenthic production is realized in two months only (Pihl and Rosenberg, 1982). Combining these two aspects would suggest that the potential for regulation through predation mortality decreases towards the poles.

Furthermore, the duration of developmental stages increases with latitude. A positive relationship between duration of egg and larval stages and latitude has been demonstrated for flatfish (Minami and Tanaka, 1992), and effects of stage duration on recruitment variability have been found for marine fishes (Pepin and Myers, 1991). Thus, at high latitudes controlling factors may be relatively more important than in lower latitudes, generally resulting in higher recruitment variability. These patterns would fit into the 'species-range' hypothesis according to which recruitment variation is least in the center of a species range as a result of density-dependent biotic factors (mainly predation) and most on the polar end as a result of abiotic factors (Miller et al., 1991). This hypothesis has been supported by some studies (Myers, 1991; Brunel and Boucher, 2006) and refuted by others (Leggett and Frank, 1997; Philippart et al., 1998). Our review of predation-induced mortality does not provide factual evidence for any latitudinal trend in regulation. Instead, population regulation appears to be overwhelmed by local factors and thus, overall patterns in recruitment might be mainly determined by controlling factors.

Despite the complexity of predator-prey interactions, the basic mechanisms underlying these interactions must be founded on the temperature-tolerance limits (determining potential presence/absence), temperature sensitivity affecting growth potential (and predator behavior) and prevailing food conditions (determining the ultimate time window of size-selective predation). In this context, it might be worthwhile to investigate whether the observed regime shifts in marine ecosystems of the North Sea and Wadden Sea (Weijerman et al., 2005) can be related to differences in temperature tolerance or in temperature sensitivity among species involved in predator-prey interactions and whether regime shifts become more pronounced when local food conditions are limiting.

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Chapter 3

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Potential impact of temperature change on epibenthic predator-bivalve prey interactions in temperate estuaries

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Abstract

Temperate estuaries are indispensable as refuelling areas for long-distance shorebirds, where they depend on intertidal benthic fauna, such as bivalves, as food source. Bivalve recruitment is thought to be, at least partly, top-down regulated by epibenthic predators (the shrimp Crangon crangon and the crab Carcinus maenas) but this interaction is part of a complex predator-prey system since various fish species prey upon the crustaceans.

The impact of climate change in temperate estuarine food web will be determined by how the various size-selective interactions are affected by temperature. This will depend on the temperature sensitivity of each species' growth and on how food conditions allow them to fill in this growth potential. In this paper, the focus is on the first aspect: temperature sensitivity of the epibenthic predators compared with that of the bivalve prey and among the various predator species. Our results show that crustaceans have higher temperature sensitivity and tolerance range compared with their potential predators and with their bivalve prey. It is hypothesized that a temperature increase can potentially lead to an overall higher predation pressure in these systems with negative impacts in bivalve recruitment and hence, in the functioning of temperate estuaries as fuelling stations. However, prevailing food conditions for bivalves and predators will determine to what extent the potential impacts of an increase in temperature will be realized. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Climate change; Temperature sensitivity; Bivalve recruitment; Predation; Predator-prey interactions

1. Introduction

Temperate estuaries are an indispensable chain of essential resting and so-called fuelling stations for millions of wading birds on their migratory pathways (e.g. Piersma, 1994; Van de Kam et al., 2004). In these shallow estuarine areas, the main food source for birds consists of intertidal benthic fauna, whereby a main component is formed by bivalves (e.g. Piersma, 1994; Zwarts, 1997). Wading birds encounter large seasonal and annual variation in their food supply, both in terms of abundance and composition, due

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to year-to-year fluctuations in the recruitment success of their bivalve prey (e.g. Zwarts and Wanink, 1993; Larsen and Guillemette, 2000).

Bivalve recruitment results from a combination of both abiotic conditions and biological interactions of which abundance of predators is one of the most important (Beukema et al., 1998; Van der Veer et al., 1998; Philippart et al., 2003) indicating, at least partly, top-down control of bivalve recruitment by predation. Among the epibenthic predators of newly settled bivalve spat, one of the most important are juvenile crustaceans, especially the brown shrimp Crangon crangon (Pihl and Rosenberg, 1984; Keus, 1986; Van der Veer et al., 1998) and the shore crab Carcinus maenas (Jensen and Jensen, 1985; Sanchez-Salazar and Seed, 1987; Van der Veer et al., 1998). This picture is even more complex because, instead of a single

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predator (shrimp)-prey (bivalve spat) interaction, mortality of bivalve spat and ultimate bivalve recruitment will be the result of multispecies interactions (Pihl, 1985a, b). Not only shrimps, but also shore crabs C. maenas and flatfish species, plaice Pleuronectes platessa, and flounder Platichthys flesus prey upon bivalve spat (De Vlas, 1979; Afman, 1980). These interactions are further complicated by the occurrence of cannibalism of adult shrimps on juveniles (Pihl and Rosenberg, 1984) and predation by Pomatoschistus species (Van Beek, 1976; Del Norte-Campos and Temming, 1994), shore crabs and flatfish upon adult shrimps (De Vlas, 1979; Afman, 1980). Finally, top predators in the system should also be considered. These include young cod (Gadus morhua) and sea bass (*Dicentrarchus labrax*), who prey upon both the predatory crustaceans and the various fish species (Pomatoschistus spp. and flatfishes) (Pihl, 1982; Van der Veer, 1986). Experimental studies (Jensen and Jensen, 1985; Keus, 1986) and field observations (Pihl and Rosenberg, 1982; Möller and Rosenberg, 1983; Günther, 1992; Van der Veer et al., 1998) have shown that predation by these species is size selective.

Since we are dealing with poikilothermic animals, both bivalve growth and shrimp predation are temperature related. Variability and trends in climate are expected to cause shifts in species distributional ranges (Kennedy et al., 2002; Walther et al., 2002) and, besides the immediate effects on interspecies competition, these changes can also have secondary impacts in predator–prey interactions (Scavia et al., 2002). In case of bivalve spat–shrimp relationship, a temperature increase could influence the recruitment success of bivalve prey. Supportive evidence is based on the observation that after severe winters, reduced and a delayed epibenthic predation occurred (Strasser and Gunther, 2001) which allowed bivalves to outgrow their predators (Hiddink et al., 2002) or at least overtake their prey size spectrum (Jensen and Jensen, 1985).

A recent analysis of various long-term data sets in the western Dutch Wadden Sea suggested that an increase in seawater temperature will result in a spring advancement of bivalve spawning, and in an overall decrease in reproductive output (Philippart et al., 2003). In addition, a narrowing of the time gap between bivalve spawning and post-settlement predation by shrimps was suggested and hence an overall decrease in recruitment at increasing seawater temperature (Philippart et al., 2003). However, these studies were based on correlations instead of causal relationships, whereby only a single predator–prey interaction and a similar reaction of both predators and prey to temperature were assumed.

The reaction of the various predators and prey to temperature depends on a combination of their temperature tolerance and sensitivity together with prevailing food conditions. For instance, on the one hand, growth in bivalves in the Wadden Sea appears to be food limited (Hummel, 1985; Kamermans et al., 1992; Kamermans, 1993; Beukema et al., 2002; Cardoso et al., 2006), while for some predators (flatfishes) food conditions seemed to be optimal and only determined by prevailing temperature (Zijlstra et al., 1982; Van der Veer et al., 1991). For most other potential predators it is unknown whether they are food limited at present or not. This means that even when the temperature dependence of the various species would be similar, their ultimate reaction to changes in temperature might be different due to differences in prevailing food conditions.

In this paper, we analyse part of the problem by focusing on the indirect effect of temperature on bivalve recruitment via predator-prev interactions. Subsequent papers will deal with the prevailing food conditions of both bivalves and various predator species. The temperature dependence is a reflection of the species type (cold water versus intermediate or warm water species), which can be illustrated and quantified by the optimal temperature of the various species, their temperature tolerance range and their sensitivity to temperature within their tolerance range. So far, such an analysis has only been made for the various bivalve prey species (Van der Veer et al., 2006) and the flatfishes as predator (Van der Veer et al., 2001). The data on flatfish suggests that their temperature tolerance and sensitivity differs from that of the bivalves, which might have large implications for the overall impact of the epibenthic predator complex on bivalve spat. However, data for the other predatory species is missing. The aim of this paper is: (1) to determine and estimate the temperature tolerance range, optimal temperature and temperature sensitivity of the various epibenthic predators, (2) to determine whether differences exist between epibenthic predators and prey and amongst the various predator species and finally, (3) to conclude whether from this point of view climate change can potentially affect bivalve spat recruitment-via changes in the epibenthic predators-prey interactions.

2. Material and methods

2.1. Methods

2.1.1. Temperature range

Each species can only perform within a specific temperature range, i.e. its temperature tolerance range. This range is a reflection of both metabolism, showing a steady increase with temperature and also ingestion, increasing only until an abrupt decline occurs at high temperatures. As a result, growth is characterized by a steady increase with increasing temperature until a maximum followed by a sharply defined upper boundary (for plaice and flounder see for instance Fonds et al., 1992). Information on the temperature tolerance of a species is based on data on food intake or growth in relation to temperature. For the temperature tolerance range, the temperature interval is determined where the reaction rate is positive, i.e. zone of above-zero performance (Huey and Kingsolver, 1989).

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Fig. 1. Estimation procedure of optimal temperature T_{OPT} , temperature tolerance range and temperature performance breadth. Left panel: relationship of temperature (T; °C) with food intake FI. Right panel: same relationship after scaling of the maximum food intake to 1. Optimal temperature T_{OPT} is the temperature at which the scaled FI is 1; and temperature performance breadth is the temperature range were activity is more than 69% of the maximum observed activity (grey area between T_L and T_H); temperature tolerance range is the range with positive FI values.

Within the temperature tolerance range, the temperature performance breadth is defined as the range of body temperatures over which performance is greater than or equal to an arbitrary level of performance (Angilletta et al., 2002). Estimation of the thermal performance breadth is based on the quantitative formulation by Sharpe and De Michele (1977) (see Kooijman, 2000). In short, this formulation is based on the idea that the rate is controlled by an enzyme that has an inactive configuration at high and low temperatures, respectively, above and below the optimum temperature. This means that the reaction rate has to be multiplied by the enzyme fraction that is in its active state in relation to prevailing temperature:

$$\left(1 + \exp\left[\frac{T_{\rm AL}}{T} - \frac{T_{\rm AL}}{T_{\rm L}}\right] + \exp\left[\frac{T_{\rm AH}}{T_{\rm H}} - \frac{T_{\rm AH}}{T}\right]\right)^{-1}.$$
 (1)

In this way, four extra parameters are needed: $T_{\rm L}$ and $T_{\rm H}$, which relate to the lower and upper boundary of the tolerance range where 69% ($=\ln 2\%$) of the enzymes are active and $T_{\rm AL}$ and $T_{\rm AH}$, which are the Arrhenius temperatures for the rate of decrease at both boundaries. In this study, the thermal performance breadth is the range between $T_{\rm L}$ and $T_{\rm H}$, where the reaction rate is above 69% ($=\ln 2$) of the maximum rate.

The optimum temperature is defined as the temperature at which the reaction rate (growth or food intake) is maximal. The various definitions are based on Willmer et al. (2000) and the procedure for estimation is illustrated in Fig. 1.

2.1.2. Temperature sensitivity

Temperature sensitivity refers to rate at which the reaction increases with temperature. Therefore, estimates of temperature sensitivity are based on the part of the temperature tolerance range where rates, preferably oxygen consumption, increase exponentially with increasing temperature. Traditionally, Q_{10} quotient has been used to provide an indication of temperature sensitivity. It quantifies the effect of temperature on reaction rates by comparing a rate at two temperatures differing by 10 °C. Despite its wide utilization, some have questioned the

accuracy and the variance of this factor within a temperature range (see for instance Willmer et al., 2000). As an alternative, the Arrhenius relationship, based on the Van't Hoff equation has been applied, usually providing a good explanation for the variation in the temperature dependence of metabolic rate across species (Gillooly et al., 2006). The Arrhenius temperature T_A can be estimated as

$$\dot{k}(T) = \dot{k}(T_1) \times \exp\left[\frac{T_A}{T_1} - \frac{T_A}{T}\right],$$
(2)

where k(T) is a physiological rate at the ambient temperature T (K), $\dot{k}(T_1)$ is the physiological rate at the reference temperature T_1 (normally set at 293 K) and T_A is the species-specific Arrhenius temperature (K). T_A results from the slope of plots of $\ln(\dot{k})$ against 1/T. The procedure is illustrated in Fig. 2.

2.2. Materials

Estimation of the various temperature dependence parameters was performed for the various epibenthic species while for the bivalve species, data published in Van der Veer et al. (2006) was used. The estimation of the temperature parameters for the epibenthic species was based on information published in various literature references in combination with experimental data.

Laboratory experiments were carried out at the NIOZ aquarium facilities over the years using standard experimental conditions as described in De Blok (1975) and Fonds et al. (1992). In brief, crustaceans and fish were caught in the neighbourhood of the institute and held in tanks of $2.5 \times 0.5 \times 0.5$ m with running seawater at constant temperatures. Small individuals were kept in perforated plastic crates of $50 \times 35 \times 25$ cm, suspended in the larger constant-temperature tanks. Tanks and crates were aerated and for flatfish a small layer of sand was put at the bottom. Crustaceans and fish were acclimatized before the start of the experiments. For more information see Fonds et al. (1992). Some information has been presented in NIOZ student reports (Van Beek, 1976; Van der Gaag, 1977; Van Lissa, 1977) and these references are

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Fig. 2. Estimation procedure of temperature sensitivity T_A (K) on respiration R. Left panel: relationship of temperature (T; °C) with respiration R. Right panel: after log transformation of Y-axes. Slope reflects the temperature sensitivity T_A (K).

available through request in the NIOZ library (E-mail address: bib@nioz.nl).

With respect to published information several references were used: temperature sensitivity was estimated mainly on experiments on oxygen consumption after Van Donk and De Wilde (1981) for the shrimp C. crangon; Klein Breteler (1975) and Young et al. (2006) for the shore crab C. maenas; Fonds et al. (1992) for plaice P. platessa, and flounder P. flesus; Fonds and Veldhuis (1973) and Petersen and Petersen (1990) for sand goby Pomatoschistus minutus and common goby Pomatoschistus microps; Jobling (1988) and Pedersen and Jobling (1989) for cod G. morhua and Claireaux and Lagardère (1999) for sea bass D. labrax. Optimal temperature and temperature tolerance was estimated based on information on growth or food intake in relation to temperature, after Van Lissa (1977) for C. crangon; Fonds et al. (1992) for P. platessa and P. flesus; Fonds (1973) and Van der Gaag (1977) for Pomatoschistus spp.; and Jobling (1988) and Pedersen and Jobling (1989) for cod G. morhua; for C. maenas information on peripheral neuronal function in relation to temperature from Young et al. (2006) was used while, for D. labrax information on metabolism in relation to temperature (Claireaux and Lagardère, 1999) was utilized.

In relation to bivalve species, the published literature list used to determine the temperature dependence parameters can be consulted in Van der Veer et al. (2006).

3. Results

3.1. Temperature range

For many species, information at both the extreme low and high ends of the temperature range was lacking and, therefore, the temperature tolerance range and thermal performance breadth had to be interpreted.

For the various bivalve species, the temperature tolerance range and thermal performance breadth differed (Fig. 3). *Macoma balthica* had the smallest tolerance range and performance breadth, 17 and 8 degrees, respectively. The tolerance range and performance breadth for the other species was larger and shifted from *Mytilus edulis*, *Mya* arenaria to Cerastoderma edule towards higher temperatures. Also the optimal temperature differed between species. *M. balthica* and *M. edulis* had the lowest optimal temperatures 283 K (10 °C) and 290 K (16 °C), respectively, followed by *M. arenaria* (293 K; 20 °C) and *C. edule* (298 K; 25 °C). Results for *M. arenaria* and *C. edule* indicate that these species are able to tolerate high temperatures in the upper 20 s °C (Fig. 3).

For the epibenthic predators, all species could tolerate temperatures as low as 273 K (0 °C), except D. labrax (Fig. 4). The high temperature tolerance limit showed larger differences between species. C. crangon could tolerate 303 K (30 °C), D. labrax 305 K (32 °C) and P. microps even 307 K (34 °C). The other fish species could only tolerate lower temperatures: the flatfish species up to 299 K (26 $^{\circ}$ C) and G. morhua only up to 297 K (24 $^{\circ}$ C). The temperature performance breadth was almost similar between species, between 10° and 13° . The optimal temperature for most species was also very similar (Fig. 4) around 293 K (20 °C). Only C. crangon and D. labrax had slightly higher values of 296 K (23 °C) and 295 K (22 °C), respectively. G. morhua has a much lower value (287 K; $14 \degree \text{C}$). A comparative overview of the different parameters can be observed in Fig. 5. No information was available for P. minutus.

The various parameters are combined for all species in Table 1 and illustrate the differences in temperature tolerance, performance breadth, optimal temperature and temperature sensitivity between the various prey and predator species.

3.2. Temperature sensitivity

The estimates of the temperature sensitivity (\pm SE) for the various bivalve species differed between 5290 \pm 1108 and 7051 \pm 453 K, however, with relatively large standard deviations (Fig. 6). The analysis for all species combined resulted in a statistically significant estimate of 5826 \pm 195 K (n = 281; $R^2 = 0.99$), and, since similarity in temperature sensitivity in related species is expected (Kooijman, 2000), a value of 5800 K was adopted for all species.



Fig. 3. Optimal temperature (vertical line) (°C), temperature performance breadth (grey range) and tolerance range (total range of positive rate) for the bivalve species *Macoma balthica*, *Mytilus edulis*, *Mya arenaria* and *Cerastoderma edule* based on data of food intake and/or growth in relation to temperature. Rates are scaled to the maximum rate, which has been set to 1.0. For more information and references see text and Van der Veer et al. (2006).

For the various epibenthic predators, the temperature sensitivity differed (Fig. 7). For crustaceans, the estimate of the Arrhenius temperature (\pm SE) for *C. crangon* was in the order of 7351 \pm 266 K, while for *C. maenas* a value of 6498 \pm 920 K was found. Low values were found in the gobies, 2963 \pm 165 K in *P. minutus* and 3418 \pm 184 K in *P. microps.* Combining the data sets for both species resulted in an average value of 3191 \pm 125 K for these two

related gobies. For both flatfish species, the estimate ranged from 6519 ± 163 K for *P. platessa* to 8974 ± 178 K in *P. flesus*. Since these two species are closely related, data were combined resulting in an estimate of 7747 ± 183 K for both species. The data for *G. morhua* resulted in an estimate of 5345 ± 220 K and for *D. labrax* an estimate of 5651 ± 298 K.

The Arrhenius temperature T_A can be compared with Q_{10} quotient using

$$\frac{1}{10}\ln Q_{10} = \frac{T_{\rm A}}{T_1(T_1 - 10)},$$

where T_1 is the reference temperature (normally set at 293 K). An Arrhenius temperature of 3000 K roughly corresponds with a Q_{10} of 1.5, and an Arrhenius temperature of 6000 K with a Q_{10} of 2.

4. Discussion

4.1. General impact of temperature

Fluctuations in water temperature in shallow coastal systems usually follow the air temperature, which in term is determined by local weather conditions. Although water temperature is buffered by the higher heat capacity of water compared to air, large changes and fluctuations in water temperature can occur not only at an annual scale but also on a daily and tidal basis (Pihl and Rosenberg, 1982; Van der Veer and Bergman, 1986). For instance, along the Swedish coast the seasonal fluctuations in water temperature are between 0 and 20 °C, however, in summer, values up to 30 °C can occur (Pihl and Rosenberg, 1982). Sessile bivalves will experience more fluctuations in temperature conditions than their mobile potential epibenthic predators that are able to carry out migration movements.

The basic action of temperature on reaction rates is via its link with the molecular motion in a material. With increasing temperature, the average motion increases and a larger portion of the molecules moves fast enough to collide and react with other molecules. In biological systems a similar process is assumed; however, instead of molecules, biochemical reactions are catalysed by enzymes, whereby, the reaction rate rises steadily with temperature due to thermal effects on the reaction of substrates with enzymes and the consequent faster release of products. Above an upper thermal limit, reactions are drastically reduced or cease altogether as the biochemical structures involved are damaged (Willmer et al., 2000). In line with the above, the temperature tolerance is quantified in this study by a formulation that is based on the idea that the rate is controlled by an enzyme that has an inactive configuration at high and low temperatures, respectively, above and below the optimum temperature (Sharpe and De Michele, 1977). Although this quantitative formulation by Sharpe and De Michele (1977) works out well, it cannot



Fig. 4. Optimal temperature (vertical line) (°C), temperature performance breadth (grey range) and tolerance range (total range of positive rate) for the crustacean species *Crangon crangon* and *Carcinus maenas*; the common goby *Pomatoschistus microps*; the flatfishes *Pleuronectes platessa* and *Platichthys flesus*; the gadoid species *Gadus morhua* and the sea bass *D. labrax*. Based on data of food intake and/or growth in relation to temperature. Rates are scaled to the maximum rate, which has been set to 1.0. For more information and references see text and Van der Veer et al. (2006).

hide our lack of detailed knowledge on the mechanistic functioning of temperature on ectotherms.

Any analysis of the impact of temperature is complicated by a number of factors. First of all, there is variability in temperature tolerance between the different life stages. For plaice, temperature tolerance is highest during the larval stages. Both during the egg stage and from the juvenile stage onwards, temperature tolerance decreases (Ryland et al., 1975; Talbot, 1976; Kuipers and Fonds, 1978; Fonds et al., 1992). This might be a general phenomenon at least in fish species and be responsible for the often observed positive relationship between fish size and water depth, the so-called Heincke's law (Heincke, 1913). Secondly, variability might occur between individuals and, also over the range of most bivalve and epibenthic species genetic subpopulation structure can be distinguished (Gysels et al., 2004a, b; Hoarau et al., 2004; Roman and Palumbi, 2004; Luttikhuizen et al., 2007). Whether genetic subpopulations also differ in their temperature tolerance and sensitivity is unclear at present. Furthermore, temperature sensitivity and tolerance range of an individual and a population can be affected by adaptation and acclimation to local conditions (Willmer et al., 2000), whereby also local temperature conditions may show spatial and temporal variability. A pronounced example of adaptation to local condition is the irreversible non-genetic adaptation (Kinne, 1962), whereby changes in the environment during the egg stage induce functional non-genetic adaptation, which was not reversible during the subsequent life of the individual. Countergradient growth compensation (Conover and Present, 1990), where populations from different latitude show compensation for length of the growing season might be a reflection of non-genetic adaptation at the population level. In the present analysis, these various factors are not taken into account and discussed and the focus is restricted to general patterns in optimum temperature, temperature performance breadth and temperature tolerance range.

4.2. Temperature effect on prey and predator species

From the optimal temperature, temperature performance breadth and tolerance range of the various bivalve prey species, it is clear that *M. balthica* with an optimal temperature at 283 K (10 °C) and a tolerance range to about 290 K (17 °C), can be considered as a cold water species. Its temperature performance breadth and tolerance range indicate that under the present conditions *M. balthica* might already suffer from suboptimal to too high temperatures in temperate areas in summer (Fig. 8), a suggestion recently confirmed for the western Wadden Sea (Cardoso et al., 2006). A slight increase in temperature might therefore have a negative effect on *M. balthica* causing a lower growth and hence longer period of predation. For the other bivalve species, an increase in temperature will remain in their tolerance range and even

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Fig. 5. Overview of optimal temperature (bold vertical bar), temperature performance breadth (grey horizontal bar) and temperature tolerance range (total horizontal bar) of the various bivalve and epibenthic predator species.

Table 1

Temperature sensitivity (T_A ; K), optimal temperature (T_{OPT} ; °C, K), temperature performance breadth and temperature tolerance range for various bivalve and epibenthic predatory species

Symbol	<i>T</i> _A (K)	$T_{\rm OPT}$ (°C (K))	Temperature performance breadth (K) (range between $T_{\rm L}$ and $T_{\rm H}$)	Temperature tolerance range (K) (range with positive reaction rate)
Bivalve species				
Macoma balthica	5800	10 (283)	8 (278–286)	17 (273–290)
Mytilus edulis	5800	17 (290)	14 (281–295)	26 (273–299)
Mya arenaria	5800	20 (293)	20 (283–303)	34 (273–307)
Cerastoderma edule	5800	25 (298)	13 (290–303)	28 (278–306)
Epibenthic predators				
Crangon crangon	7351 + 266	23 (296)	10 (291–301)	30 (273-303)
Carcinus maenas	6498 ± 920	20 (293)	11 (290–301)	30 (273–303)
Pomatoschistus minutus	3191 + 125			
Pomatoschistus microps	3191 ± 125	20 (293)	13 (288–301)	34 (273–307)
Pleuronectes platessa	7749 ± 183	20 (293)	11 (286–297)	26 (273–299)
Platichthys flesus	7749 + 183	20 (293)	12 (285–297)	26 (273–299)
Gadus morhua	5345 ± 345	14 (287)	12 (280–292)	24 (273–297)
Dicentrarchus labrax	5651 ± 298	23 (296)	11 (290–301)	26 (280–306)

For more information see text and Van der Veer et al. (2006). Interpolated values in italic.

in their temperature performance breadth in the neighbourhood of their optimal temperature.

With respect to the predator species, the present environmental conditions in most temperate areas along the European coast (Fig. 8) are near the optimal temperatures for most species, except for the cod *G. morhua.* Therefore, any increase in temperature will release the other epibenthic species from predation by cod; however, its role in the food web will probably be replaced by sea bass *D. labrax*, a species with a higher temperature tolerance and a similar function in the trophic web. For the other species, an increase in temperature will fall within

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Fig. 6. Arrhenius plot (ln rate versus 1/T) for the oxygen consumption data for various bivalve species. Each line represents a different data set. Arrhenius temperature (±SE)—*Macoma balthica*: 5672±522 K (n = 57; $R^2 = 0.94$); *Mya arenaria*: 7051±453 K (n = 30; $R^2 = 0.95$); *Cerastoderma edule*: 5290±1107 K (n = 11; $R^2 = 0.98$); *Mytilus edulis*: 7022±552 K (n = 11; $R^2 = 0.94$). All species together (including estimates for *Crassostrea gigas*): 5826±195 K (n = 281; $R^2 = 0.99$). For references see text.

their temperature performance breadth, which means that this will not result in a change in species composition. The present distribution pattern of the various crustaceans, flatfish and gobies species at their southern edge all along the Portuguese coast confirms this analysis (Campos and Freitas, unpublished). The various epibenthic predatory species show differences in their Arrhenius temperature. Since predator-prey relationships are often size-based (Pihl and Rosenberg, 1984; Van der Veer et al., 1997; Van der Veer et al., 1998), differences in Arrhenius temperature will potentially be able to change interactions between the epibenthic species because it implies a difference in reaction and hence in growth between them. In this respect, cod, sea bass and both goby species show much lower values that the crustaceans and the flatfishes. This means that an increase in temperature will relatively release the crustaceans from predation by cod and sea bass and especially by gobies. As a consequence, crustaceans may become a more dominant component of the epibenthic predator complex.

4.3. Temperature effect on predator-prey interactions

The fact that in the present situation, *M. balthica* already suffers from suboptimal temperature conditions means that any further increase in temperature will have a negative impact on the *M. balthica* population. This implies that the relative contribution of the other bivalve species will increase, becoming more vulnerable to predation. In addition, an increase in temperature will automatically imply a higher predation pressure by the epibenthic predators through an increase in their food intake. The lower Arrhenius temperature of bivalves (5800 K) compared with that of its main predators, the crustacean species (6500–7350 K), and especially the shrimp *C. crangon*,

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Fig. 7. Arrhenius plot (ln rate versus 1/T) for the oxygen consumption data for various bivalve species. Each line represents an individual data set. Arrhenius temperature (\pm SE)—*Crangon crangon:* 7351 \pm 266 K (n = 42; $R^2 = 0.99$); *Carcinus maenas:* 6498 \pm 920 K (n = 38; $R^2 = 0.95$); *Pleuronectes platessa:* 6519 \pm 163 K (n = 100; $R^2 = 0.97$); *Platichthys flesus;* 8974 \pm 178 K (n = 100; $R^2 = 0.97$); *Pomatoschistus minutus:* 2963 \pm 165 K (n = 50; $R^2 = 0.97$); *P. microps:* 3418 \pm 184 K (n = 50; $R^2 = 0.97$); *Gadus morhua:* 5345 \pm 220 K (n = 24; $R^2 = 0.98$); *Dicentrarchus labrax:* 5651 \pm 298 K (n = 12; $R^2 = 0.99$). See text.

implies that the growth potential of the predators increases more than that of their prey.

Within the epibenthic predator complex also a shift will occur in favour of the crustaceans and especially the shrimp *C. crangon* because of the exclusion of cod, an important predator. The implications for the food web structure and the various predator–prey interactions might be insignificant in case other predator species fill in the gap,



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Fig. 8. Seasonal pattern in water temperature along the European Atlantic coast. Data source: Valosen Norway (Campos and Freitas, unpublished), Sandvik Sweden (Pihl and Rosenberg, 1982), Balgzand The Netherlands (Van der Veer and Witte, unpublished), Gironde France (Bachelet, 1986), Minho Portugal (Campos and Freitas, unpublished) and Vaccarès (Gellin et al., 2000). Mean values are presented together with observed range (if present).

for instance, in case sea bass replaces cod as predator. However, if the disappearance of an important predator is not filled in, it might imply a change in predator–prey interactions and result in shifts in the food web structure. Such regime shifts related to changes in environmental conditions have already been observed for the Wadden Sea (Weijerman et al., 2005). This study corroborates with the suggestion of other studies, that climate induced changes in different trophic levels of the ecosystem can have important consequences in food web structure and
functioning (Frank et al., 2005) and, in this specific situation, a potential change in species composition in favour of some key species, such as *C. crangon* may have cascade effects in all the food web.

These three main impacts of temperature on the predator-prey interaction ((1) a general increase in absolute predation pressure; (2) release of main predators of bivalve spat, the shrimps, from predation by fish species and (3) increase in relative growth potential of predators), all work out in a similar way towards a higher potential predation pressure by *C. crangon* upon the bivalve spat. A next step will be detailed studies on the food conditions for the predator and prey species in the field. Ultimately, the processes determining recruitment of the predatory species should also be taken into account. In this respect, regulating mechanisms might even vary between areas as it has been suggested for *C. crangon* by the work of Siegel et al. (2005) and Henderson et al. (2006).

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Chapter 4

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Reconstruction of food conditions for Northeast Atlantic bivalve species based on Dynamic Energy Budgets

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ABSTRACT

Required assimilated energy to support observed growth was reconstructed for four common bivalve species (*Mya arenaria, Cerastoderma edule, Mytilus edulis* and *Macoma balthica*) from various Northeast Atlantic coastal areas, along the species distributional range. The approach applied was based on the Dynamic Energy Budget (DEB) theory whereby observed growth patterns in the field, in combination with prevailing temperatures, were used to reconstruct the average food intake experienced in the field scaled to the maximum possible. For all species, results suggest food limitation over the range of locations. In general, reconstructed food intake indicated better conditions for *C. edule* compared to the other species, while *M. edulis* presented the lowest food conditions in all the areas. Despite the indications for a latitudinal trend in primary production, no clear pattern or relationship between reconstructed food conditions and latitude was observed suggesting that any trend may be overruled by local conditions.

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SEA RESEARCH

1. Introduction

Temperate estuarine and coastal systems function as important nursery areas for various fish species (Zijlstra, 1972; Bergman et al., 1989) and offer essential feeding grounds to coastal and migratory birds (Piersma, 1994; Van de Kam et al., 2004). For both predator groups, intertidal bivalves form an important component of the available food sources (Wolff, 1983; Piersma, 1994; Van de Kam et al., 2004; Moreira, 1997; Santos et al., 2005) due to their overall high abundance and biomass (Beukema, 1976; Bocher et al., 2007) and hence, the use of these areas by birds and fishes is strongly linked to the local productivity of bivalve stocks. Along the Northeast Atlantic coast, the same bivalve species are consistently present (see, for instance Bocher et al., 2007). Over broad latitudinal gradients, trends in temperature and in food availability are expected to occur which may affect differently the energy budget and, consequently, the growth of these bivalves.

Several studies have suggested the occurrence of food limitation in intertidal bivalves (Fréchette and Bourget, 1985; Beukema and Cadée, 1991; Kamermans et al., 1992; Kamermans, 1993; De Montaudouin, 1996; Bos et al., 2006; Cardoso et al., 2006; Dekker and Beukema,

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2007). Most of these studies were, however, restricted to specific areas as well as to particular species and hence it is still unclear whether food limitation is a widespread phenomenon among various species of bivalves and whether it occurs over larger spatial scales. Typical tools for the analysis of prevailing food conditions are either statistical analyses of field studies or direct comparison of observed growth in the field with maximum growth from laboratory experiments under ad libitum food conditions, as has been extensively used in fishes (Zijlstra et al., 1982; Van der Veer, 1986). However, such a speciesspecific approach is not applicable for an interspecies comparison. The latter requires a conceptual framework, describing growth in relation to environmental conditions in a consistent way. The Dynamic Energy Budget (DEB) theory (Kooijman, 1988, 2000) offers such a framework. The elegance of the DEB model is that it describes processes such as feeding, growth and reproduction in relation to environmental conditions (average food and/or temperature levels) in a general way, whereby differences between species are reflected in differences in parameter values only (Kooijman, 2000; Van der Veer et al., 2001; Sousa et al., 2008). A powerful aspect of the DEB model is that it can also be applied to reconstruct food intake from observed growth and/ or reproductive patterns under the experienced temperature conditions (Kooijman, 2000). Such an approach based on growth has already been applied to several bivalve species from the Dutch Wadden Sea (Cardoso et al., 2006), although in this case, it has been assumed that food conditions were constant over the whole life span

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Fig. 1. Energy flux through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake); 2 defecation; 3 assimilation; 4 demobilization of energy into reserves; 5 mobilization of energy from reserves; 6 utilization; 7 growth; 8 somatic maintenance; 9 maturation maintenance; 10 maturation; 11 reproduction. The rounded boxes indicate sources or sinks; the rectangles indicate state variables.

of the species and thus an average food level was used over time. However, the DEB model allows a more dynamic reconstruction of food intake whereby the resolution of the analysis is dictated by the frequency of sampling (annually, seasonally, monthly or even daily).

In the present paper, the DEB approach is applied to dynamically reconstruct the food conditions of Northeast Atlantic coastal bivalve species. The goals are [1] to investigate if food limitation is a common phenomenon and how it may influence individual growth; [2] to analyse whether patterns in food conditions exist over the distributional range of the various species; [3] to determine whether similar patterns occur among species. The analysis is restricted to the most abundant intertidal species: the Baltic clam *Macoma balthica* (L.), the soft-shell clam *Mya arenaria* L., the cockle *Cerastoderma edule* (L.) and the blue mussel *Mytilus edulis* L.

2. DEB model

2.1. DEB theory

The DEB theory provides a mechanistic and quantitative description of energy fluxes through an individual organism that assimilates and utilizes energy for maintenance, growth and reproduction (Fig. 1), and how these fluxes change in environments with varying food densities and temperatures. An individual is characterized by three state variables: structural volume V (cm³), reserve energy E (J) and reproductive reserves E_R (J). In terms of dynamics, DEB theory assumes that ingested food is converted, with a constant efficiency, into assimilates which are first incorporated in a reserve pool from where energy is mobilized to the various metabolic processes. Mobilization of reserves follows the so-called ' κ -rule': a fixed fraction

Table 1

DEB paramete	r set for	the various	bivalve species	at 293 K	(20°	'C).
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of the energy (κ) is allocated to growth and somatic maintenance, with priority for maintenance processes, while the remainder portion $(1-\kappa)$ is directed to maturity maintenance and maturation (in embryos and juveniles) or reproduction (in adults). The description of any metabolic process with a DEB model requires adequate parameters (Table 1) and a few differential equations that describe the change in state variables for a given trajectory of food density and temperature conditions.

2.2. Relationships between food conditions, temperature and growth

In DEB theory, the energy costs of maintenance are proportional to structure's volume while food uptake (ingestion, assimilation) is taken to be proportional to the surface area of structure. This aspect in combination with priority rules in energy allocation implies that, as the organism grows, somatic maintenance will, at some point, mobilize all the available energy and thus, impose a maximum size within a species:

$$V_{\rm max}^{1/3} = \kappa \{ \dot{p}_{\rm Am} \} / [\dot{p}_{\rm M}]$$
 (1)

where $V_{\text{max}}^{1/3}$ is the theoretical maximum volumetric length (cm), κ is the fraction of reserve spent on somatic maintenance plus growth (dimensionless), { \dot{p}_{Am} } is the maximum surface area-specific assimilation rate (J cm⁻² d⁻¹) and [\dot{p}_{M}] is the volume-specific cost of maintenance (J cm⁻³ d⁻¹).

In DEB theory, growth is only indirectly related to ingestion, as energy is mobilized from reserves and not directly from food. Feeding and assimilation rates may change in response to the state of the organism and to environmental conditions but the utilization rate of reserves is only dependent on the internal state of the organism, (i.e. on reserve density and body volume).

In the DEB model, ingestion rate relates to food density through a Holling's type II curve and can be represented as:

$$\dot{p}_{\rm X} = \{\dot{p}_{\rm Xm}\} \cdot f \cdot V^{2/3} \tag{2}$$

where $\{\dot{p}_{Xm}\}$ is the maximum ingestion rate per unit of surface area $(J \text{ cm}^{-2} \text{ d}^{-1})$ and f is the scaled functional response (dimensionless), corresponding to a function of food density. In bivalves, the relationship between filtration rate and food density is generally well described by this type of function (Kooijman, 2000) (Fig. 2) although, for low food concentrations, it is not very clear how the clearance rate changes with food concentration (Ren and Ross, 2005).

Temperature controls rates (Fry, 1947, 1971) typically according to the relationship proposed by Arrhenius (see Kooijman, 2000, p. 53). DEB theory uses this formulation to describe the effect of temperature on physiological rates within a species-specific range of temperatures. A

Symbol	Dimension	Interpretation	M. balthica	M. arenaria	C. edule	M. edulis
T _A	K	Arrhenius temperature	5800	5800	5800	5800
{ <i>p</i> _{Xm} }	$J cm^{-2} d^{-1}$	Maximum surface area-specific ingestion rate	43.9	177.3	91.5	196.8
$\tilde{\rho}$	_	Losses due to digestion	0.25	0.25	0.25	0.25
{ <i>p</i> _{Am} }	$J cm^{-2} d^{-1}$	Maximum surface area-specific assimilation rate	32.9	133.0	68.6	147.6
[p _M]	J cm ⁻³ d ⁻¹	Volume-specific maintenance costs	24	24	24	24
$[E_{\rm m}]$	J cm ⁻³	Maximum storage density	2085	2180	2115	2190
$[E_G]$	J cm ⁻³	Volume-specific costs of growth	1900	1900	1900	1900
$[E_V]$	J cm ⁻³	Volume-specific structural energy content	1350	1350	1350	1350
к	_	Fraction of utilized energy spent on maintenance plus growth	0.80	0.75	0.80	0.70
δm	-	Shape coefficient	0.365	0.277	0.381	0.287
ν̈́	cm d ⁻¹	Energy conductance	0.016	0.061	0.032	0.067
k _м	d ⁻¹	Maintenance rate coefficient	0.013	0.013	0.013	0.013
g	-	Investment ratio	1.139	1.162	1.123	1.239
r _B	y ⁻¹	Von Bertalanffy growth constant	1.097	0.730	1.150	0.848

Adapted from Van der Veer et al. (2006).

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Fig. 2. Schematic representation of the type II functional response describing the relationship between food intake rate and food density in bivalves (Kooijman, 2000). Values of the scaled functional response vary between 0 (corresponding to starvation) and 1 (representing food *ad libitum*). Modified from Cardoso et al. (2006).

similar Arrhenius temperature (T_A) is taken for all physiological processes under the reasoning that conversion efficiencies (e.g. from food to biomass and offspring) generally do not depend on temperature. In the present analysis, rates affected by temperature are ingestion, assimilation and maintenance. Temperature effects on rates outside the temperature tolerance range are discussed in Kooijman (2000).

2.3. Food reconstruction

The link between food availability and the energy that is actually assimilated into reserves is captured by the value of f, the scaled functional response. The scaled functional response is not an absolute measure of the available food conditions and gives no indication on the food source and/or quality. However, it can be used as a measure of the assimilated food in terms of energy, ranging between 0 (representing starvation) and 1 (representing food *ad libitum*, allowing maximum growth). Values of f lower than 1, indicate food limitation which, in this context, refers to a lower energy uptake by the organism in relation to the maximum possible.

The reconstruction of scaled *f* from growth trajectories (seasonal, annual or over the life span of the individual) requires reliable datasets of length-at-age and accurate temperature data. This approach can be applied to individual bivalves if growth of marked individuals has been followed over time. However, most often, this type of data is not available and the reconstruction has to be based on observed patterns in size distribution of the entire population or age classes sampled over time.

2.4. Assumptions

Crucial for applying the DEB model are accurate parameter estimates. So far, estimates of the DEB parameters of bivalve species were based on a combination of several datasets from published and unpublished laboratory experiments, conducted with different populations and under different environmental circumstances (Van der Veer et al., 2006). Some intraspecific variation in parameter values, whether related to phenotypical plasticity to local environmental features or to genetic subpopulation structuring has been suggested (Van Haren and Kooijman, 1993; Kooijman, 2000). Nevertheless, the parameter set for bivalves described in Van der Veer et al. (2006) appears to be a rather generic and robust set as, for various species, it has been successfully applied to different datasets (field, laboratory observations) in very different areas (Bacher and Gangnery, 2006; Casas and Bacher, 2006; Cardoso et al., 2006; Pouvreau et al., 2006; Maar et al., 2009-this issue; Rosland et al., 2009-this issue). Similar assumptions have been made with respect to parameter constancy over time. Physiological acclimation and genetic adaptation of the population may occur (Hummel et al., 1997) which might cause subtle changes in energy budgets and affect parameter values. However, due to the lack of more precise information for each population, the DEB parameter set is assumed to be constant in space and time.

3. Materials and methods

3.1. Data acquisition

Literature data and unpublished datasets on shell length-at-age from several areas along the Northeast Atlantic coast were used (Fig. 3). Information from literature presented in graphical form (length-at-age and temperature data) was scanned and digitalized using the software Grab-it![™] XP 10 (Datatrend software). Details on the sampling procedures of published datasets can be found in the original papers (for references see legend of Fig. 3).

In addition, a monthly sampling program was carried out in the northern part of the distributional range of the four studied bivalve species, in Bodø (Norway), during 2005. Every month, 50 individuals of



Fig. 3. Map of the NE Atlantic coast with indication of the areas from which shell lengthat-age data were taken. 1 Balsjord, Norway (69°N, Drent, unpubl.); 2 Bodø, Norway (67°N, own unpubl. data); 3 Kandalaksha Bay, White Sea (66°N, Zotin and Ozernyuk, 2004; Sukhotin et al., 2006); 4 Oslofjord, Norway (59°N, Winther and Gray, 1985); 5 Gullmarsvik, Sweden (58°.2′N, Möller and Rosenberg, 1983); 6 Roskilde fjord, Denmark (55°.4′N, Munch-Petersen, 1973); 7 North Sea, Germany (54°N, Sukhotin et al., 2006); 8 Dundalk Bay, Ireland (53°.5′N, Fahy et al., 2005); 9 Wadden Sea, Netherlands (53°N, Cardoso et al., 2006); 10 Gironde estuary, France (45°N, Drent, unpubl.); 11 Mundaka estuary, Spain (43°N, Iglesias and Navarro, 1990).

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Fig. 4. Sequence of steps used in the dynamic reconstruction of scaled food conditions. Example using *Cerastoderma edule* from the Dutch Wadden Sea. a) Spline curve fitted to observed shell length-at-age data (mean), b) reconstructed scaled *f* as a function of time, c) annual temperature cycle observed in the field, repeated over the entire period considered, d) predicted mean growth trajectory based on the temperature data and on the reconstructed scaled *f*.

each species were collected in an intertidal area at low tide. Individual shell length (along the anterior–posterior axis) was measured with digital callipers and age was determined by counting the external shell annuli, following the methodology described in Cardoso et al. (2006). For each age class, shell length was averaged per sampling date and length was plotted as a function of age (in days). Since the month of birth is difficult to assess, age in days was calculated in relation to January of the year of birth. The same procedure was applied to all the areas.

With respect to temperature, for most areas only data recorded during sampling was available. Since the use of long-term temperature measurements is preferable compared to single year temperature records, for some areas, long-term data series were used to reconstruct seasonal temperature patterns. For Mundaka estuary (Spain), a 20-year dataset was obtained via http://www.surf-forecast. com and, for the White Sea, a 36-year sea-surface temperature dataset from Berger et al. (2003) was used. In Bodø, temperature was continuously monitored, from April till October, using temperature loggers placed in the sediment. In order to obtain the entire annual temperature cycle, temperature data from the field was compared to a 20-year temperature series from a nearby location (obtained from the Norwegian Institute of Marine Research via http://www.imr.no).

3.2. DEB model simulations

Standard DEB model equations (see Appendix A) and speciesspecific parameter values (Table 1) for the various species were coded in Octave (http://www.octave.org). Some routines from the software package "DEBtool" (freely downloadable from http://www.bio.vu.nl/thb/deb/deblab/) were also used namely for data interpolation and for parameterisation. Due to the large scatter in the length-at-age of some datasets, a cubic spline function was used to obtain a smooth growth curve that could be used as an input in the model. The seasonal temperature pattern from each area was also included in the model as a forcing variable. Under the assumption that seasonal temperature cycles in each area were roughly similar across years, a Fourier series was used to produce a periodic function over the entire simulation period. The scaled food density *f* trajectory over the whole period was then reconstructed using a regression routine based on the Nelder Mead method for parameter estimation (for more details see DEBtool manual index.html in the subdirectory 'manual' of DEBtool).

Resulting f(t) functions (food conditions over time) for the various species and areas were subsequently used in an inverse routine to back-calculate length as a function of time. An example of the sequence of steps of this procedure applied to *C. edule* from the Dutch Wadden Sea can be seen in Fig. 4.

Finally, *f* values obtained for the various areas were compared in order to look for trends in scaled food conditions with latitude.

4. Results

In total, datasets from 11 different locations were used. In most cases, reconstructed scaled functional response f fluctuated widely over the time periods considered (Fig. 5). Despite using a scaled function, in some areas, f values slightly overshot 0 and 1 which relates to technical problems caused by the use of periodic functions in the definition of the scaled functional response.

Although the output is considerably variable, some intra- and interspecies comparisons could be performed, on a general basis. *C. edule* was the species with the highest f values, generally above 0.6, with the exception of the population from Mundaka estuary (Spain) for which f was below this level over the entire life span. For the other species, f was close to 0.6 in case of *M. arenaria*, usually lower than 0.6 in *M. balthica*, and lower than 0.4 in *M. edulis*, which showed the lowest range of the four species.

In respect to the variation of scaled food conditions within a species, similar ranges of *f* values were observed among sites. Since the number of available sites was low, a meaningful latitudinal analysis could not be performed and thus, only tendencies are indicated. In *M. balthica*, for which the available datasets covered most of the species distributional range, there was no trend with latitude. For *C. edule*, scaled functional response values varied more between areas than in the other species. However, due to the wide fluctuations in the reconstructions, a clear latitudinal trend in food conditions could not be assessed.

5. Discussion

5.1. Bivalve food conditions

In this paper, food intake was reconstructed for several intertidal species from various areas using a model based on Dynamic Energy Budget (DEB) theory. By focusing on the food (energy) assimilated rather than on the absolute food available, it was possible to assess food limitation overcoming the difficult task of evaluating directly food quantity and/or quality in the field. The approach presented here represents an improvement to the method of Cardoso et al. (2006) in which food intake was reconstructed by changing scaled functional response until predicted values matched field observations. Nevertheless, the overshooting in some results points to the need of further

Fig. 5. Reconstructed scaled food conditions for *C. edule, M. balthica, M. edulis* and *M. arenaria* in various locations along the NE Atlantic coast (right panel). On the left panel, mean shell length-at-age growth curves used to derive the scaled functional response *f*. References for the original datasets can be seen in the legend of Fig. 3. For *M. edulis*, in the White Sea, two datasets were available: (a) from Zotin and Ozernyuk (2004), (b) from Sukhotin et al. (2006).

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refinement, either of the quality of the datasets or the statistical analysis.

Despite differences in intertidal habitat use and in feeding mode (suspension- versus deposit-feeding), stomach content analysis has revealed that the various bivalve species rely on the same food sources (Kamermans, 1994), suggesting that potential food conditions might also be similar. However, overall, reconstructed scaled food conditions were better for *C. edule* compared to the other species with average values of scaled functional response generally above 0.6. An exception was the C. edule population from Mundaka estuary (Spain) where the high tidal position and the particular poor productivity conditions of the area could be responsible for the lower growth observed (Iglesias and Navarro, 1990). Food conditions were the lowest for M. edulis which might be related to its specific life history traits. M. edulis is a gregarious species forming dense banks and hence, intraspecific competition for resources might cause food limitation (Kautski, 1982; Fréchette and Bourget, 1985). The reasons beneath the relative advantage of C. edule in relation to the other species are not clear. In a comparison of the feeding morphology of various intertidal bivalves from the Wadden Sea, C. edule showed the highest gill-to-palp mass ratio (Compton et al., 2007) indicating a greater pumping capacity in detriment of a sorting ability which might confer higher intake rates under the prevailing environmental conditions in which this species lives.

Based on these results, most species in the analysed areas are assimilating less than 60% of their maximum capacity. Furthermore, these figures might be even overestimated as they are based on growth in shell length and not on the seasonal pattern in somatic mass which has been shown to result in lower f values (Cardoso et al., 2006). In fact, it is questionable whether optimal food conditions do exist for bivalves during their whole life span. In coastal waters, temporal variability (on a scale ranging from days to weeks) in composition, concentration and nutritional quality of the available food occurs (Bayne et al., 1993). Feeding in bivalves is responsive to these changes as suggested by several studies indicating plasticity in feeding behaviour (Bayne, 2004). Morphological dynamics in the foraging apparatus of bivalves, indicated by plasticity in gills and/or palps mass, is well known (Honkoop et al., 2003; Drent et al., 2004; Compton et al., 2007) and seems to represent an adaptive mechanism to adjust the feeding system to foraging environment. Nevertheless, there is no information on the rate at which these adjustments occur and it is, therefore, likely that prevailing food conditions (in terms of quantity and/or quality) will often not match with size (mass) of these processing organs. In addition, sediment load in the water column may also affect the efficiency of the food-acquisition apparatus with consequences for the amount of food ingested (Pouvreau et al., 2006). Therefore, scaled food conditions lower than 0.8 might already indicate and reflect the most favourable food conditions possible under field conditions.

5.2. Implications for latitudinal trends

Our results suggest that, over the areas analysed, scaled food conditions are generally quite similar as a trend over the years. These results are based on a small number of areas so the representativeness of these sites for latitudinal comparisons may be questionable. Nevertheless, these areas correspond to a clear latitudinal trend in seasonal water temperature patterns. From an energetic point of view, within a species, higher temperatures cause higher maximum surface area-specific assimilation rates and maintenance costs while volumespecific costs of growth are not affected by temperature. A lack of a clear trend in scaled food conditions over the distributional range of a species, if it is assumed to represent a thermal gradient, implies that absolute energy uptake from food should increase from colder to warmer areas, as the increased maintenance needs depend strongly on a concurrent match in food availability.

Global trends in oceanic primary production available for benthic consumption seem to indicate a trend of increasing food availability towards higher latitudes (Petersen and Curtis, 1980; Warwick and Ruswahyuni, 1987; Gross et al., 1988). Despite the increased seasonality towards the poles, food availability per individual in the growth season generally increases with latitude (Kooijman, 2000). Patterns in coastal productivity, however, and particularly in the intertidal, are more difficult to analyse since regional weather patterns, local hydrodynamic and morphological conditions may modify the outcome in terms of food availability. Herman et al. (1999), in a review of several shallow temperate estuarine systems, observed a linear relationship between primary production and macrobenthic biomass. However, no suggestion of large spatial scale trends in benthic biomass was made. In fact, available studies indicate that there is substantial local variability in primary (benthic and pelagic) productivity among areas unrelated to latitude (Heip et al., 1995; Herman et al., 1999; Tillmann et al., 2000; Struski and Bacher, 2006).

Therefore, at present, it is not possible to discriminate if there is a latitudinal trend in food conditions or whether any latitudinal trend is being overruled by local factors in our relatively small dataset.

5.3. Limitations of the study and suggestions for future research

The present analysis was based on a restricted dataset collected over a number of years. Preferably, an increased number of datasets should have been used whereby also growth and reproductive output were monitored. However, at present, only a few of such datasets are available from Bodø, northern Norway (own unpubl. data) and from the Wadden Sea (Cardoso et al., 2006, 2007a,b). Some of the growth curves used in this study refer to the bivalve growth during the decades of 70s and/or 80s and hence, may not represent the present situation in terms of food conditions. As has been observed in the Dutch Wadden Sea, eutrophication events can modify prevailing food conditions with consequences on zoobenthos biomass and annual growth rates (Beukema and Cadée, 1991; Philippart et al., 2007). Therefore, this approach is important to suggest patterns in food conditions and to perform comparisons but should not be used in terms of absolute statements on site-specific food conditions.

Furthermore, the DEB model used was built on species-specific parameters which are assumed to be constant over time and space. When comparing different populations distributed across a wide latitudinal gradient the potential existence of specific phenotypic and/ or genetic adaptations cannot be excluded. One particular assumption is related to the energy allocation to growth and body maintenance (κ rule). In the present analysis, a fixed κ is assumed indicating that reproduction does not compete directly with growth. Nevertheless, bivalves are known to be able to resorb their gametes in case of food shortage to sustain maintenance demands (a.o. Bayne et al., 1978; Drent and Honkoop, 2004). In addition, the fraction of energy devoted to reproduction may differ between populations as has been shown in M. edulis (Van Haren and Kooijman, 1993) and M. balthica (Drent, 2004). It appears to be also the case of *M. balthica* population from Bodø (own unpubl. data) in relation to the intertidal Wadden Sea population (Cardoso et al., 2007b). Deviations from the *k*-rule such as energy resorption can be incorporated in the DEB model, however, there is at present lack of detailed information on the extent of this phenomenon. Clarifying these questions would require following seasonal patterns in reproduction and growth of different populations, preferably over long-time scales, which could shed some light on the flexibility in energy allocation rules. In the future, a sensitivity analysis should also be performed to assess the individual influence of the main parameters on the model predictions.

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Appendix A. DEB model equations used in food reconstruction routines

The change in scaled reserve density $e = [E]/[E_m]$ (-) and in volumetric length $L = V^{1/3}$ (cm) are given, respectively, by:

$$\frac{\mathrm{d}}{\mathrm{d}t}e = (f - e)^* v T C / L;$$
$$\frac{\mathrm{d}}{\mathrm{d}t}L = \frac{v T C}{3} \frac{e - L / L \mathrm{m}}{e + g};$$

where *f* is the scaled functional response (-), *g* is the investment ratio $g = [E_G]v/(k\{\dot{p}_{Am}\})$ (-), L_m is the maximum volumetric length $L_m = k \{\dot{p}_{Am}\}/[\dot{p}_M]$ (cm), *vTC* is the energy conductance *v* multiplied by the temperature correction factor *TC*. Temperature correction has been performed with the routine *tempcorr* which can be found in the toolbox 'lib/misc' of the software package 'DEBtool' freely downloadable from http://www.bio.vu.nl/thb/deb/deblab/. The temperature correction factor is an exponential function of the type:

$$kT = k_1 e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)} \frac{1 + e^{\left(\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_1}\right)}}{1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_H}\right)}}$$

where *T* is the absolute temperature (K), T_{AL} and T_{AH} are the Arrhenius temperatures (K) for the rate of decrease at respectively the lower (T_L) and upper (T_H) boundaries; T_1 is the reference temperature (293 K), T_A is the Arrhenius temperature, k_1 is the rate at the reference temperature and kT is the rate at ambient temperature (T).

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Chapter 5



Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species

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Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species

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Temperature tolerance and sensitivity were examined for some North Atlantic marine species and linked to their energetics in terms of species-specific parameters described by dynamic energy budget (DEB) theory. There was a general lack of basic information on temperature tolerance and sensitivity for many species. Available data indicated that the ranges in tolerable temperatures were positively related to optimal growth temperatures. However, no clear relationships with temperature sensitivity were established and no clear differences between pelagic and demersal species were observed. The analysis was complicated by the fact that for pelagic species, experimental data were completely absent and even for well-studied species, information was incomplete and sometimes contradictory. Nevertheless, differences in life-history strategies were clearly reflected in parameter differences between related species. Two approaches were used in the estimation of DEB parameters: one based on the assumption that reserve hardly contributes to physical volume; the other does not make this assumption, but relies on body-size scaling relationships, using parameter values of a generalized animal as pseudo-data. Temperature tolerance and sensitivity seemed to be linked with the energetics of a species. In terms of growth, relatively high temperature optima, sensitivity and/or tolerance were related to lower relative assimilation rates as well as lower maintenance costs. Making the step from limited observations to underlying mechanisms is complicated and extrapolations should be carefully interpreted. Special attention should be devoted to the estimation of parameters using body-size scaling relationships predicted by the DEB theory.

Keywords: dynamic energy budget theory; dynamic energy budget parameters; temperature dependence; growth; energetics; marine species

1. INTRODUCTION

In general, life cycles of marine organisms comprise several distinct life-history stages (egg, larvae, juvenile, adult). Each of these successive stages often differs in their habitat requirements and, as a consequence, might depend on different and frequently spatially separated habitats (Rijnsdorp *et al.* 1995). For marine populations, it is a prerequisite that successive habitats are connected to allow survivors to mature

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Electronic supplementary material is available at http://dx.doi.org/ 10.1098/rstb.2010.0049 or via http://rstb.royalsocietypublishing.org. and return to the spawning grounds for successful reproduction (the concept of life cycle closure; Sinclair 1988).

At each life-history stage and/or within each habitat, the spatio-temporal window of opportunity for development (somatic growth and reproduction) is set by both biotic factors (prey availability) and tolerance limits to abiotic factors whereby, for ectotherms, prevailing temperature conditions are a controlling factor (Fry 1947; Neill *et al.* 1994). The response to temperature conditions is frequently characterized in terms of temperature sensitivity and temperature tolerance range (Huey & Kingsolver 1989). Temperature tolerance range is the temperature zone where growth rates are positive. Within the range of tolerable temperatures, an optimal temperature, preferred

One contribution of 14 to a Theme Issue 'Developments in dynamic energy budget theory and its applications'.

temperatures and temperature sensitivity (reflecting the rate at which physiological reactions change with temperature) can be distinguished using different criteria. Besides an acute response to temperature, an individual can show acclimatization as a chronic response and adaptation, measured in timescales of generations, as an evolutionary response. The latter will ultimately allow a modification of the physiological performance and response of an organism over time. Furthermore, there is some evidence for ontogenetic changes in the range of tolerable temperatures (Irvin 1974; Rijnsdorp et al. 2009) and temperature sensitivity (Peck & Buckley 2007), indicating that optimal thermal habitats for growth may vary for different life stages. This has wide implications in terms of defining 'ecologically relevant' thermal tolerance of a species purely based on laboratory experiments conducted on specific life stages (Jobling 1994). In this respect, the lack of information regarding the physiology of late-larval/early-juvenile stages of many marine species is rather surprising, given that processes acting during these stages can create a bottleneck to successful life closure and have important consequences for recruitment strength (Bailey & Houde 1989; Sogard 1997).

Within the window for somatic growth and reproduction, any prediction of the physiological performance requires a general framework that describes the relationship between prevailing abiotic and biotic conditions and fish growth and reproduction rates. At the organismal level, the use of balanced energy budgets to predict various aspects (e.g. prey consumption and growth) has become common in the last five decades (Winberg 1956; Brett & Groves 1979; Hanson *et al.* 1997). However, the various allometric relationships are a purely statistical description of species-specific measurements and not physiologically based on first principles. These budgets are also unable to describe the energetics of an organism within variable environments.

Dynamic energy budgets (DEBs) are a framework describing the quantitative aspects of energy flows through an organism in a systematic and dynamic way (Kooijman 1988, 1993, 2000, 2010; Ross & Nisbet 1990). DEBs are based on first principles and can capture the energetics of species in a single model whereby interspecific differences are reflected by differences in parameter values. A second application of the DEB theory is the prediction of various body-size scaling relationships. Such relationships have been previously studied and debated for decades (see the pioneering work of Kleiber (1961) on the scaling of metabolic rate with body size) and, over time, numerous empirical relationships of biological rates as simple functions of body size and other variables have been established (for overview, see Peters (1983)). Although this descriptive ecology has proved to be valuable, it is criticized for seeking post hoc explanations of observed patterns without experimental tests of hypotheses (Blackburn & Gaston 1999). The DEB theory of Kooijman (1993, 2000, 2010), based on surface- and volume-related processes, is a clear response to this criticism but has not vet been recognized as such. Body-size scaling relationships provide basic information that can be

applied to predict species characteristics in cases where basic information is lacking. In addition, the DEB theory can be used to analyse the discrepancy between modelled and observed growth rates based on energetic constraints, and to potentially identify important intrinsic and extrinsic (environmental) factors in species life-history strategies.

Finally, combining information on tolerance limits to environmental factors, particularly water temperature, and growth energetics by means of DEBs, can give considerable insight on the physiological plasticity of a species. Insight at the species level provides a sound foundation for analyses of ecosystem functioning and response to environmental variability such as climate change. Unfortunately, these bioenergeticallybased analyses are largely unexplored.

In the present paper, we attempt to fill a critical gap in knowledge by examining interspecific differences in the temperature dependence of growth (reflected in species-specific differences in optimal temperatures, range in tolerable temperatures and thermal sensitivity), and relating these to differences in species bioenergetics as revealed by DEB parameters. For this purpose, information on the temperature tolerance and sensitivity was combined with estimates of the DEB parameters and with predictions of bodysize scaling relationships based on DEB theory for fish and crustacean species of the northeast Atlantic, North Sea and coastal Wadden Sea ecosystems.

2. MATERIAL AND METHODS

The main focus of this paper is on marine northeast Atlantic fish species. A set of species was selected that contained different, commercially important resources, ecosystem components (pelagic, demersal) and species with different positions in the food web (forage species, wasp-waist, apex predators). In addition, other abundant coastal species were added, including crustaceans. The initial list was reduced during the process of parameter estimation owing to a lack of basic data for some species. Furthermore, most information reported in the literature was only available for females. At the end, the following species remained: the flatfish species, plaice (Pleuronectes platessa), flounder (Platichthys flesus), dab (Limanda limanda) and sole (Solea solea), the common goby (Pomatoschistus microps) and the sand goby (Pomatoschistus minutus), the eelpout (Zoarces viviparous), bull-rout (Myoxocephalus scorpius), sea bass (Dicentrarchus labrax), Atlantic cod (Gadus morhua), Atlantic herring (Clupea harengus), sprat (Sprattus sprattus), European anchovy (Engraulis encrasicolus) and the crustacean species brown shrimp (Crangon crangon) and shore crab (Carcinus maenas).

(a) Temperature tolerance and sensitivity

(i) *Temperature tolerance*

Each species can only obtain positive rates of growth within a specific range of tolerable temperatures. This range is a reflection of both metabolism (showing a steady increase with temperature) and ingestion (increasing only until an abrupt decline occurs at high temperatures). As a result, growth is characterized by a steady increase with increasing temperature until a maximum, followed by a sharply defined upper boundary. Information on temperature tolerance is based on data on food intake or growth in relation to temperature.

(ii) Optimum temperature

The optimum temperature is defined as the temperature at which growth is maximal. Optimum temperature for growth has been shown to vary depending on food conditions and decline when food is limited (Brett 1979; Jobling 1994). In the present study, ad libitum (unrestricted) feeding was assumed.

(iii) Temperature sensitivity

Temperature sensitivity is an indication of the temperature dependence of physiological rates, i.e. the rates at which a reaction changes with temperature. Growth is an integrative process and an end product of the interaction among other physiological parameters affected by temperature. In the present study, temperature sensitivity was based on the exponential rate of increase in metabolism, preferably oxygen consumption rate, with increasing temperature commonly observed within a portion of the temperature tolerance range. In this paper, the Arrhenius relationship has been applied, usually providing a good explanation for the variation in the temperature dependence of metabolic rates across species (Gillooly et al. 2006). The species-specific Arrhenius temperature (T_A, K) can be estimated as:

$$\dot{k}(T) = \dot{k}(T_{\rm ref}) * \exp\left[\frac{T_{\rm A}}{T_{\rm ref}} - \frac{T_{\rm A}}{T}\right], \qquad (2.1)$$

where k(T) is a physiological rate at the ambient temperature T(K), and $\dot{k}(T_{ref})$ the physiological rate at the reference temperature T_{ref} . T_A can be determined from the slope of plots of $\ln(\dot{k})$ against 1/T. The procedure is illustrated in Freitas *et al.* (2007).

(b) Auxiliary theory for the standard DEB model

The state variables of the standard DEB model (reserve, structure, maturity; Sousa *et al.* 2010) can only be measured indirectly. This consequently applies to the parameter values and calls for auxiliary theory, which links quantities that can be measured to variables in the model. Progress has been made in recent years in developing auxiliary theory for the standard DEB model (e.g. Kooijman *et al.* 2008; Kooijman 2010).

The contribution of reserves to physical volume is no longer neglected, while physical length is still used as a proxy for structural volumetric length. This affects the way the shape coefficient δ_M (which converts physical length into volumetric length) is obtained from data. Previously, the volumetric structural length was identified with the volumetric length, but in the new approach it is obtained, together with the zoom factor z and other parameters simultaneously, from data on lengths, weights and other measurements (see next section).

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Continued research also converted some compound parameters of the standard DEB model to primary ones and vice versa, to enhance the link with underlying processes (table 1); the electronic supplementary material gives a detailed account of the changes. These changes did not affect the standard DEB model as such.

(c) Estimation procedure

Two approaches were used to determine the speciesspecific DEB parameters. The first was based on empirical derivation of individual parameters, from compilation of datasets for a species and checking the consistency of the individual parameter set with related species a posteriori. The second approach was based on body-size scaling relationships of the DEB theory and more oriented for an interspecies comparison. A direct comparison of the two approaches, however, is complicated, on one hand because the first approach does not allow estimating all the primary parameters that DEB 3 version now considers and, on the other hand, because they differ in the assumption of reserves contribution to body volume. Total body volume (V_w) includes not only structural volume (V)and reproduction volume (V_R) , but also a contribution from reserves $(V_{\rm E})$:

$$V_{\rm w} = V + V_{\rm R} + V_{\rm E}.$$

So far, previous parameter estimates for flatfish species (van der Veer *et al.* 2001) and bivalves (van der Veer *et al.* 2006) have neglected the contribution of reserves to volume, because differences in maximum size were small (bivalves) or because of the assumption that species replace energy reserves by water (flatfishes). However, the range in maximum sizes differs by more than a factor of 10 in the present study, and since reserve density scales with volumetric length, ignoring the contribution of reserves to total volume might introduce a more serious bias. To account for these differences, the two approaches are distinguished as:

- estimation of parameters based on datasets, i.e. in line with previous studies and assuming that the contribution of reserves to volume can be neglected $(V_{\rm E} = 0);$
- estimation of parameters based on DEB model predictions of body-size scaling relationships, and taking into account the contribution of reserves to body volume ($V_E \neq 0$).

(i) Parameter estimation assuming $V_E = 0$

The methodology and required datasets followed those outlined by van der Veer *et al.* (2006, 2009). Parameter estimation could not be based on measurements made on a single individual owing to a general lack of complete datasets. Datasets were collected from the Web of Science and other sources. Information on maximum size (length) and wet mass was taken from Wheeler (1978), Fishbase (www.fishbase.org) and other data sources. Information on maximum observed length referred mostly to females. Maximum length of males was interpolated based on the ratio between

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Table 1. Parameters of the standard DEB model in a time-length-energy frame with symbols and units used in this paper, together with other species-specific physiological parameters. Typical values for a generalized animal at 20°C are also indicated. The length measure in the specific searching rate refers to the environment, all other length measures to structure. Square brackets mean 'per structural volume', curly braces mean 'per structural surface area' and dots denote 'per time'. Changes in the choice of primary parameters (P) and compound parameters (C) from DEB 2 (Kooijman 2000) to DEB 3 (Kooijman 2010) are indicated.

symbol	units	interpretation	DEB 2	DEB 3	typical values
paramet	ers				
$\{\dot{F}_{\rm m}\}$	$cm^2 \text{ or } 3 cm^{-2} d^{-1}$	maximum surface-area-specific searching rate		Р	$6.5 \text{ dm}^3 \text{cm}^{-2} \text{ d}^{-1}$
$\{\dot{p}_{Am}\}$	$J cm^{-2} d^{-1}$	maximum surface-area-specific assimilation rate	Р	Р	$22.5 \mathrm{J}\mathrm{cm}^{-2}\mathrm{d}^{-1}$
KX	_	assimilation efficiency		Р	0.8
\dot{v}	$\mathrm{cm} \mathrm{d}^{-1}$	energy conductance	С	Р	$0.02 \mathrm{~cm~d}^{-1}$
к	_	fraction of used energy spent on maintenance plus growth	Р	Р	0.8
κ _R	_	reproduction efficiency	Р	Р	0.95
$\dot{p}_{\rm M}$	$J cm^{-3} d^{-1}$	volume-specific maintenance costs	Р	Р	$18 \mathrm{J}\mathrm{cm}^{-3}\mathrm{d}^{-1}$
$[E_{\rm G}]$	$\rm Jcm^{-3}$	volume-specific cost for structure	Р	Р	$2800 \mathrm{J} \mathrm{cm}^{-3}$
\dot{k}_i	d^{-1}	maturity maintenance rate coefficient	_	Р	$0.002 \mathrm{d}^{-1}$
$E_H^{\rm b}$	J	maturation at birth	—	Р	275 mJ
$E_H^{ m p}$	J	maturation at puberty	—	Р	166 J
\ddot{h}_{a}	d^{-2}	Weibull ageing acceleration	Р	Р	
\$ _G	—	Gompertz stress coefficient	—	Р	
$L_{\rm m}$	cm	maximum structural length: $k\{\dot{p}_{\mathrm{Am}}\}/[\dot{p}_{\mathrm{M}}]$	С	С	
K	$\mathrm{Jcm}^{-2 \text{ or } -3}$	half-saturation coefficient: $\{\dot{p}_{Am}\}/\kappa_X\{\dot{F}_m\}$	Р	С	
\dot{k}_{M}	d^{-1}	maintenance rate coefficient: $[\dot{p}_{\rm M}]/[E_{\rm G}]$	С	С	
g	—	energy investment ratio: $[E_G]/\kappa[E_m]$	С	С	
$[E_{\rm m}]$	$\rm Jcm^{-3}$	maximum reserve density: $\{\dot{p}_{ m Am}\}/\dot{v}$	Р	С	
scaling p	parameters				
z	—	zoom factor			
$\delta_{\mathbf{M}}$	—	shape coefficient			
conversi	on parameters				
μ_X	$\mathrm{J}\mathrm{mol}^{-1}$	energy-mass coupler for assimilation			

the Von Bertalanffy L_{∞} parameter for males and females, whenever available. For flatfish, information published by van der Veer *et al.* (2001, 2009) was incorporated and for brown shrimp, the estimates were taken from Campos *et al.* (2009). The complete list of references used in the parameter estimation is given in electronic supplementary material.

The parameter set presented here differs slightly from previously published values (van der Veer et al. 2001, 2009) in the first place because we now assume that the energy conductance \dot{v} is unlikely to vary substantially among species, and does not scale with body size, with the consequence that the maximum reserve capacity [E_m] of a species is proportional to maximum (structural) length. Furthermore, the specific cost for structure $[E_G]$ and specific somatic maintenance costs $[\dot{p}_{\rm M}]$ are related to cell complexity and, therefore, we assume that for related species, as well as for different sexes, their values will be similar (Kooijman 2000); sexes differ in maximum size because of their specific assimilation rate, and maybe because of κ , but not in specific somatic maintenance.

The resulting estimated parameter set was validated with data on maximum growth in relation to water temperature from different sources other than those used for parameter estimation. Observed discrepancies in predicted values on maximum growth were adjusted under the assumption that:

- differences between DEB simulations and growth observations indicated by different slopes in the simulated and observed growth relationships with temperature, imply an incorrect Arrhenius temperature;
- a systematic difference between DEB simulations and growth observations in absolute values indicate too high or too low values for $\{\dot{p}_{Am}\}$ and $[\dot{p}_{M}]$ or $[E_G]$ and $[E_m]$.

(ii) Parameter estimation assuming $V_E \neq 0$

For the parameter estimation based on body-size scaling relationships, the typical set of primary parameters of the standard DEB model for a generalized animal (theoretical reference for maximum structural length of 1 cm at 20° C) was used (table 1). The specific assimilation rate $\{\dot{p}_{Am}\}$ and the ageing acceleration $h_{\rm a}$ are primary parameters that are proportional to maximum length and the maturity thresholds proportional to maximum structural volume. All other primary parameters are intensive and do not depend on maximum length. This covariation is reflected in a scaling zoom factor z, i.e. the ratio of the maximum (structural) lengths of the two compared species. Structural length is obtained from an appropriately chosen actual (physical) length by multiplication with the shape coefficient δ_{M} .

The zoom factor z, the shape coefficient δ_M and all primary parameters are estimated simultaneously from

a (small) set of available data and the abovementioned parameter values for a generalized animal by minimization of a weighted sum of squared deviations between data and predictions. The parameter values of the generalized animal are thus treated as pseudo-data, and given small weight coefficients to ensure that if the real data have information about some primary parameter, it gets priority. The nature of the real data differs between species (depending on availability), and typically include maximum length and weight, length and age at birth and puberty and maximum reproduction rate. This one-step procedure is illustrated in electronic supplementary material. Scripts can be downloaded from the DEB laboratory (http:// www.bio.vu.nl/thb/deb/) and are explained in the add_my_pet document (http://www.bio.vu.nl/thb/deb/ deblab/add_my_pet/).

(c) Interspecies comparisons

Species-specific parameters were determined for different reference temperatures $T_{\rm ref}$ and, hence, interspecies comparisons require a previous conversion of the DEB parameters that represent physiological rates (e.g. $\{\dot{p}_{\rm Am}\}$ and $[\dot{p}_{\rm M}]$) to a common temperature using formula (2.1). The new reference temperature was selected in such a way that it lies within the range of preferred temperatures, but below the optimal temperature.

Subsequently, the comparison of both sets of parameters (*set I*, based on the empirical procedure, and *set II*, based on the minimization procedure) was made, keeping in mind the different assumptions regarding reserves as previously stated. The comparison between the two parameter sets was done at reference temperatures of 10, 15 or 20° C, depending on the species.

3. RESULTS

(a) Temperature

Estimates of temperature tolerance of the various species were based on experimental data on juveniles, except where otherwise stated. Information was taken from Freitas et al. (2007), except for dab (Fonds & Rijnsdorp 1988), sole (Lefrançois & Claireaux 2003), cod (Pörtner et al. 2001), eelpout and bullrout (Fonds et al. 1989) and shore crab (McDonald et al. 2006). For herring, sprat and anchovy, either larval or juvenile data were used (Brawn 1960; M. Peck 2010, unpublished data). The latter species was assumed to have a similar tolerance as found for northern anchovy (Engraulis mordax) by Theilacker (1987). Species showed clear differences in optimal temperature and tolerance range (table 2). Most species could endure temperatures below 10°C, and interspecific differences were most pronounced at the upper temperature limit. The shore crab had the largest tolerance range of more than 30°C.

Information on temperature sensitivity T_A (K) for cod, sea bass, common goby, sand goby, plaice, flounder, brown shrimp and shore crab was taken from Freitas *et al.* (2007); data for dab and sole were obtained from van der Veer *et al.* (2001) and for anchovy from Pecquerie (2008). For bull-rout and

Table 2. Temperature tolerance (range with positive reaction rate) and sensitivity parameters set for various North Atlantic marine species. For more information and references, see text. Interpolated values are in italic.

	T _A (K)	$T_{ m opt} ^{\circ}{ m C}$ (K)	temperature tolerance range °C (K)
P. platessa	7000	20 (293)	26 (273-299)
L. limanda	4000	20 (293)	26 (273-299)
P. flesus	7000	20 (293)	26 (273-299)
S. solea	8500	20 (293)	27 (276-303)
P. microps	3500 ^a	20 (293)	33 (273–306 ^a)
P. minutus	3500 ^a		
G. morhua	7400	14 (287)	24 (273-297)
M. scorpius	4000	15 (288)	23 (273-296)
Z. viviparous	5000^{a}	13 (286)	20 (273-293)
D. labrax	5700	23 (296)	>33 (273-306)
C. harengus	8000	18 (291)	>24 (273-297)
S. sprattus	9300	19 (292)	>25 (275–300 ^a)
E. encrasicolus	9800	24 (297)	>27 (278-305)
C. crangon	9000 ^a	23 (296)	30 (273-303)
C. maenas	6400	20 (293)	35 (273–308 ^a)

^aIn some cases, the DEB parameter validation procedure resulted in a correction of the estimates (see text for further explanations).

eelpout, $T_A(K)$ was calculated from data on oxygen consumption in relation to temperature published by Fonds *et al.* (1989). DEB parameter validation resulted in some cases in a correction of the Arrhenius temperature (table 2).

With respect to the various temperature parameters, there was a significantly positive relationship between temperature tolerance range and optimal temperature (figure 1*a*; Spearman rank correlation test: $r_s = 0.79$, d.f. = 8, p < 0.025). A positive, but non-significant trend was present between temperature tolerance range and the Arrhenius temperature (figure 1*b*; $r_s = 0.12$, d.f. = 8, p > 0.1), and between the optimal temperature and the Arrhenius temperature (figure 1*c*; $r_s = 0.26$, d.f. = 12, p = 0.36).

For a few species, information for different life stages was available. Information on plaice was based on Ryland *et al.* (1975), Talbot (1977) and Fonds *et al.* (1992); for cod it was based on a compilation made by Graham & Harrod (2009) and for brown shrimp it was based on Campos & van der Veer (2008). Temperature tolerance range varied during ontogeny, and the largest tolerance range occurred during the juvenile stage (figure 2).

(b) *Energetics*

(i) Set I: parameter estimation assuming $V_E = 0$

The estimated values for the various species based on empirical data, as well as the estimation procedures, are described in more detail in electronic supplementary material. This set was validated and adjusted based on a comparison with maximum growth data in relation to temperature (figure 3). Final estimates at the species-specific reference temperatures are shown in table 3.

(ii) Set II: parameter estimation assuming $V_E \neq 0$ Estimated values based on body-size scaling relationships, using typical parameter values of a generalized

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Figure 1. Relationships for a number of North Atlantic marine species between (*a*) temperature tolerance range (°C) and optimal temperature (°C); (*b*) temperature tolerance range and the Arrhenius temperature (K); and (*c*) optimal temperature (°C) and the Arrhenius temperature (K). Filled circles, demersal fish; open circles, pelagic fish; filled inverted triangles, crustaceans.

animal as pseudo-data, are presented in table 4. The estimates for the primary parameters $[E_G]$ and \dot{k}_j were for all species very close to the values of the generalized animal, i.e. $[E_G] = 2800 \text{ J cm}^{-3}$ and $\dot{k}_j = 0.002 \text{ d}^{-1}$. The rest of the primary parameters were not estimated because data on feeding, maturation, reproduction and lifespan were not available for all species. Values for assimilation and maximum storage density varied for the different species by a factor of about 22 in line with differences in the zoom factor z. Table 4 also presents the fraction of maximum body weight that is structure, δ_{V_2} for individuals with an empty reproduction buffer. This fraction is a function of parameter values (Kooijman 2010), and illustrates that



Figure 2. Temperature tolerance range (°C) of (a) place (*Pleuronectes platessa*), (b) cod (*Gadus morhua*) and (c) brown shrimp (*Crangon crangon*) in relation to life stages. For references, see text.

the contribution of reserves in total body volume should not be neglected.

(iii) Parameter set I versus parameter set II

The order of magnitude of set II parameter values was lower than that of set I. For instance, for flatfishes, the volume-specific maintenance costs $[\dot{p}_{\rm M}]$ at 15°C obtained with the minimization procedure varied from 12 to 15 J cm⁻³ d⁻¹, while the value empirically derived amounted to about 29.8 J cm⁻³ d⁻¹. The same was true for assimilation rate $\{\dot{p}_{\rm Am}\}$. The low energy conductance assumed in the minimization approach resulted in high predictions of the maximum storage density $[E_{\rm m}]$. For both assimilation rate and maximum storage density, set II (table 4) and set I (table 3) values were strongly correlated (figure 4*a*; set II $\{\dot{p}_{\rm Am}\}$ versus set I $\{\dot{p}_{\rm Am}\}$: $r_{\rm s} = 0.90$, d.f. = 13, p < 0.001; figure 4*c*; set II $[E_{\rm m}]$ versus set I $[E_{\rm m}]$:



Figure 3. Comparison of observed maximum growth under laboratory conditions and DEB simulations for both females and males. For more information about the individual species and references, see text. Solid circles with solid lines, experimental data; open circles with dashed lines, DEB simulations female and crosses with dashed lines, DEB simulations male.

 $r_{\rm s} = 0.86$, d.f. = 13, p < 0.001). However, estimated values were on average approximately four times higher for assimilation rate and approximately 3.5 times lower for the maximum storage density. No significant correlation was found between the values of the volume-specific somatic maintenance rate $[\dot{p}_{\rm M}]$ from the two sets (figure 4*b*).

(c) Link between temperature parameters and energetics

For comparison of the various species, the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the

volume-specific maintenance rate $[\dot{p}_{\rm M}]$ empirically derived were related with the optimal temperature, the Arrhenius temperature and temperature tolerance range, respectively, after conversion to 10°C using equation (2.1) (figure 5).

Surface-area-specific assimilation rate $\{\dot{p}_{\rm Am}\}$ showed a significantly negative relationship with temperature tolerance range (figure 5*b*; $r_{\rm s} = -0.58$, d.f. = 8, p < 0.05), and negative but non-significant trends with the optimal temperature (figure 5*a*; $r_{\rm s} = -0.39$, d.f. = 12, p = 0.17) and the Arrhenius temperature (figure 5*c*; $r_{\rm s} = -0.007$, d.f. = 13, p = 0.98).

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Table 3. DEB parameter set for various North Atlantic marine species, for females and males (between brackets), based on experimental data after validation with maximum growth data in relation to water temperature. For more information, see electronic supplementary material and text.

	$T_{ m ref}$ (°C)	T _A (K)	$\delta_{ m M}$ (–)	L _{max} (cm)	$\{\dot{p}_{Am}\}\ (J\ cm^{-2}\ d^{-1})$	$[\dot{p}_{\rm M}]$ (J cm ⁻³ d ⁻¹)	$[E_{\rm m}]$ (J cm ⁻³)	$[E_{\rm G}]$ (J cm ⁻³)	к (-)
P. platessa	15	7000	0.219	78 (52)	599 (358)	29.8	2500 (1500)	5600	0.85 (0.95)
L. limanda	15	4000	0.216	51 (43)	317 (240)	29.8	1585 (1200)	5600	0.85 (0.95)
P. flesus	15	7000	0.224	56 (47)	576 (335)	29.8	2400 (1400)	5600	0.65 (0.95)
S. solea	20	8500	0.192	75 (64)	864 (697)	54.1	1986 (1600)	5600	0.90 (0.95)
P. microps	20	3500	0.190	6.5	65	33.6	272	5600	0.65
P. minutus	20	3500	0.190	9.5	93	33.6	390	5600	0.65
G. morhua	10	7400	0.209	190	1144 (1024)	24.5	7330 (6565)	5600	0.85 (0.95)
M. scorpius	10	4000	0.230	60 (51)	385 (293)	23.8	5000 (3800)	5600	0.85 (0.95)
Z. viviparous	10	5000	0.157	50 (42)	355 (170)	39.5 (24.5)	2275 (1090)	5600	0.85 (0.95)
D. labrax	20	5700	0.217	103 (87)	1194 (864)	41	3850 (2790)	5600	0.85 (0.90)
C. harengus	15	8000	0.190	43	468	46	1840	5600	0.80
S. sprattus	15	9300	0.180	16.5	180	46	652	5600	0.90
E. encrasicolus	20	9800	0.172	20 (17)	329	62	645	5600	0.65
C. crangon	20	9000	0.213	9.5 (7.5)	112 (75)	47.1	850 (565)	2500	0.80 (0.95)
C. maenas	20	6400	0.581	8.5 (10)	212 (210)	34.4	2211 (2191)	2500	0.80 (0.95)

Table 4. DEB parameter set based on body-size scaling relationships, using the typical parameter values of a generalized animal as pseudo-data. Temperature-dependent DEB parameters were converted to a species-specific reference temperature $T_{\rm ref}$ for comparison with the estimates in table 3, using the species-specific Arrhenius temperature $T_{\rm A}$ from table 2. $\delta_{\rm V}$ is the fraction of body weight that is structure.

	$T_{ m ref}$ (°C)	$\delta_{ m M}$ (-)	z(-)	$\{\dot{p}_{Am}\}\$ (J cm ⁻² d ⁻¹)	$[\dot{p}_{\rm M}]$ (J cm ⁻³ d ⁻¹)	\dot{v} (cm d ⁻¹)	$[E_{\rm m}]$ (J cm ⁻³)	к (-)	$\delta_{ m V}$ (-)
standard DEB (generalized animal)	20		1	22.5	18.0	0.0200	$\{\dot{p}_{ m Am}\}/\dot{v}$	0.80	
P. platessa	15	0.121	9.4	148	12.2	0.0129	11 473	0.78	0.143
L. limanda	15	0.130	6.6	125	14.9	0.0151	8278	0.79	0.187
P. flesus	15	0.131	7.4	115	12.4	0.0126	9127	0.79	0.173
S. solea	20	0.109	8.2	200	18.9	0.0196	10 204	0.77	0.157
P. microps	20	0.169	1.1	24	18.0	0.0203	1182	0.82	0.616
P. minutus	20	0.158	1.5	35	18.4	0.0197	1777	0.78	0.516
G. morhua	10	0.097	18.5	218	10.0	0.0082	26 585	0.85	0.067
M. scorpius	10	0.136	8.2	110	11.2	0.0123	8943	0.83	0.176
Z. viviparous	10	0.102	5.1	66	10.0	0.0106	6226	0.77	0.236
D. labrax	20	0.110	11.3	286	19.7	0.0184	15 543	0.78	0.109
C. harengus	15	0.122	5.3	77	11.4	0.0123	6260	0.78	0.233
S. sprattus	15	0.142	2.3	30	10.4	0.0127	2362	0.81	0.447
E. encrasicolus	20	0.130	2.6	60	18.2	0.0199	3015	0.79	0.387
C. crangon	20	0.175	1.7	36	17.7	0.0207	1739	0.82	0.526
C. maenas	20	0.565	4.8	95	15.9	0.0200	4750	0.80	0.286

Volume-specific maintenance rate $[\dot{p}_{\rm M}]$ showed a strong negative correlation with the optimal temperature (figure 5*d*; $r_{\rm s} = -0.80$, d.f. = 12, p = 0.001) and a significant negative trend with tolerance range (figure 5*e*; $r_{\rm s} = -0.69$, d.f. = 8, p < 0.025). With respect to the Arrhenius temperature, no relationship with $[\dot{p}_{\rm M}]$ was found.

4. DISCUSSION

The idea behind this paper is to compare the physiological performance of species by combining species-specific differences in temperature tolerance and sensitivity with their energetics reflected in the DEB parameters. The availability of reliable datasets is an important requirement but, unfortunately, basic information on temperature tolerance and sensitivity for many species is lacking. The absence of data on pelagic, schooling species, such as herring, sprat and anchovy, is somewhat understandable as laboratory rearing can be technically more challenging, but the lack of information on one of the most abundant, widely distributed and easy to handle species, the shore crab C. maenas, is more striking. An additional complication is that tolerance and temperature sensitivity appear to be flexible, causing plasticity of a species' physiology in response to short- and longterm environmental conditions (adaptation, etc.). Furthermore, nonlinear changes in sensitivity and tolerance during ontogeny may occur as has been found for C. crangon (Campos & van der Veer 2008). Finally, it is currently unknown whether there are



Figure 4. Relationship between DEB parameters empirically derived (set I; table 3) and DEB parameters estimated by minimization procedures (set II; table 4). (*a*) maximum surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$; (*b*) maximum volume-specific somatic maintenance rate $[\dot{p}_{M}]$; and (*c*) maximum storage density $[E_m]$. Filled circles, demersal fish; open circles, pelagic fish; filled inverted triangles, crustaceans.

differences between males and females. Therefore, although the present limited set of information should be interpreted with caution, it can, nevertheless, be seen as a step forward, advancing in our understanding of how organismal-level energetics are related to interspecific differences in thermal biology and, consequently, the impact of climate change on species interactions and community structure.

(a) Temperature

Based on tolerance range and optimal temperature, cold/temperate water (eelpout, bull-rout, herring, cod, sprat, various flatfishes) and warm water

(gobiidae, shrimp, crab, sea bass, anchovy) species could be identified. This classification fits generally with the one based on biogeographic affinities (Boreal, Lusitanian) proposed by Yang (1982) and that has been followed in more recent studies (Tulp et al. 2008; Rijnsdorp et al. 2009). However, some discrepancies still occur, namely for sprat, a species occurring over a relatively large geographical (latitudinal) range, which has been considered both as a warm-water or cold-water species depending on the author. Species such as sprat challenge rigid classification schemes that separate groups based on thermal preference/tolerance, attributes that are more likely continuous (and not categorical) in nature. More importantly, species with wide geographical (latitudinal) ranges may show specific population adaptations to local environmental conditions, which also need to be considered.

With respect to temperature tolerance range, the high-temperature limit is more variable than the lowtemperature limit. The lower limit was down to 10°C in almost all the species examined in this study, and approached 0°C in more than half of them. The high temperature limit was more variable, from 20°C to even 35°C, indicating that increasing temperatures, owing to either seasonal or longer term climatedriven changes, will modify the species composition of fish and crustacean assemblages. For instance, the nursery function of the Wadden Sea for plaice and herring (Zijlstra 1972) is restricted to maximum temperatures in the low 20s. At higher temperatures, not only shrimps but also crabs and gobiidae will become the dominant species, as has already been recently observed in intertidal areas during warm periods (H. W. van der Veer & J. IJ. Witte 2009, unpublished data). The fact that young (small) juvenile fishes seem to exploit a larger range in temperatures than either earlier or later life stages (e.g. Pörtner & Farrell 2008; Rijnsdorp et al. 2009) and that juvenile fishes select higher temperatures than do older (larger) conspecifics (McCauley & Huggins 1979; Lafrance et al. 2005) points to a differential vulnerability to changes in temperature, which should be accounted for when trying to predict individual responses to climate change. In coastal ecosystems, typically with larger variation in thermal regimes, these differential individual responses to increasing temperatures may result in a decrease in fish size or mass with consequences in the ecosystem structure and local production.

As expected, temperature tolerance range and optimal temperature are positively related. In this respect, mobile species do not deviate from sessile bivalves (van der Veer *et al.* 2006). The slightly positive trend of the Arrhenius temperature with temperature tolerance range diverges from the suggestion by Kooijman (2010): species with a large tolerance range that typically inhabit more variable temperature environments are expected to have lower temperature sensitivity (lower Arrhenius). However, in this respect, the dataset exhibits a large variation and thus no clear conclusions can be drawn. Moreover, the variability also masked any potential differences between pelagic and demersal species.



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Figure 5. Relationships between, respectively, maximum surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ (a-c) and maximum volume-specific somatic maintenance rate $[\dot{p}_{M}]$ (d-f), at 10°C, with optimal temperature (°C) (a,d), temperature tolerance range (°C) (b,e) and Arrhenius temperature (K) (c,f). DEB parameter values from set I. Filled circles, demersal fish; open circles, pelagic fish; filled inverted triangles, crustaceans.

(b) *Energetics*

An energetic-based comparison of species with DEBs seems to be a promising route as only a few parameters are necessary to characterize a species. However, the token of the DEB model is energy, which requires a conversion for comparison of model simulations with observations. An issue is the general lack of reliable datasets preventing the use of standard protocols (Kooijman *et al.* 2008). For the pelagic species analysed, experimental data are completely absent and even for more well-studied species, information is often incomplete and/or contradictory. Moreover, some parameters are difficult to determine. Therefore, part of the analysis was based on the assumption that

both $[E_G]$ and $[\dot{p}_M]$ are related to cell complexity, and hence similar in related species as well as among sexes (Kooijman 2010). In a number of species, predicted maximum growth corresponded well with observations. However, in other cases discrepancies could not be reconciled or there was a lack of growth observations in relation to temperature. Information on growth of juvenile stages was particularly difficult to find, highlighting the fact that there is still lack of knowledge on the ecology of specific life stages for important species. This indicates that parameter estimates can only be considered exploratory, a rough approximation of the real values, requiring further experimental support and data for fine-tuning. The estimates for the pelagic species are particularly questionable.

Some parameters, such as the volume-specific maintenance costs, represent different components depending on the type of species examined. In more active schooling species, higher maintenance costs reflect the higher cost of swimming compared with less active demersal species such as flatfishes with reduced swimming activity (Fonds et al. 1992). Therefore, differences in volume-specific maintenance costs between other fish species such as cod, sea bass and pelagic species reflect differences in activity patterns rather than differences in cell complexity. Differences in cell complexity are visible when comparing bivalves $(12 \text{ J cm}^{-3} \text{ d}^{-1} \text{ at } 10^{\circ}\text{C}; \text{ van der Veer et al. 2006})$ with shrimps and shore crabs $(16 \text{ J cm}^{-3} \text{ d}^{-1})$. Differences in life-history strategies (cf. Stearns 1992) are clearly reflected in the parameter values of the various flatfish species. Although being characterized by a similar blueprint (maintenance costs and costs for growth) the various species showed a large variability in energy uptake $(310-490 \text{ J cm}^{-2} \text{ d}^{-1} \text{ at } 10^{\circ}\text{C})$ and in energy allocation (κ in females varies from 0.65 to 0.90).

In DEB models, differences in energy budgets between sexes are reflected in different parameter values as in the case of different species (Kooijman 2010). Since DEB parameters are coupled to each other, dimorphism in ultimate size is related to differences in energy allocation (reflected in κ) and/or energy acquisition (ingestion, assimilation). In male fish, including flatfishes, reproductive investment in terms of energy used for gonadal production is typically lower than in females (Rijnsdorp & Ibelings 1989). However, males can also have additional 'reproduction-related' costs, namely territorial behaviour or parental care, which should be accounted. Differences in energy acquisition and assimilation seem to be the underlying cause for sexual differences in some flatfishes like dab L. limanda (Lozán 1992) and in percids (Rennie et al. 2008).

Our second approach to estimate parameters, based on body-size scaling relationships, is motivated by the observation that essential data are lacking for most species. Since maximum reserve capacity $[E_m]$ is expected to increase with maximum length, the assumption that reserve hardly contributes to physical volume is hard to substantiate for large-bodied species; wet-weight/dry-weight ratios do not vary that much with maximum length, so reserve is probably not replaced by water in small-bodied species. Deviations from predictions within this framework can be useful to detect species-specific adaptations in an evolutionary context (Kooijman *et al.* 2008).

We observed differences in results between both approaches. With the present dataset, it is unclear whether this indicates that for marine species the parameter values are different from those of other groups or whether the estimates are biased. The fact that predicted parameter values for plaice did not result in a good correspondence with observed growth patterns (not shown) might suggest that for marine species, typical values deviate from those presented by Kooijman (2010) for a generalized animal. However, more data are required to resolve this aspect.

(c) Are temperature tolerance and sensitivity linked with energetics?

Any discussion concerning a link between temperature tolerance and sensitivity with the energetics of a species should be considered as preliminary owing to the relatively small dataset and to uncertainties in some DEB parameter estimates for various species. From the DEB parameters, the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the volume-specific somatic maintenance costs $[\dot{p}_{\rm M}]$ are, in this respect, the key parameters. First of all, they are temperature dependent and second, they reflect important energy fluxes. $\{\dot{p}_{Am}\}$ is the link with the environment that integrates feeding mode and prey species in one parameter. $[\dot{p}_{\rm M}]$, on the other hand, is linked to turnover/activity processes reflecting the building design of the species and its complexity, and is a major factor in determining allocation to growth and reproduction. Differences in life-history strategies are therefore expected to act on (and to be reflected in) these parameters (Stearns 1992).

Both surface-area-specific assimilation rate and volume-specific maintenance rate appeared to decrease with increasing optimal temperature, temperature sensitivity and range of temperature tolerance. This might suggest that species with high optimal temperatures, living in fluctuating temperature environments, or those having greater metabolic sensitivity are compensated by having relatively lower assimilation rates and, surprisingly, lower maintenance costs. Generalizing these tendencies, species living under low and constant temperatures can afford a relatively high assimilation. On the other hand, species living in warm-water conditions may pay the price of a relatively low assimilation rate. Making the step from limited observations into underlying mechanisms is complicated especially because of the intimate coupling of processes of energy uptake and utilization. However, the preliminary work presented here is a promising approach to understand the response of species to temperature changes and is worth expanding in the near future. As noted by Rijnsdorp et al. (2009), responses at the population, community and ecosystem levels to climate change are ultimately the outcome of differences in individual physiological responses that affect trophic interactions. Integrating thermal tolerance and sensitivity information seems thus fundamental to understanding and predicting biological responses to global change.

The present study also highlights the need for additional, basic physiological data collected during controlled, multifactorial experiments quantifying rates of growth and metabolism (i.e. at different temperatures and feeding rates; cf. Peck *et al.* 2003). Parametrizations that embrace observed ontogenetic changes in metabolic scaling, which account for variability in prey energy densities within species with different feeding habitats, and which mechanistically couple resource allocation to other key environmental regulators (e.g. photothermal cues for the seasonal allocation of reserves), should also be pursued.

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ELECTRONIC SUPPLEMENTARY MATERIAL

Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species

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1. Primary parameters in DEB 2 versus DEB 3

Although the standard DEB model did not change, ten years of research between the two editions (Kooijman 2000, 2010) identified different primary parameters. To illustrate the problem: if a, b and c are parameters, while c = a/b, two parameters are primary and the third one is compound. The choice is arbitrary from a mathematical point of view, but not from a biological point of view. Parameters that are most close to the underlying processes are selected as primary parameters. Changes of selection occurred for the following parameters:

- Specific searching rate $\{\dot{F}_m\} = \{\dot{J}_{XAm}\}/K$ is preferred above half saturation constant K
- Digestion efficiency $\kappa_x = \{\dot{p}_{Am}\}/\{\dot{p}_{Xm}\}\$ is preferred above specific feeding rate $\{\dot{p}_{Xm}\}$
- Energy conductance $\dot{v} = \{\dot{p}_{Am}\}/[E_m]$ is preferred above maximum reserve capacity $[E_m]$

The latter change in selection results from the discovery of a mechanism for the reserve dynamics (Kooijman & Troost 2007).

Another important development affected the way maturity is treated. In the second edition, for maximum simplicity reasons, maturity maintenance was set to be equal to $p_J = \min(V, V_p) [p_M] (1-\kappa)/\kappa$. The only motivation for this choice was that maturity density (maturity per structure) then does not change, and stage transitions occur when structure exceeds threshold values, V_b and V_p . Further consequences are that there is no need to monitor maturity as state variable and the costs of an egg is a relatively simple explicit function of parameters and of the reserve density of the mother at egg formation. This simplification turned out to be problematic in several contexts and is no longer done in the third edition. The consequences are that maturity is now an explicit state variable, the maturity maintenance rate coefficient k_J is a primary parameter, the amount of structure at stage transitions becomes dependent on food availability (so structure thresholds V_b and V_p

must be replaced by maturity thresholds E_{H}^{b} and E_{H}^{p}) and the costs of an egg are much more difficult to obtain (and must be obtained numerically).

The final change concerns the ageing module. The single-parameter ageing module of the second edition did not capture observed ageing patterns of endotherms well. An extension that involves a second ageing parameter, the Gompertz stress coefficient, repaired the problem. Progress has been made to quantify the ageing process dynamically, which involves two extra state variables, the ageing acceleration and the hazard rate.

The change in the selection of primary parameters simplified the argument on the co-variation of parameter values, since less primary parameters are design-parameters (which depend on the maximum size of organisms).

2. Parameter estimation assuming $V_E = 0$

2.1. Parameter estimation based on datasets

The DEB parameter estimation procedure for the various species is described for both females and males of each species separately, whenever information for both sexes is available. Parameter sets are applicable for the isometric growth phase of juveniles and adults. Temperature dependent parameters are listed at the reference temperature. Values for males are indicated between brackets. In addition to the DEB parameters $[E_{\nu}]$ i.e. the energy content of structure without reserves was also included in the parameter list. For fish species, the energy conductance $\dot{\nu}$ is taken to be similar to the value estimated for plaice *Pleuronectes platessa*, 0.156 cm d⁻¹ at 10°C (Van der Veer et al. 2009). For crustaceans, the energy conductance value published for *Crangon crangon*, 0.045 cm d⁻¹ at 10°C (Campos et al. 2009) is used. Although in these studies $\dot{\nu}$ has been estimated as a compound parameter, due to the considerations addressed above, it is now treated as a primary parameter.

For each species, a block summarizes the datasets used and the estimates for the various parameters. Next, parameter calibration and validation for the various species based on laboratory experiments on maximum growth in relation to temperature are described. Table 3 in the paper summarizes the final set of DEB parameters for the various species after conversion to an appropriate species-specific reference temperature (10, 15 or 20°C depending on the species).

Pleuronectes platessa

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.219	The shape coefficient was estimated from length–wet mass data of juveniles (5 - 45 cm total length).	Van der Veer et al. 2001
L _{max}	78 (52)	Maximum size of males was based on the ratio between the von Bertalanffy growth curves of males and females.	Deniel 1981 Van der Veer et al. 2001
$[\dot{p}_M]$	19.4	The volume-specific maintenance costs were based on field data. This value includes not only body maintenance but also cost for feeding and activity (swimming). These values were expected to be similar for males and females.	Van der Veer et al. 2001
$[E_G]$	5600	The costs of structure were estimated under the assumption of a conversion efficiency of about 60% resulting in 7 kJ cm ⁻³ (Van der Veer et al., 2001). However, information on the energetic efficiency of synthesizing material indicates, in general, costs for protein and fat synthesis on the order of maximum 20% (Aoyagi et al. 1988, Roberts and Young 1988). Assuming that the costs for material synthesis for other components are in the same order of magnitude and that a similar amount is required for establishing and completing the cellular metabolism, indicates that total energy costs would be less than 40%. Therefore, a conversion efficiency of 60% might be an overestimation and hence the volume-specific costs of structure were lowered from 7 to 5.6 kJ cm ⁻³ .	Van der Veer et al. 2009 and references therein
K	0.85 (0.95)	κ was determined by model simulations. In female plaice, gonadal mass of relatively large individuals (with a high body mass that are well fed) just before spawning is about 20% of the total mass which would imply a κ slightly higher than 0.85. Plaice is a capital spawner, whereby the gonad and testis are a store where energy/chemicals are passing through from body reserves to develop and shed eggs and sperm. This means that the total energy lost in reproduction is larger than the gonad and testis mass at any time. Therefore, the estimate of κ was rounded down to 0.85. For males a value of 0.95 was taken based on Deniel (1981).	Deniel 1981 Rijnsdorp & Ibelings 1989
$\left\{\dot{p}_{Xm}\right\}$	487 (291)	Under the assumption of losses of 20% due to digestion (Brett and Groves 1979) this would mean for $\{\dot{p}_{Xm}\}$ a value of 487 J cm ⁻² d ⁻¹ for females and 291 J cm ⁻² d ⁻¹ for males.	Van der Veer et al. 2009
$\{\dot{p}_{Am}\}$	390 (233)	This parameter was determined based on the formula for maximum volumetric length under optimal food conditions: $V_m^{\frac{1}{3}} = k \frac{\{\dot{p}_{Am}\}}{[\dot{p}_M]}$. Volumetric length of plaice was calculated by multiplying the shape coefficient (0.219) with the expected maximum length, about 78 cm for females and 52 cm for males. Together with the other parameters (<i>K</i> and $[\dot{p}_M]$), this means a value for $\{\dot{p}_{Am}\}$ of 390 for females and 233 J cm ⁻² d ⁻¹ for males.	Van der Veer et al. 2009

[E] 2500 Maximum storage of females was based on Van der Veer et al. (2009) For males Van der Veer et al. 2	
	2009
(1500) since $[E_m]$ is a compound parameter, it was estimated from the energy conductance	
and the maximum surface-area-specific assimilation ($[E_m] = \{\dot{p}_{Am}\}/\dot{v}$) resulting in the	
estimate of 1500 J cm ³ .	
$[E_{v}]$ 4000 Energy content of structure without reserves. Van der Veer et al. 2	2009

Limanda limanda

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.216	The shape coefficient was estimated from length–wet mass data of juveniles (5 - 30 cm total length).	Van der Veer et al. 2001
$L_{\rm max}$	51 (43)	The Von Bertalanffy curves suggested a ratio between L_{∞} for males and females of 0.85 which means a maximum size for males of 43 cm.	Deniel 1981 Van der Veer et al. 2001
$[\dot{p}_M]$	19.4	The volume-specific maintenance costs were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2009
К	0.85 (0.95)	κ was determined on model simulations comparing simulated reproductive investment with observations along the French coast. For females this resulted in a value of 0.85 and for males a value of 0.95 was taken.	Deniel 1981 Van der Veer et al. 2001
$\{\dot{p}_{Xm}\}$	310 (240)	$\left\{\dot{p}_{Xm} ight\}$ was calculated under the assumption of losses due to digestion of 20%.	Brett and Groves 1979
$\left\{ \dot{p}_{Am} \right\}$	248 (188)	Based on the formula for maximum volumetric size, $\left\{\dot{p}_{Am} ight\}$ could be calculated.	This paper
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	1600 (1200)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for females and males.	This paper
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001

Platichthys flesus

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.224	The shape coefficient was estimated from length–wet mass data of juveniles (5 - 30 cm total length).	Van der Veer et al. 2001
$L_{\rm max}$	56 (47)	The Von Bertalanffy curves suggested a ratio between L_{∞} for males and females of 0.85 which means a maximum size for males of 47 cm.	Deniel 1981 Van der Veer et al. 2001
$[\dot{p}_M]$	19.4	The volume-specific maintenance costs were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2009
К	0.65 (0.95)	κ was determined on model simulations comparing simulated reproductive investment with observations along the French coast. For females this resulted in a value of 0.65 and for males a value of 0.95 was taken.	Deniel 1981 Van der Veer et al. 2001
$\left\{ \dot{p}_{Xm} \right\}$	468 (272)	$\left\{\dot{p}_{_{Xm}} ight\}$ was calculated under the assumption of losses due to digestion of 20%.	Brett & Groves 1979
$\left\{ \dot{p}_{Am} \right\}$	375 (218)	Based on the formula for maximum volumetric size, $\left\{ \dot{p}_{\scriptscriptstyle Am} ight\}$ could be calculated.	This paper
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	2400 (1400)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for females and males.	This paper
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001

Solea solea

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{_M}$	0.192	The shape coefficient was estimated from length–wet mass data of juveniles (5 - 35 cm total length).	Van der Veer et al. 2001
$L_{\rm max}$	75 (64)	The Von Bertalanffy curves suggested a ratio between L_{∞} for males and females of 0.85 and this means a maximum size for males of 64 cm.	Deniel 1981 Van der Veer et al. 2001.
$[\dot{p}_M]$	19.4	The volume-specific maintenance costs were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2009
К	0.90 (0.95)	<i>K</i> was determined on model simulations comparing simulated reproductive investment with observations along the French coast. For females this resulted in a value of 0.65 and for males a value of 0.95 was taken.	Deniel 1981 Van der Veer et al. 2001.
$\{\dot{p}_{Xm}\}$	388 (312)	$\{\dot{p}_{\chi_m}\}$ was calculated under the assumption of losses due to digestion of 20%.	Brett & Groves 1979
$\{\dot{p}_{Am}\}$	310 (250)	Based on the formula for maximum volumetric size, $\left\{ \dot{p}_{\scriptscriptstyle Am} ight\}$ was calculated.	This paper
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	2000 (1600)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for females and males.	This paper
$\left[E_{v}\right]$	4000	The energy content of structure were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	Van der Veer et al. 2001

Pomatoschistus microps

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{_M}$	0.190	The estimate of the shape coefficient was based on data from Minho, Portugal. The value of 0.199 \pm 0.008 (n=216; r ² = 0.86) included gonad mass and will be slightly overestimated. Therefore, a value of 0.190 was taken.	V. Freitas unpubl.
L _{max}	6.5	Value assumed for females.	Wheeler 1978
$[\dot{p}_M]$	45	The volume-specific maintenance costs were calculated based on the formulae of maximum volumetric length, knowing the estimates of $\{\dot{p}_{Am}\}$ and κ .	This paper
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken.	Van der Veer et al. 2009
К	0.65	Reproductive effort in <i>P. microps</i> was studied by Rogers (1988). He estimated a total caloric investment in reproduction of 12 kJ in relation to a total annual input -calculated in the form of dietary energy content- in the order of 35 kJ. This would mean a K of ~ 0.65.	Rogers 1988
$\{\dot{p}_{Xm}\}$	106	A rough estimate of $\{\dot{p}_{\chi_m}\}$ based on the dietary energy content at the end of April at a temperature of 10°C was 95.97 J d ⁻¹ per fish. Assuming a fish length of 5 cm, this means a surface-area-specific ingestion rate of ~ 106 J cm ⁻² d ⁻¹ .	Rogers 1988
$\left\{\dot{p}_{Am}\right\}$	85	$\{\dot{p}_{Am}\}$ was calculated from $\{\dot{p}_{Xm}\}$ under the assumption of 20% losses due to digestion.	Brett & Groves 1979
\dot{v}	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	545	The maximum storage was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{\rm Am}\}$.	This paper
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken.	Van der Veer et al. 2001
Pomatoschistus minutus

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.190	The estimate of the shape coefficient for <i>P. microps</i> was taken.	This paper
L _{max}	9.5	Value assumed for females.	Wheeler 1978
$[\dot{p}_M]$	19.4	The estimate for plaice was taken.	This paper
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The estimate for <i>P. microps</i> was taken.	This paper
К	0.65	The estimate for <i>P. microps</i> was taken.	This paper
$\{\dot{p}_{Xm}\}$	155	$\left\{\dot{p}_{_{Xm}} ight\}$ was calculated under the assumption of losses due to digestion of 20%.	Brett & Groves 1979
$\left\{ \dot{p}_{Am} \right\}$	125	Based on the formula for maximum volumetric size, $\{\dot{p}_{Am}\}$ was calculated for females.	This paper
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	801	The maximum storage was based on the energy conductance \dot{v} value for plaice and on	This paper
		the estimated $\{\dot{p}_{Am}\}$.	
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken.	Van der Veer et al. 2001

Gadus morhua

Symbol	Value	Description	Reference
T _{ref}	10	Reference temperature	
$\delta_{_M}$	0.209	The shape coefficient was estimated from length–wet mass data of juveniles (10 - 20 cm total length).	M. Fonds unpublished data.
$L_{\rm max}$	190	No evidence for sexual dimorphic growth has been reported.	This paper
$[\dot{p}_M]$	24.5	The maintenance rate was estimated via the formulae of maximum volumetric length.	This paper
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper
К	0.85 (0.95)	The gonad investment in terms of energy in Balsfjord cod amounted to ~ 15%. For males an investment of 5% was taken.	Jobling 1982 This paper
$\{\dot{p}_{Xm}\}$	1430 (1280)	Food intake in relation to body mass and temperature was determined as: Ln FI = $(0.104T - 0.000112T^3 - 1.500) + 0.802$ ln W (n=50; r ² =0.91 where FI is food intake in kJ d ⁻¹ ; T is temperature in °C and W is wet mass in grams. For a fish with a mass of 1000 g this would mean a food intake of 143.74 kJ d ⁻¹ at 10°C, which corresponded with an ingestion of 1.43 kJ cm ⁻² d ⁻¹ .	Jobling 1988
$\left\{\dot{p}_{Am}\right\}$	1144 (1024)	$\{\dot{p}_{Am}\}\$ was calculated from $\{\dot{p}_{Xm}\}\$ under the assumption of losses due to digestion of 20%.	Brett & Groves 1979
ż	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	7330 (6565)	The energy density of full stores (muscle + liver) was on average 8700 J g ⁻¹ and the energy density of somatic tissues (whole body energy content minus liver) amounted 4000 J g ⁻¹ . This suggested an $[E_m]$ of at least ~ 4700 J cm ⁻³ . However, the	Jørgensen & Fiksen 2006 This paper
		assumption that \dot{v} would be similar among related species would imply a $[E_m]$ in the order of 7330 for females and for males 6565 J cm ⁻³ .	
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper

Myoxocephalus scorpius

Symbol	Value	Description	Reference
T_{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.230	The shape coefficient was estimated from length–wet mass data of juveniles (10 - 20 cm total length).	M. Fonds unpublished data.
L _{max}	60 (51)	For males a maximum size of 85% of that of a female was assumed.	This paper
[<i>p</i> _M]	23.8	Maintenance requirements were calculated from the relationship between daily food intake and daily growth at different rations. Daily growth was zero at a food level of $37.2 \text{ J} \text{ d}^{-1}$ per gram metabolic mass and for a fish with a wet mass of 11 g (and a metabolic mass of 7.04 g), this means a maintenance rate of 262 J d ⁻¹ or 23.8 J cm ⁻³ d ⁻¹ .	Fonds et al. 1989
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper
К	0.85 (0.95)	For females, kappa was estimated via the formulae of maximum volumetric length. For males a value of 0.95 was taken.	This paper
$\{\dot{p}_{Xm}\}$	481 (366)	Maximum food intake of 350 J d ⁻¹ per gram metabolic mass. For a fish with a wet mass of 11 gram (and a metabolic mass of 6.81 g) this would mean a maximum food intake of 2383 J d ⁻¹ or a { \dot{p}_{Xm} } of 481.8 J cm ⁻² d ⁻¹ . For males, { \dot{p}_{Xm} } was estimated from { \dot{p}_{Am} } under the assumption of losses due to digestion of 20%.	Fonds et al. 1989
$\left\{ \dot{p}_{Am} \right\}$	385 (293)	For females, $\{\dot{p}_{Am}\}$ was calculated from $\{\dot{p}_{Xm}\}$ under the assumption of losses due to digestion of 20%; for males it was estimated via the formulae of maximum volumetric length.	Brett & Groves 1979
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	2470 (1880)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for both sexes.	This paper
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper

Zoarces viviparous

Symbol	Value	Description	Reference
T_{ref}	14	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.157	The shape coefficient was estimated from length–wet mass data of juveniles (7 - 20 cm total length).	M. Fonds unpublished data.
$L_{\rm max}$	50 (42)	For males a maximum size of 85% of that of a female was assumed.	This paper
[<i>p</i> _M]	62	Maintenance requirements were calculated from the relationship between daily food intake and daily growth at different rations. Daily growth was zero at a food level of 107.3 J d^{-1} per gram metabolic mass. For a fish with a wet mass in the range of $10-30$ g (and a metabolic mass of 7.04 to 15.9 g), this would mean a maintenance rate in the range of 68.9–56.9 (average 62) J cm ⁻² d ⁻¹ . For males, the estimate of the maintenance rate appeared to be unrealistically high.	Fonds et al. 1989 This paper
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper
K	0.85 (0.95)	For females, Kappa was estimated via the formulae of maximum length. For males a value of 0.95 was taken.	This paper
$\{\dot{p}_{Xm}\}$	732 (366)	Maximum food intake of 551 J d ⁻¹ per gram metabolic mass was found. For a fish with a wet mass of 11 gram (and a metabolic mass of 6.81 g) this would mean a maximum food intake of 3024 J d ⁻¹ or a $\{\dot{p}_{Xm}\}$ of 731.8 J cm ⁻² d ⁻¹ . For males, $\{\dot{p}_{Xm}\}$ was estimated from $\{\dot{p}_{Am}\}$ under the assumption of losses due to digestion of 20%.	Fonds et al. 1989
$\left\{\dot{p}_{Am}\right\}$	585 (293)	For females, $\{\dot{p}_{Am}\}$ was calculated from $\{\dot{p}_{Xm}\}$ under the assumption of losses due to digestion of 20%; for males it was estimated via the formulae of maximum volumetric length.	Brett & Groves 1979
, v	0.228	Value assumed to be similar to that of plaice at 10°C and converted to 14°C based on an Arrhenius temperature of 7000 K.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	2565 (1285)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for both sexes.	This paper
$[E_v]$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper

Dicentrarchus labrax

Symbol	Value	Description	Reference
T _{ref}	20	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.217	The shape coefficient was estimated from length–wet mass data of juveniles (10 - 20 cm total length).	Coull et al. 1989
$L_{ m max}$	103 (85)	For males a maximum size of 85% of that of a female was assumed.	This paper
[<i>p</i> _M]	41	Maintenance requirements were based on growth experiments with different ration level at 25°C. Maintenance was deduced from the energy intake level at which growth was zero (56.8 J cm ⁻³ d ⁻¹ at 25°C). Zero growth means that still some energy (1 - κ) is stored in reproduction. However, on the other hand, in captivity activity levels in sea bass will be lower than in the field. Therefore, the volume-specific maintenance rate was not altered.	Peres & Oliva-Teles 2005
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper
К	0.85 (0.90)	For females, Kappa was estimated via the formulae of maximum length. This value seems realistic since gonad mass can account for more than 10% and sea bass is a fractional spawner meaning that reproductive investment underestimates κ . Males have a relatively high gonadosomatic index of above 5%. Therefore a κ of 0.90 was taken.	Kennedy and Fitzmaurice 1972 Rodriguez et al. 2001 This paper
$\{\dot{p}_{Xm}\}$	1493 (1080)	Food intake was based on Hidalgo et al. (1987) and in Person-Le Ruyet et al. (2004). At 20°C, maximum food intake was 0.025 g dry mass per gram fish mass and for a 23 g fish (surface area 8.08 cm ²) 0.575 g dry mass, which corresponded with 12.08 kJ. This means a maximum ingestion rate $\{\dot{p}_{Xm}\}$ of 1.493 J cm ⁻² d ⁻¹ . For males, $\{\dot{p}_{Xm}\}$ was estimated from $\{\dot{p}_{Am}\}$ under the assumption of 20% losses due to digestion.	Fonds et al. 1989 Hidalgo et al. 1987 Person-Le Ruyet et al. 2004
$\left\{ \dot{p}_{Am} \right\}$	1194 (864)	For females $\{\dot{p}_{Am}\}$ was calculated from $\{\dot{p}_{Xm}\}$ under the assumption of losses due to digestion of 20%. For males it was estimated via the formulae of maximum volumetric length.	Brett & Groves 1979 This paper
v.	0.310	Value assumed to be similar to that of plaice at 10°C and converted to 20°C based on an Arrhenius temperature TA of 5700 K.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	7600 (5540)	The maximum storage of females and males was based on the energy conductance \dot{v} value for plaice and on the estimated $\{\dot{p}_{Am}\}$ for both sexes.	This paper
$[E_v]$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper

Clupea harengus

Symbol	Value	Description	Reference				
T _{ref}	16	Reference temperature					
$\delta_{\scriptscriptstyle M}$	0.190	The shape coefficient was estimated from length–wet mass data directly after spawning in April.	Coull et al. 1989				
$L_{\rm max}$	43	Value assumed for females.	This paper				
$[\dot{p}_M]$	79.5	aintenance requirements were based on growth experiments at 16°C. Juvenile fish Bernreuther et a ith a wet mass of ~ 6.5 g had a maintenance rate of 517 J per fish per day or 79.5 J $m^{-3} d^{-1}$.					
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken.	This paper				
К	0.80	For the Atlantic herring from Canada, gonadosomatic index (GSI) of spring-spawners was around 20%. With the above parameter set, a GSI of 0.20 was achieved with a K of 0.80 (not shown).	Grégoire & Lefebre 2003				
$\left\{ \dot{p}_{Xm} \right\}$	574	Food intake was based on experiments at 16°C. Juvenile fish with a wet mass of ~ 6.5 g had a maximum food intake of 2000 J per fish per day or 574 J cm ⁻² d ⁻¹ .	Bernreuther et al. 2007				
$\left\{ \dot{p}_{Am} \right\}$	515	Assimilation was estimated from maximum food ingestion under the assumption of losses due to digestion of 10% as in sprat.	JP. Herrmann unpublished data				
<i>v</i>	0.280	Value assumed to be similar to that of plaice at 10°C and converted to 16°C based on an Arrhenius temperature TA of 8000.	This paper				
$\begin{bmatrix} E_m \end{bmatrix}$	1840	Body composition of metamorphosed herring showed a seasonal fluctuation from 2900 to 4800 J g ⁻¹ wet weight and in two-year old herring from ~ 5000 to 6000 J g ⁻¹ wet weight. This implied a maximum storage density of 6000 – 2900 = 3100 J cm ⁻³ . Under the assumption of a similar \dot{v} as in the other species at 10°C, this would imply a $[E_m]$ in the order of 1840 J cm ⁻³ for females.	Arrhenius & Hansson 1996 This paper				
$\left[E_{v}\right]$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper				

Sprattus sprattus

Symbol	Value	Description	Reference
T_{ref}	15	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.180	The shape coefficient was estimated from length–wet mass data directly after spawning in April.	Coull et al. 1989
$L_{ m max}$	16.5	Value assumed for females.	This paper
$[\dot{p}_M]$	45.8	Maintenance requirements were considered to be similar as in herring, a related species: 50.4 at 16°C or 45.8 at 15°C	This paper
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper
К	0.90	A maximum gonadosomatic index of 0.07 for both males and females was found and this would correspond with a κ of 0.90 (not shown).	Veiga 1976
$\{\dot{p}_{Xm}\}$	200	Food intake was determined based on laboratory experiments. At 15°C, YOY juvenile sprat (5-7 cm TL) consumed 330 nauplii per hour. With an energy content of 0.0272 J per nauplii, this means a maximum surface-area-specific ingestion rate of 136 – 266 J cm ⁻² d ⁻¹ .	JP. Herrmann unpublished data
$\left\{\dot{p}_{Am}\right\}$	180	Assimilation was estimated from maximum food ingestion under the assumption of losses due to digestion of 10%, between $123 - 240 \text{ J cm}^{-2} \text{ d}^{-1}$.	JP. Herrmann unpublished data
<i>v</i>	0.276	Value assumed to be similar to that of plaice at 10°C and converted to 15°C based on an Arrhenius temperature TA of 9300.	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	652	Under the assumption of a similar \dot{v} as in the other species at 10°C, this would imply a maximum storage $[E_m]$ in the order of 652 J cm ⁻³ for females.	This paper
$[E_v]$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper

Engraulis encrasicolus

Symbol	Value	Description	Reference	
T_{ref}	10	Reference temperature		
$\delta_{\scriptscriptstyle M}$	0.172	The shape coefficient was estimated from length-wet mass data of juveniles.	Pecquerie 2008	
$L_{\rm max}$	20 (17)	For males a maximum size of 85% of that of a female was assumed.	Pecquerie 2008	
[ṕ _M]	19	The mass loss during the night in the larval growth model could be considered as an approach for metabolism. At 10°C, the losses were 0.003 dry mass per h during the night (Fig. 5). For a 6 mm larvae with a dry mass of 60 µg (Theilacker 1987), this means a loss of 4.32 µg dry mass d ⁻¹ or, considering a caloric value of larval tissue of 185.2 µg dry mass cal ⁻¹ (Urtizberea et al. 2008), 0.02333 cal d ⁻¹ , corresponding with 0.00558 J d ⁻¹ . Assuming a wet–dry mass ratio of 5 to 6 this means a volume-specific maintenance rate $[\dot{p}_M]$ between 15.5 and 18.6 J cm ⁻³ d ⁻¹ . In line with the other species, the value at the upper range was taken.		
$\begin{bmatrix} E_G \end{bmatrix}$	5600	The costs for structure were assumed to be similar in fish species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper	
К	0.65	The value of κ results from calibration exercises to best fit the lengths-at-age and weight-at-length data.	Pecquerie 2008	
$\{\dot{p}_{Xm}\}$	112	Ingestion was estimated from maximum food assimilation under the assumption of losses due to digestion of 10% as in sprat.	JP. Herrmann unpublished data	
$\left\{\dot{p}_{Am}\right\}$	101	Based on the formulae for maximum volumetric length, a κ of 0.65 and $L_{max} = 20$ cm (V $L_{max} = 3.42$ cm) implies that the ratio between $\{\dot{p}_{Am}\}$ and $[\dot{p}_{M}]$ is 5.26. This results in a $\{\dot{p}_{Am}\}$ of 100.6 J cm ⁻² d ⁻¹ for females.	Brett & Groves 1979 This paper	
<i>v</i>	0.156	Value assumed to be similar to that of plaice.	This paper	
$\begin{bmatrix} E_m \end{bmatrix}$	645	Under the assumption of a similar \dot{v} as in the other species, this would imply a maximum storage $[E_m]$ in the order of 645 J cm ⁻³ for females.	This paper	
$\begin{bmatrix} E_v \end{bmatrix}$	4000	The energy content of structure was assumed to be similar in related species and the value of plaice was taken. The value was expected to be similar for males and females.	This paper	

Symbol	Value	Description	Reference
T_{ref}	10	Reference temperature	
$\delta_{\scriptscriptstyle M}$	0.213	The shape coefficient was based on the total length-wet mass relationship.	Van Lissa 1977
L _{max}	9.5 (7.5)	Maximum carapace width was predicted based on observations in the German Wadden Sea.	Tiews 1970
$[\dot{p}_M]$	15.9	The estimate was based on parameter validation.	Campos et al. 2009
$\begin{bmatrix} E_G \end{bmatrix}$	2500	The estimate previously published for <i>C. crangon</i> was taken.	Campos et al. 2009
К	0.80 (0.95)	Reproductive investment in females was at least 17 % in July and hence a value of 0.80 was taken. For males a value of 0.95 was taken.	J. Campos and J. IJ. Witte unpublished data.
$\left\{ \dot{p}_{Xm} \right\}$	59 (38)	$\left\{ \dot{p}_{_{Xm}} ight\}$ was calculated under the assumption of 33% losses due to digestion.	Campos et al. 2009
$\left\{ \dot{p}_{Am} \right\}$	38 (25)	$\left\{ \dot{p}_{_{Am}} ight\}$ was calculated according to the formulae of maximum volumetric size.	Campos et al. 2009
<i>v</i>	0.045	Value assumed.	Campos et al. 2009
$\begin{bmatrix} E_m \end{bmatrix}$	850 (566)	The maximum storage of females was based on experimental data by Fonds (unpubl.) and field data for the Baltic (Swaniawska 1983). For males it was calculated based on the energy conductance \dot{v} value for females and on the estimated $\{\dot{p}_{Am}\}$ for males.	Campos et al. 2009
$\left[E_{v}\right]$	1750	The energy content of structure was based on experimental data by Fonds (unpubl.). The value was expected to be similar for males and females.	Campos et al. 2009

Carcinus maenas

Symbol	Value	Description	Reference
T_{ref}	10	Reference temperature	
$\delta_{_M}$	0.581	The shape coefficient was based on the carapace width-AFDM relationship (in combination with an AFDM/wet mass ratio of 17.4%.	Klein Breteler 1975 V. Freitas unpublished data
$L_{\rm max}$	8.5 (10)	For females, a maximum carapace width of 85% of that of a male was assumed.	This paper
$[\dot{p}_M]$	15.9	The estimate for <i>C. crangon</i> was taken.	This paper
$\begin{bmatrix} E_G \end{bmatrix}$	2500	The estimate for <i>C. crangon</i> was taken.	This paper
К	0.80 (0.95)	For both females and males the estimate for <i>C. crangon</i> was taken.	This paper
$\left\{ \dot{p}_{Xm} \right\}$	147.2 (146.0)	The estimate of food intake in the field (22.04 mg AFDM per gram AFDM crab at 17°C) by Afman (1980) resulted in a value for $\{\dot{p}_{Am}\}$ of 168.8 at 17°C or 98.1 J cm ⁻² d ⁻¹ at	Afman 1980
		10°C, for a female which are in the same order of magnitude as the estimates for other species. The values were corrected based on the formulae of maximum volumetric size.	
$\left\{ \dot{p}_{Am} \right\}$	98 (97)	${\dot{p}}_{Am}$ was calculated from ${\dot{p}}_{Xm}$ under the assumption of losses due to digestion of 33% similar as in <i>C. crangon.</i>	This paper
<i>v</i>	0.045	Value assumed to be similar to that of <i>C. crangon</i> .	This paper
$\begin{bmatrix} E_m \end{bmatrix}$	2205 (2185)	The maximum storage of females and males was based on the energy conductance \dot{v} value for <i>C. crangon</i> and on the estimated $\{\dot{p}_{Am}\}$ for both sexes.	This paper
$[E_v]$	1750	The energy content of structure was assumed to be similar in related species and the value of <i>Crangon crangon</i> was taken. The value was expected to be similar for males and females.	This paper

2.2. Parameter calibration and validation

Plaice *Pleuronectes platessa.* Experimental data on maximum growth of juvenile plaice in relation to water temperature were published by Fonds et al. (1992). DEB model simulations showed a good correspondence (similar shape and magnitude of the growth curve) with laboratory observations of juvenile maximum growth for both females and males. In the simulations however, the reduction in growth at the higher temperature range started later than in the observations. Females showed a faster simulated growth rate than males.

Dab *Limanda limanda.* Experimental data on maximum growth of juvenile dab in relation to water temperature were published by Fonds and Rijnsdorp (1988). DEB model simulations for females and males showed a good correspondence with the laboratory observations.

Flounder *Platichthys flesus.* Information on juvenile growth under optimal food conditions was published by Fonds and Rijnsdorp (1988). A comparison of DEB model simulations with laboratory observations showed for both males and female flounder a good fit.

Sole Solea solea. Data on juvenile growth of sole in relation to temperature (5-20°C) was published by Fonds and Rijnsdorp (1988). Simulated growth rates were slightly lower than observed values. This might be caused by a slight underestimation of maximum length. Nevertheless, no changes in the DEB parameters values were made.

Gobiidae *Pomatoschistus microps* and *P. minutus*. Only few data were available for gobies. The maintenance rate costs estimated from the ingestion data available in the literature resulted in a high value (45 J cm⁻³ d⁻¹) compared to other species. A maintenance rate of about half the initial value was considered to be more realistic and in line with data for the other species. The reduction in $[\dot{p}_M]$ led, as a result, to lower values for ingestion and assimilation. Additional data on oxygen consumption for both species (Penning de Vries 1969) resulted in a suggestion that the Arrhenius temperature published (~ 3000 K) (Freitas et al. 2007) was slightly too low, therefore a value of 3500 K was adopted. The same parameters were taken for *P. minutus*. For a *P. microps* individual in the size range of 2-3 cm, growth rates predicted by the DEB model using this parameter set seem too low compared with the field growth reported in Atlantic waters (Healey, 1972). However, due to a lack of experimental data on maximum growth in relation to water temperature, no validation of the parameter estimates could be done.

Cod *Gadus morhua.* Information on maximum juvenile growth of cod in relation to water temperature can be found in Fonds and Rijnsdorp (1988). There was a good correspondence with DEB simulations for both males and females. The optimal growth rate might be slightly overestimated suggesting a small overestimation of T_A , however we did not find it necessary to change the parameter estimates.

Bull-rout *Myoxocephalus scorpius.* Fonds et al. (1989) published information on the maximum growth rate of juveniles in relation to water temperature. DEB simulations overestimated growth rates. All parameters appeared to be based on reliable estimates (maintenance, assimilation, κ) or in line with other species (cost for structure, energy content of structure), suggesting that $[E_m]$ was the only parameter

that could be changed. Increasing the values for both females and males by a factor 2 to respectively 5000 and 3800 J cm⁻³ resulted in simulations that agreed with observations.

Eelpout *Zoarces viviparous.* Information on juvenile growth of eelpout was published by Fonds et al. (1989). For both females and males, the DEB simulations resulted in too steep increase with temperature. Therefore, T_A estimate of 7700 (Fonds et al. 1989) was lowered to 5000 K. At the higher tolerance range, DEB simulations showed a very steep decrease in rate and as a consequence T_{AH} was lowered to 5000 K. With these two adaptations, for both females and males, the pattern of the simulations was similar to that of the observed growth rates. The fact that eelpout are viviparous fish caused problems with the estimation of the maintenance rate (and hence the assimilation and ingestion rate) and κ . After mating in August-September, young are born between December and February fully formed at a length of ~ 4 cm, nourished by special tissues of the ovary. Reproductive output in the Dutch Wadden Sea for a female of 20 cm is on average 24 offspring (Witte NIOZ pers. comm.). Assuming a similar shape of 0.157, the offspring represented a mass of 5.95 g. This mass has been built up over a period of 6 months and has increased maintenance load for the female. These costs included the costs for structure (33.2 kJ), maintenance costs (roughly 40 J cm⁻³ d⁻¹ for 180 d, assuming a similar rate as for cod, see below) and reserves (maximum of 10 kJ), which were in total ~ 65 kJ or 9 J cm⁻³ d⁻¹ for a female with a mass of 20 cm³. During the period of reproduction (6 months) this means a contribution of ~ 15 - 20 J cm⁻³ d⁻¹. A better alternative would be to incorporate this energy flux in κ . The consequence is that in males the maintenance rate is overestimated. Therefore, a similar rate as for cod was assumed. For females, a higher value (+ 15 J cm⁻² d⁻¹) was taken in line with the viviparous character of the species (see above). This means that also the values of assimilation, ingestion and maximum storage density were adjusted.

Sea bass Dicentrarchus labrax. Information on juvenile growth was published by Person-Le Ruyet et al. (2004). DEB simulations resulted in good fit with the experimental data, without a need to change parameter values.

Herring *Clupea harengus.* The estimate of the upper temperature tolerance limit was very low and based on only a few data. The value was increased to 297 K more in line with the other cold water species. The difference in food intake of juvenile herring of about three times between 6.5 and 14.5°C (De Silva and Balbontin 1974) suggested an Arrhenius temperature in the order of 8000 K. For the relationship between oxygen uptake and temperature in larvae a Q_{10} of 2.6 (Almatar 1984) is given, corresponding with a T_A of 7400 K. A maximum size in the order of 43 cm, a shape coefficient of 0.190 and a κ of 0.80, resulted in a ratio between maximum surface-area-specific assimilation and volume-specific maintenance of 10.2, while the estimates of ingestion and maintenance only differ by a factor 7.5. The estimate of maintenance was high compared to the other species. Therefore the maintenance rate was lowered to 50.4 J cm⁻³ d⁻¹, which corresponds with 28 J cm⁻³ d⁻¹ at 10°C and is in line with the estimates for other species. There are no experimental data to compare the simulated growth

rates with, in relation to water temperature. No reproductive data are available for males and, therefore, only estimates for females were calculated.

Sprat *Sprattus sprattus.* The estimate of the upper temperature tolerance limit was very low and based on only a few data. The value was increased to 300 K in line with other species. There were no experimental growth data to validate the parameter set.

Anchovy *Engraulis encrasicolus.* Pecquerie (2008) calculated that the average water temperature experienced by anchovy was about 13°C. Observed growth rates in the field suggested a growth of about 8 cm in 100 days (Pecquerie, 2008). At this temperature a maximum growth rate of ~ 0.25 mm d⁻¹ was simulated corresponding with 7 cm per year. There were no experimental data on growth in relation to water temperature to validate the parameter estimates and therefore only estimates for females were calculated.

Brown shrimp *Crangon crangon.* A comparison of DEB model simulations with laboratory observations of maximum growth of juvenile shrimps (M. Fonds unpublished data cited in Kuipers and Dapper 1981) indicated a difference in slope suggesting that the estimate of the Arrhenius temperature of about 7351 K (Freitas et al. 2007) might be too low and would be in the order of T_A = 9000 K. Experimental data were slightly above the DEB simulations for female shrimp. However, this difference was considered as too small to justify an adaptation of parameter values. Females showed a higher growth rate than males.

Shore crab *Carcinus maenas.* There are only a few experimental growth data of juvenile shore crabs to validate the DEB parameters. DEB simulated growth of 0.2 mm d⁻¹ for small <2cm female crabs at 20°C, fitted those found by Klein Breteler (1975). There was a suggestion that the Arrhenius temperature should be higher, however the data were too few to justify an adaptation.

3. Parameter estimation assuming $V_E \neq 0$

This section is based on the *add-my-pet* action which aims to connect easy-to-measure quantities to parameters in a consistence and objective way. How far one can go with parameter estimation depends greatly on how much information is available for the species under consideration. The first step avoids the estimation of parameter values and works with very little information namely only with maximum body length and weight data. The starting point is the parameter set of a "generalized animal" and the basic procedure is exemplified for plaice *Pleuronectes platessa*.

- Start by downloading <u>DEBtool</u>. Copy <u>pars_my_pet</u> to the location where you want to work. Rename the file to the latin name of the species '*pars_Pleuronectes_platessa*' (see below).
- Create a path from your work location to *Debtool* so that Octave (or Matlab) can find the *Debtool* routines it needs.

- Temperature is set by default to a reference temperature (293 K) for comparison purposes. Adjust the actual body temperature, by selecting a temperature that lies within the species-specific tolerance range (for plaice, 288K).
- Leave all parameters at their default values and play with the scaling parameters: zoom factor z and the shape coefficient $\delta_M \cdot z$ controls the maximum length via the specific assimilation and it also affects life stage parameters and ageing parameters. In combination with the zoom factor, the shape coefficient controls the length-weight relationship, where weight has contributions from reserve. At constant energy conductance, the consequence of an increase in the zoom factor is an increase in the specific assimilation rate and so a rise in the maximum reserve capacity and in the contribution of reserve to weight.
- Information available for plaice indicates a maximum length of 78 cm and a maximum wet weight of around 5 Kg (wet).
- Adjust the zoom factor to match a maximum dry weight of 500 g (assuming a wet to dry mass ratio of 10%). Run the file and study the output in terms of maximum dry weight. We arrive at z = 9.4 which represents the maximum volumetric length.
- The fraction between the maximum volumetric length and the maximum physical length gives the shape coefficient δ_M = 9.4/78 = 0.121.
- Maximum surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ is computed from the zoom factor, the specific maintenance costs and the allocation fraction to soma. It is proportional to the maximum structural length and hence it cannot be edited.
- The specific maturity at birth E_H^b and at puberty E_H^p (controlling respectively, the timing of switching assimilation and allocation) depend on the zoom factor as they are proportional to the maximum structural length; however since these are highly species-specific they probably need adjustment. Tune these parameters to match size at birth and at puberty reported in the literature. Ageing acceleration \ddot{h}_a is also affected by the zoom factor and thus should be adjusted to match mean life span.
- Study the output statistics which correspond to the implied properties for the species.

The more general and objective way to arrive at adjustments of the parameter values of the generalized animal for a species is to minimize the weighted sum-of-squared deviations between DEB predictions and known data for species. This applies to species for which more information is available (often commercial species) but, for species relatively unstudied it is not possible to proceed further. The general methodology for estimation of DEB parameters from data is described in Van der Meer (2006); the aim is to estimate all parameters using circumstantial information (real data and pseudo-data) and the body-size scaling relationships of the DEB theory.

The *mydata_my_pet* file contains both "real data" (information for the species under consideration) and "pseudo-data" (information from the generalized animal). These are combined and treated as facts. The relative confidence of these facts is quantified by the *weight coefficients* which are added to the data. The weight coefficients are chosen to be inversely proportional to the squared facts' values to avoid dimensional problems and effects of units, such as centimeters (cm) versus millimeters (mm) or meters (m). A good general strategy is to increase the weight coefficient of the real data relative to the pseudo-data. In this way, the fit to the real data will be better than that to the pseudo-data. Choosing the best weight coefficients is relatively subjective and there is no satisfying general strategy. However, the aim should be getting the best possible fit between observations and parameters, keeping in mind that parameter values should make physiological sense. The routine used to find the best fit is *nmregr* found in *debtool/lib/regr* of the DEBtool software. It minimizes the weighted sum-of-squared deviations between the data (real and pseudo) and the expected values based on the output of *get_pars_my_pet*.

The basic steps are:

- Copy, paste and edit a *mydata_my_pet* file. Replace data by that of your species. Add references and comments to identify where the datasets come from.
- Copy, paste and edit the corresponding get_pars_my_pet file that makes all calculations and computes the expected values.
- Look in *DEBtool/animal/statistics* if you need more expected values.
- Run the mydata_my_pet file and copy the resulting parameter estimates to the pars_my_pet file
- Run the *get_pars_my_pet* file and analyze the reported implied properties. If an output statistics presents an unrealistic value, include a realistic value for it in the *mydata_my_pet* file, include its computation in *get_pars_my_pet* and re-estimate the parameters.

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Chapter 6

Food limitation in epibenthic species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes platessa*

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ABSTRACT: The Balgzand intertidal is an important nursery area for early life stages of various epibenthic crustacean and fish species. Especially in summer, extremely high numbers of individuals occur. This study analyses whether these high densities in summer lead to food limitation using 0-group plaice Pleuronectes platessa L. as a model species. Between 1975 and 2007, this species was quantitatively monitored during 20 yr. The aim of this study is twofold: (1) a statistical analysis of field growth in relation to density, whereby negative density-dependent growth is considered as an indication of intraspecific competition, and (2) a comparison of observed field growth with predicted maximum growth according to the dynamic energy budget (DEB) model, to detect whether growth reduction occurs during the growing season as an indication of interspecies competition. The statistical analysis indicated no negative density-dependent growth during the whole growing season, suggesting the absence of intraspecies competition for food. The comparison of observed growth with DEB-predicted maximum growth showed that field growth was lower than the possible maximum, and that the difference increased over time until about the end of July, suggesting interspecies competition for food in summer. The stabilization in growth rate from July onwards might be related to a change in food quality: a shift from small bivalve siphons as main food items to larger tail tips of the lugworm Arenicola marina. These findings illustrate that not only food quantity but also food quality affects growth rates, at least in 0-group plaice.

KEY WORDS: Plaice \cdot Pleuronectes platessa \cdot Wadden Sea \cdot Growth \cdot Dynamic energy budget \cdot Intertidal \cdot Food quantity \cdot Food quality \cdot Food limitation

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INTRODUCTION

Shallow coastal systems are considered to be hostile environments, subject to strong variations in abiotic parameters that determine a relatively low species diversity (for overview see Goodall 1983). Regardless, shallow areas are used as nursery grounds by various epibenthic fish and crustacean species. Only a few species account for most of the numbers and biomass in shallow coastal systems, and these species are widely distributed (Haedrich 1983, Wolff 1983). This means that over a large latitudinal gradient, the same group of species is dominating. Along the European coast, the most abundant epibenthic species include the mobile invertebrates *Crangon crangon* and *Carcinus maenas* and the fishes *Pomatoschistus minutus*,

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P. microps, and the juvenile flatfishes *Pleuronectes* platessa, *Platichthys flesus*, *Limanda limanda* and *Solea solea* (Zijlstra 1972, Jensen & Jensen 1985, Pihl 1985, Ansell et al. 1999, Amara 2003, Amara & Paul 2003, Freitas et al. 2010a).

For those species, shallow coastal areas are typically important habitats as nursery grounds for early life stages due to presumed favourable conditions for growth and survival (Zijlstra 1972, Bergman et al. 1988). In general, juveniles arrive and settle in the intertidal with rising temperatures in spring and disappear with decreasing temperatures at the end of the growing season, emigrating to deeper waters. As a result, high densities (10s to 1000s of ind. m^{-2}) of epibenthic consumers build up in these shallow areas in the course of the season. Since the various species have overlapping food spectra, these high numbers, and hence high biomass, have raised questions about their growth conditions, suggesting that food might be limited by either intra- and/or interspecies competition (Pihl 1985). For most species, growth is difficult to monitor due to more or less continuous settlement cohorts. The various flatfish species are an exception with, in general, a single cohort of settling larvae in spring. Therefore, flatfishes have become popular model species for the analysis of growth conditions in coastal nurseries, whereby the basic approach has been the comparison of observed field growth with predictions from a laboratory-based relationship of maximum growth in relation to water temperature (Zijlstra et al. 1982, van der Veer et al. 1991, 2001b, Jager et al. 1995). A potential problem with these growth models is that they are applicable over a restricted size range corresponding in most areas with the spring-early summer growth period only, although highest temperatures and biomasses occur in the summer-autumn period.

In most cases, the growth rate of juvenile flatfish in the field in spring and early summer was at a maximum level and only determined by temperature, as found for the Balgzand area in the western Dutch Wadden Sea, Loch Ewe, Scotland and Filey Bay, England (Zijlstra et al. 1982, van der Veer 1986), in Swedish bays (van der Veer et al. 1990), in the Dollard, Netherlands (Jager et al. 1995) and during part of the year in Port Erin Bay, Irish Sea (Nash et al. 1994). In some cases, negative density-dependent growth (Modin & Pihl 1994) or reduced growth was observed, due to poor food conditions (van der Veer & Witte 1993, Berghahn et al. 1995). Back-calculation of juvenile plaice growth based on otolith microstructure analysis showed an increase in growth rate from the 1950's onwards (Rijnsdorp & van Leeuwen 1992), which was suggested to be related to an increase in availability of food in the coastal zone over that time period. However, for the period mid-June until September, observed growth rates of juvenile flatfish (plaice) in the field were much lower than the predicted maximum values, a phenomenon observed at Balgzand (Teal et al. 2008), the Dollard (Jager et al. 1995), the Irish Sea (Nash et al. 1994) as well as in northern Norway (Freitas et al. 2010a). This discrepancy between maximum possible and observed growth might suggest food limitation in summer due to the outburst of gobiids and crustaceans (Kuipers & Dapper 1984), or it might be an experimental bias, since the plaice population from July onwards starts outgrowing the range where the maximum growth model can be applied (van der Veer et al. 2009). Solving the question of food and growth conditions in summer would require extensive laboratory experiments with larger-sized fish.

In this paper, an innovative approach that does not suffer from this size limitation, and which can be applied for the whole growing season, including the summer-autumn period, is used: the standard dynamic energy budget (DEB). The DEB is based on surfaceand volume-related processes and provides a framework describing the quantitative aspects of energy flows through an organism (Ross & Nisbet 1990, Kooijman 2010). The energetics of a species is captured in a single model, where intraspecies variability (in size or length) is caused by differences in state variables (as a result of differences in environmental conditions, i.e. temperature, food), and interspecies variability is caused by differences in parameter values (Kooijman 2010). Applying the DEB model requires a set of species-specific parameters, which can be estimated from the result of experimental studies (van der Veer et al. 2006). For flatfishes, parameters were published in van der Veer et al. (2001a, 2009) and Freitas et al. (2010b). Once such a set is available, maximum possible growth (corresponding with a model situation of ad libitum food) can be estimated in relation to prevailing temperature conditions and compared with observed growth in the field. Subsequently, observed and predicted growth can be compared and used as an indicator of food conditions and hence of competition.

The present study analyses the food conditions in a temperate coastal nursery area in summer in the Balgzand intertidal area in the western Dutch Wadden Sea, where plaice *Pleuronectes platessa* is used as a model species. Between 1975 and 2007, 0-group plaice has been monitored quantitatively during 20 years. The aim of this study is twofold: (1) a statistical analysis of field growth in relation to density, whereby negative density-dependent growth is considered as an indication of intraspecific competition and (2) a comparison of observed field growth with predicted maximum growth according to the DEB model, to detect whether growth reduction occurs during the growing season as an indication of interspecies competition.

MATERIALS AND METHODS

Field observations. Seasonal patterns of 0-group plaice were monitored in the Balgzand intertidal area in 20 yr during the period 1975 to 2007. Sampling generally started in February and continued at frequent intervals (2 to 4 wk) until about October. During each survey, 9 transects distributed over the area were sampled, each consisting of 4 stations (Fig. 1). Sampling occurred within a 3 h period around high tide, during which the flatfish population is assumed to be randomly distributed over the area (Kuipers 1977). Hauls were taken during the day with a 1.9 m beam trawl with 1 tickler chain, a net mesh size of 5×5 mm, towed by a rubber dinghy with a 25 hp outboard motor at a speed of ~35 m min⁻¹ (Riley & Corlett 1966). Location of the hauls was initially established by fixed poles at the beginning of each transect and later by GPS. Exact length of the hauls was assessed with a meter wheel fitted to the trawl. Occasionally, some stations could not be sampled due to extreme weather conditions (wind stress, reduced water depths). During all cruises, except for 1975 and 1976, bottom water temperature measurements were taken to the nearest °C. For 1975 and 1976, water temperature was estimated from a nearby station, Marsdiep (Fig. 1), based on a linear regression model for the mean monthly Marsdiep temperatures for 1977 to 2002 (van Aken 2003) and those



Fig. 1. The Balgzand intertidal area in the western Dutch Wadden Sea. Each transect consisted of 4 hauls (**O**). Thin lines indicate the low water mark, dashed lines the high water mark

of the Balgzand area. The regression model ($T_{Marsdiep}$ = $1.02 \times T_{Balgzand}$ + 0.36) indicated a strong relationship (R^2 = 0.95, n = 228, p < 0.01) between temperature at high water at Balgzand ($T_{Balgzand}$, °C) with that of the nearby Marsdiep station ($T_{Marsdiep}$, °C).

Catches were immediately stored in a 4 % formalin solution (until 1990) or deep-frozen (from 1991 onwards) and sorted within a few days. The 0-group plaice present in the catches were preserved in 70% ethanol and, within a few days, total length (TL) was measured to the nearest mm. No correction for shrinkage was applied. For each haul, numbers caught were corrected for size-selective mesh and catch efficiency after Kuipers (1975) and Dapper (1978) and then converted into ind. per 1000 m² (ind. $[10^3 m^2]^{-1}$). The arithmetic mean density and mean size in TL, considering all stations sampled during a cruise, was taken as an index of the population (cf. Kuipers 1977, Zijlstra et al. 1982).

To eliminate a bias in growth rate estimates due to settlement of larvae in spring, data analysis was restricted to the period from peak settlement in May, which generally coincided with a peak in maximum abundance, and until the end of September, to limit the potential bias introduced by autumn emigration of juveniles. Daily growth in length (dL_i cm d^{-1}) was estimated from the changes in population mean TL between consecutive sampling periods (cf. Zijlstra et al. 1982, van der Veer 1986).

DEB model. The DEB theory (Kooijman 2010) describes energy flows through an animal (Fig. 2) under conditions in which food densities and temperatures vary. Food uptake is assumed to follow a functional response relationship with food density. In line with observations on juvenile flounder (Kiorbøe 1978, Mattila & Bonsdorff 1998), a Holling type-II hyperbolic function seems to be sufficient to quantitatively reproduce ingestion rate in plaice. Environmental food conditions are described in the form of a scaled functional response f, where 0 reflects starvation, and 1 optimal food conditions (feeding ad libitum). Food uptake is proportional to organism surface area and converted into reserves with a constant efficiency. Mobilized reserves are allocated to growth, to maintenance of existing body tissues (somatic and gonadal) and to maturation or reproduction. A fixed fraction (κ rule) of reserve is allocated to growth plus somatic maintenance while the remaining fraction $(1-\kappa)$ is allocated to maturity maintenance plus maturation and/or reproduction. Maintenance has priority over growth, and hence, growth ceases when all reserve that is allocated to somatic maintenance plus growth is required for somatic maintenance. The mobilization rate of reserve is proportional to the ratio of reserve density (i.e. the ratio of reserve and body structure) and volumetric length (the cubic root of structure's volume), and the



Fig. 2. Energy flow through an organism in the DEB model, after van Haren (1995). Rates = 1: ingestion (uptake), 2: defecation, 3: assimilation, 4: demobilization of energy into reserves, 5: mobilization of energy from reserves, 6: utilization, 7: growth, 8: maintenance, 9: maturation maintenance, 10: maturation, 11: reproduction. Rounded boxes: sources or sinks, Squares: state variables. κ and $1-\kappa$: fractions of energy allocated to, respectively, growth + somatic maintenance and maturity maintenance + maturation and/or reproduction

energy costs of maintenance are proportional to the volume of the structure.

With a set of species-specific parameters, the DEB model can be applied for all combinations of fish size, food conditions and temperature. At constant food densities, the reserves are in equilibrium with the environment and consequently growth of structural biovolume represents a weighted difference between surface area and volume, which corresponds with the von Bertalanffy growth curve (Kooijman 2010):

$$\frac{d}{dt}L = \dot{r}_{\rm B}(L_{\infty} - L) \tag{1}$$

The parameters L_{∞} (ultimate size; cm) and $\dot{r}_{\rm B}$ (von Bertalanffy growth rate constant, d⁻¹) can thus be written as a combination of DEB parameters:

$$L_{\infty} = f \frac{L_{\rm m}}{\delta_{\rm M}} = f \frac{\dot{\mathbf{v}}}{g \dot{\mathbf{k}}_{\rm M} \delta_{\rm M}}$$
(2)

$$\dot{r}_{\rm B} = \frac{1}{3/\dot{k}_{\rm M} + 3fL_{\rm m}/\dot{\nu}} = \frac{\dot{k}_{\rm M}/3}{1+f/g}$$
(3)

where *f* is the scaled functional response (dimensionless), $\delta_{\rm M}$ is the shape coefficient (-), $L_{\rm m}$ the maximum volumetric length an individual can reach (cm), $\dot{\bf v}$ is the energy conductance (cm⁴ d⁻¹), a parameter related to reserve dynamics, *g* is the investment ratio (-) that stands for the costs of new biovolume relative to the maximum potentially available energy for growth and maintenance, and $\dot{k}_{\rm M}$ is the maintenance rate coefficient (d⁻¹), which stands for the ratio of somatic maintenance costs to structure. This means that the DEB theory gives a physiological interpretation to the von Bertalanffy parameters (see Kooijman 2010). Justification for applying Eq. (1) for plaice is the fact that plaice growth follows von Bertalanffy growth (van der Veer et al. 2001a).

Changes in food conditions (f) are expected to affect both L_{∞} and \dot{r}_B , while temperature conditions affect \dot{r}_B only due to the temperature dependence of physiological rates. In the DEB model, the temperature effect is based on an Arrhenius type relation that describes the rates at ambient temperature, $\dot{k}(T)$, as follows:

$$\dot{k}(T) = k_{1} e^{\left(\frac{T_{A}}{T_{1}} - \frac{T_{A}}{T}\right)} \cdot \frac{1 + e^{\left(\frac{T_{AL}}{T_{1}} - \frac{T_{AL}}{T_{L}}\right)} + e^{\left(\frac{T_{AH}}{T_{H}} - \frac{T_{AH}}{T_{1}}\right)}}{1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_{L}}\right)} + e^{\left(\frac{T_{AH}}{T_{H}} - \frac{T_{AH}}{T}\right)}}$$
(4)

where *T* is absolute temperature (K), T_{AL} and T_{AH} are Arrhenius temperatures (K) for the rate of decrease at the lower (T_L) and upper (T_H) boundaries, respectively. T_1 is the reference temperature (*k*), T_A the Arrhenius temperature (*k*), and k_1 is the rate at the reference temperature.

Data analysis. To test for intraspecies competition, the variability in the observed growth rate dL (cm d^{-1}) between time t = i and t = i + 1 was analysed as a function of mean population length, density and water temperature at t = i. A significant negative relationship of population density with growth was considered as an indication of intraspecies competition.

Secondly, for all field observations, dL was expressed as the ratio of maximum possible growth predicted by the DEB model. Differences in the ratio over time, especially a decrease in summer onwards was considered as an indication of interspecies competition.

Field observations: Prior to the statistical analysis of the field growth rates, a data exploration was carried out following the protocol described in Zuur et al. (2010). Potential outliers were checked using Cleveland dotplots, and multi-panel scatterplots were used to identify the type of relationships between variables (e.g. linear versus non-linear) and the presence of collinearity among covariates.

To investigate the relationships of field growth rates (*DL*) with temperature, plaice mean length and population density, a linear regression model was applied:

$$DL_{ij} = \alpha + \beta_1 \times \text{Length}_{ij} + \beta_2 \times \text{Density}_{ij} + \beta_3 \times \text{Temperature}_{ii} + \epsilon_{ij}$$
(5)

where DL_{ij} is the growth rate (cm d⁻¹) between sampling day *j* and *j* + 1 in year *i*, Length (cm), Density (ind. $[10^3 \text{ m}^2]^{-1}$) and Temperature (°C) are covariates, and ε_{ij} is the residual. Model validation showed that the residuals exhibited some heterogeneity (a decrease in variation along day of the year) and presented a year effect. To avoid the violation of heterogeneity and dependence problems, linear mixed effects models were applied (Zuur et al. 2009) in which year was used as random intercept:

$$DL_{ij} = \alpha + \beta_1 \times \text{Length}_{ij} + \beta_2 \times \text{Density}_{ij} + \beta_3 \times \text{Temperature}_{ij} + a_i + \varepsilon_{ij}$$
(6)

The random intercept a_i is assumed to be normally distributed with mean 0 and variance σ^2_{year} , and ε_{ij} is normally distributed with mean 0 and variance σ^2_{ε} . The random intercept a_i is imposing a temporal correlation structure on the observations within a year, namely the so-called compound symmetric correlation (Pinheiro & Bates 2000). This means that the correlation between 2 observations from the same year is equal to ρ , where ρ (also called the intra-class correlation [ICC]) is estimated by:

$$\rho = \frac{\sigma_{\text{year}}^2}{\sigma_{\text{year}}^2 + \sigma_{\epsilon}^2}$$
(7)

Because the observed time series within a year are short, irregularly spaced, and unbalanced over the years, a more sophisticated correlation structure was not considered.

We also considered smoothing equivalents of the model in Eq. (6). In such additive mixed effects models (AMMs), the parametric terms are replaced by smoothing splines, resulting in:

$$DL_{ij} = f (\text{Length}_{ij}) + f (\text{Density}_{ij}) + f (\text{Temperature}_{ii}) + a_i + \varepsilon_{ij}$$
(8)

Cross-validation was used to estimate the optimal amount of smoothing for each smoother.

All calculations were carried out in R version 2.9.1 (R Development Core Team 2009). Linear mixed effects models were fitted using the nlme package (Pinheiro et al. 2009) and the AMMs using the mgcv package (Wood 2006).

DEB predictions: Growth rates predicted by the DEB model under constant and maximum possible food conditions (f = 1) at various temperatures were estimated by Eqs. (1) & (4). DEB parameter values were taken from van der Veer et al. (2009) and Freitas et al. (2010b). Due to differences in food intake and in energy participation, males and females have different parameter sets (Table 1), and hence, growth characteristics (Freitas et al. 2010b). Therefore, maximum growth predictions in relation to temperature were made for both sexes separately.

The ratio of observed and DEB predicted maximum growth rates was estimated and analyzed over time. To help visualize patterns, a smoothing curve was added using the LOESS function in R (R Development Core Team 2009).

RESULTS

The seasonal patterns in 0-group plaice density, mean length, water temperature and daily growth rate were rather consistent over the years (Fig. 3). Maximum numbers occurred by the end of April and beginning of May, followed by a reduction and a stabilization from about July onwards. Over this period of time, mean length increased continuously

Table 1. Dynamic energy budget (DEB) model parameters for male and female plaice *Pleuronectes platessa* at 283 K (10°C). Parameters after van der Veer et al. (2009) and Freitas et al. (2010b). For details on the notation used see Kooijman et al. (2010)

Symbol	Units	Interpretation	Male plaice	Female plaice
T_{A}	K	Arrhenius temperature	7000	7000
$\{\dot{p}_{Am}\}$	$J\ cm^{-2}d^{-1}$	Maximum surface area specific assimilation rate	234	390
[$\dot{p}_{\rm M}$]	$J\ cm^{-3}d^{-1}$	Volume specific maintenance costs	19.4	19.4
[<i>E</i> _M]	$\rm J~cm^{-3}$	Maximum storage density	1500	2500
$[E_G]$	$\rm J~cm^{-3}$	Volume-specific costs of growth	5600	5600
κ	-	Fraction of utilized energy spent on maintenance plus growth	n 0.95	0.85
δ _M	-	Shape coefficient	0.219	0.219
v	$\mathrm{cm} \mathrm{d}^{-1}$	Energy conductance	0.156	0.156
$\dot{k}_{\rm M} = [\dot{p}_{\rm M}]/[E_{\rm G}]$	d^{-1}	Maintenance rate constant	0.0035	0.0035
$g = [E_{\rm G}]/\kappa[E_{\rm M}]$	_	Investment ratio	3.930	2.635
$L_{\rm m} = k \{ \dot{p}_{\rm Am} \} / [\dot{p}_{\rm M}]$] cm	Maximum volumetric length	52	78
$T_{ m L}$	K	Lower boundary of tolerance range	277	277
$T_{ m H}$	K	Upper boundary of tolerance range	295	295
$T_{ m AL}$	К	Rate of decrease at lower boundary	50000	50000
$T_{ m AH}$	K	Rate of decrease at upper boundary	75000	75000

from 1.5 cm at settlement in spring to a size of around 9 to 10 cm at the beginning of autumn. Water temperature showed a clear seasonal pattern with a maximum of ~20°C in July and August. Mean growth rate decreased from 0.08 in spring to 0.02 cm d^{-1} in autumn.

Field observations

A multi-panel plot showed similar patterns for the various years where a steady decrease in growth rates was associated with an increase in mean length, a decrease in population density and a dome-shaped curve in water temperature (Fig. 4). In some years, the pattern in population density and water temperature was irregular. Cleveland dotplots (not shown) of the various variables did not indicate outliers in any of the variables except for population density. Four observations were considerably larger

than the rest, 3 from 1996 and 1 from 2001 (Fig. 5). Instead of transforming the data, 2 statistical analyses were conducted: one where the extreme cases were omitted and another containing all data. Multi-panel scatterplots suggested a slightly non-linear relationship between growth rate and mean length as well as some degree of collinearity between the covariates (Fig. 5). To deal with collinearity, one factor had to be dropped and temperature was chosen as it had a less clear relationship with growth rate.

The linear mixed effects model (Eq. 5), in which mean length and population density were used as the remaining covariates, showed that only mean length was significant. However, a plot of residuals against mean length revealed a slight non-linear pattern (see also scatterplots of Fig. 5). Therefore, additive mixed modelling was applied (Eq. 8), starting with mean length and density as covariates. Cross-validation indicated that density could be fitted as a linear term, but since it did not have a significant effect at the 5% level,



Fig. 3. Pleuronectes platessa. Seasonal patterns in 0-group plaice (a) density (ind. $[10^3 m^2]^{-1}$), (b) mean length (cm), (c) water temperature (°C), and (d) growth rate (cm d⁻¹) at Balgzand for the period 1975–2007. Circles indicate observed values for various years together



Fig. 4. Pleuronectes platessa. Time series plot of 0-group growth rates (thick black solid line), temperature (dashed red line), mean length (dotted green line) and density (dash-dotted blue line). The y-scale for growth rates and all variables were rescaled to fit between 0 and 0.08

it was removed from the model. Therefore, the optimal final model was given by:

$$DL_{ii} = f(Length_{ii}) \tag{9}$$

with an ICC (Eq. 7) of 0.175, meaning that the correlation between any 2 observations from the same year was 17.5%.

The need of a random intercept was tested by fitting 2 AMM models, one with and another without a random intercept, and applying a likelihood ratio test while correcting for testing on the boundary (Zuur et al. 2009). Results gave $\chi^2 = 3.289$ (df = 1, p < 0.05), indicating that the best model was the one including the random intercept. The estimated df for the smoother of mean length was 2.35, and the resulting smoother was slightly non-linear (Fig. 6). The residuals of the model were homogeneous and approximately normally distributed. The statistical analysis including extreme cases for density did not deviate from these results and similar conclusions were obtained: a negative and slightly non-linear length effect on growth rate and no impact from density.



Fig. 5. *Pleuronectes platessa*. Multipanel scatterplots between 0-group growth rate (cm d⁻¹) and each covariate. Pearson correlation values: size of characters is proportional to the correlation found

DEB predictions

DEB parameters for males and females are listed in Table 1. At 10°C, the growth rates of female and male plaice amounted to 0.065 and 0.048 cm d^{-1} , respectively. After incorporating the temperature effect, DEB model predictions showed a similar pattern as in the experimental observations by Fonds et al. (1992), and similar ranges in the case of males (Fig. 7a). Furthermore, growth rate was negatively related to fish length (Fig. 7b).

In relation to predicted maximum DEB growth rates, observed growth rates showed a decrease over time and were generally lower for both males and females (Fig. 8), although the differences were stronger for females for which the DEB model predicted higher growth rates. Overall, the discrepancy increased over time, stabilizing from about Day 240 onwards (Fig 8).

DISCUSSION

The diet of juvenile plaice consists of a variety of macroozoobenthic prey items, including both polychaetes and bivalves, varying from body parts (siphon



Fig. 6. *Pleuronectes platessa*. Estimated smoothing function obtained from a generalized additive mixed model (GAMM) for 0-group growth rate as a function of mean fish length. Mean length (vertical lines; cm) vs. contribution of the smoother to the fitted values of growth rate (cm d^{-1}). Solid curve: cubic smoothing spline fit for the continuous covariate, Dashed lines: 95% confidence bands around the fit. The smoother df (2.35) were calculated with cross-validation

tips, tail tips) to whole individuals (Kuipers 1977, De Vlas 1979). Plaice is an opportunistic feeder whose diet generally reflects the composition of the benthic fauna (De Vlas 1979) and is in competition with other epibenthic species that also prey upon macrozoobenthos such as other juvenile flatfishes Platichthys flesus, Limanda limanda and Solea solea, fish species Pomatoschistus minutus, P. microps, and mobile invertebrates Crangon crangon and Carcinus maenas (Kühl & Kuipers 1983). Since 0-group plaice consists of a single settlement cohort, it was selected as a model species. With respect to location, the Balgzand intertidal is an isolated important nursery area in the Dutch Wadden Sea, allowing quantitative studies in plaice (Zijlstra et al. 1982, van der Veer & Witte 1999), as well as in other flatfish species (van der Veer et al. 1991, 2001b, Bolle et al. 1994), gobiids (van Beek 1976) and crustaceans (Kuipers & Dapper 1981, 1984). Moreover, especially in summer, extremely high numbers of early life stages of various epibenthic species occur in the area, making the Balgzand intertidal a suitable area for studies on food competition.

Intraspecies competition

The statistical analysis to test whether growth is (negatively) density-dependent is straightforward. Since plaice growth depends not only on prevailing water



Fig. 7 Pleuronectes platessa. Maximum daily growth (cm d⁻¹) of 0-group plaice under optimal constant food conditions (f = 1) according to the DEB model for females (dashed line) and males (dotted line) in relation to (a) water temperature (°C) together with Fonds et al.'s (1992) laboratory-derived growth model (solid line) and (b) total length (cm)

temperature (Fonds et al. 1992) but also on fish size (van der Veer et al. 2009), these 2 factors had to be included in the statistical model of field growth. However, this was impossible due to the collinearity between temperature and plaice length. One factor had to be dropped and temperature was selected since it had a less clear relationship with growth rates. The consequence is that the statistical model cannot be applied for growth predictions in other areas with different temperature regimes. However, this was not the aim of this study. The observed inverse relationship between growth and mean length is according to expectations.

One problem concerned the variability in the data especially caused by the extremely high peak densities of the 1996 year class. An option would have been to transform this variable, but it would have resulted in reduced resolution between the individual observations. Therefore, no transformation was applied and instead 2



Fig. 8. *Pleuronectes platessa*. Seasonal pattern in the ratio between observed growth and predicted maximum growth (DEB model) for (a) female and (b) male 0-group plaice. Smoothing curve added using LOESS function in R to capture patterns over time. All years together

different analyses were run: one excluding the extreme cases and another including them. The fact that the results of both analyses did not deviate justified, in our opinion, the decision of not transforming the data.

The autocorrelation in the data set is another aspect that should be kept in mind. Since the estimates are based on the differences between 2 successive observations, a biased sample immediately introduces variability in successive estimates. In the beginning of the season, just-settled plaice redistribute from the settlement areas over the Balgzand area (van der Veer 1986) and this might have introduced some variability in the estimates. In fact, the correlation between any 2 observations from the same year was about 18 %.

The statistical analysis did not indicate a relationship with density, suggesting the absence of intraspecies competition for food during the whole growing season including the summer period. These findings are in line with previous analyses of population growth in the Dutch Wadden Sea (van der Veer & Witte 1993). More detailed analyses based on otolith microstructure analysis of individual fish showed that only in exceptional cases, negative density-dependent growth could be observed: in small Swedish bays at densities of several ind. m⁻² (Modin & Pihl 1994). These densities are far above those occurring at the Balgzand intertidal: only in exceptional cases and for a short period during settlement, densities >1 ind. m^{-2} were observed (van der Veer et al. 2000) and, during the growing season, are in general an order of magnitude lower. The absence of intraspecies competition for food at Balgzand is in support of the 'maximum growth/optimal food conditions' theory (Karakiri et al. 1991).

Interspecies competition

In line with previous research, the analysis of interspecies food competition was based on whether growth is maximal or reduced compared with a predictive maximum growth model. Different from previous studies, the maximum growth model of Fonds et al. (1992) was replaced by a DEB model (Kooijman 2010) and instead of comparisons of absolute growth rates, a ratio was introduced. The main reason for using the DEB approach was that it allowed an estimate of maximum possible growth rates in relation to prevailing temperature irrespective of fish size. In this way, a direct comparison between observed and maximum possible growth could be made for the whole season, disposing of the limitations of the growth model of Fonds et al. (1992). The fact that male and female growth differs, as has been described in detail for dab Limanda limanda by Lozán (1992), implies that maximum growth predictions had to be made for each sex.

The DEB model can mimic and predict the maximum growth experiments of Fonds et al. (1992). Experimental data represented observations on small groups of unknown mixtures of males and females. Hence, experimental data would be expected to fall in between the maximum prediction for both sexes. However, experimental data corresponded with maximum predictions for males, most likely because experimental observations represent mean values of small groups of fish compared with a DEB prediction of theoretical maximum growth.

The comparison of observed with model-predicted maximum growth showed that growth was generally

not maximal irrespective of the season and that the difference even increased until July. These results slightly differ from the analysis by Teal et al. (2008) where growth rates in spring were found to be close to experimental growth rates. These differences reflect the use of different models: the mean observed growth of a group of fish that performed well (Fonds et al. 1992) versus maximum possible growth of an individual fish (DEB predictions).

A more detailed look into the growth analysis by Teal et al. (2008) suggests different periods with different patterns: first, a period of lower than possible growth until about the end of the period of larval immigration (~Day 125). Next, a second period until ~Day 180 with field growth rates in line with predicted maximum growth; hereafter, a period in summerautumn with lower growth rates than maximum predicted rates. The first period is characterized by a continuous immigration of settling larvae ranging in length from 10 to 15 mm (van der Veer 1986). As a consequence, mean growth estimates during this period will be underestimated. Just-settled plaice pass through a period of predation by shrimps until the population has reached a size of 3 cm (van der Veer & Bergman 1987). This predation is size-selective and stronger on the lowest size classes (van der Veer & Bergman 1987, van der Veer et al. 1997). Therefore, in the second period, length growth estimates may be slightly biased and overestimated. After this period, growth estimates appear to be lower than maximum possible growth. The observations of this study, after accounting for these sampling biases by restricting the analysis to the period after peak settlement, are in line with the findings of Teal et al. (2008): more or less maximum growth just after settlement, followed by a continuous reduction in growth performance until stabilization at ~40% of the maximum possible growth from the end of July onwards.

The results of the present study eliminate experimental bias as a cause of the observed patterns and confirm the view of Kuipers & Dapper (1984), Pihl (1985) and Teal et al. (2008) of food competition among epibenthic species in summer. Which other species are involved is unclear at present; however, other flatfish species are less likely than crustaceans and gobiids, which occur in much higher numbers. The underlying mechanisms of the competition for food might be related to interference affecting prey searching, capturing and handling, and reducing and limiting food intake. In this respect it is of interest that the difference between field and maximum predicted growth stabilized after July (~Day 225) for plaice >8 cm: at a size of ~8 cm, plaice shifts from small bivalve siphons to larger, more energy containing tail tips as main food items (Kuipers 1977, De Vlas 1979). This is in line with 🍗 Ansell AD, Comely CA, Robb L (1999) Distribution, move-

the observations on the feeding behaviour of young plaice, which seems to depend particularly on the nature and density of available prey (Gibson 1980). It indicates that food quality is also of importance: shifts in prey species composition from small siphon tips to Arenicola tail tips affect plaice growth performance.

Long-term trends in nursery ground quality

Based on the assumption that food was already limiting for 0-group plaice in summer, Teal et al. (2008) argued that a further increase in seawater temperature may negatively affect the nursery quality if the production rate of benthic food cannot meet the increase in energy requirements of 0-group plaice. However, instead of food conditions, prevailing temperature might be more important. The high temperature sensitivity of plaice makes it relatively vulnerable to temperature changes and hence climate change (Freitas et al. 2007). The key factor for plaice might be its relatively low upper tolerance limit: under experimental conditions, growth starts to decrease at ~20°C (Fonds et al. 1992). In recent years, I- and II-group plaice have disappeared from the intertidal (H. W. van der Veer & J. IJ. Witte pers. obs.) and moved to deeper waters (van Keeken et al. 2007). Also, 0-group plaice disappears from the intertidal area in late summer (H. W. van der Veer & J. IJ. Witte pers. obs.), which is much earlier than in the past (Kuipers 1977). Therefore, a further increase in water temperature might imply that temperate estuaries such as the Wadden Sea may become unsuitable as nursery areas for plaice from a physiological point of view, irrespective of prevailing food conditions. Whether this also holds true for the other epibenthic species remains unclear. However, it might be of interest to find out whether and to what extent competition for food occurs in the other epibenthic species.

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Chapter 7

Latitudinal trends in nursery quality of temperate coastal areas for juvenile flatfish

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Abstract

Latitudinal trends in nursery quality of temperate coastal areas in terms of growth conditions were studied in three flatfish species differing in timing of settlement (plaice *Pleuronectes platessa* L. versus flounder *Platichthys flesus* L.) and in prey spectrum (sole *Solea solea* L. versus the other species). Field growth of 0-group plaice, flounder and sole were compared to maximum growth predicted by a bioenergetic model based on the Dynamic Energy Budget (DEB) theory. Patterns in realized growth for plaice showed a decrease in growth performance during the season suggesting increased food competition. For flounder, in general settling later, growth performance also declined throughout the season but was generally lower compared to plaice. For sole, preying mainly on polychaetes, growth performance was not maximal, but contrarily to the other species, no clear trend over time was observed. In flounder, and to a lesser extent in plaice, a trend with latitude was observed with increased growth performance at northern latitudes.

Keywords: flatfishes, plaice, flounder, sole, growth potential, Dynamic Energy budgets, temperature, food limitation

1. Introduction

Temperate estuarine and coastal systems function as important nursery areas for various fish and crustacean species and feeding grounds to coastal and migratory birds (Zijlstra, 1972; Bergman et al., 1988; Piersma, 1994; Van de Kam et al., 2004) due to overall high abundance and biomass of macrozoobenthos (Beukema, 1976; Wolff, 1983; Bocher et al., 2007). In these systems, intertidal macrozoobenthos are preyed upon almost continuously: at low tide, emerged areas are subjected to bird predation and during inundation migratory fish and crustaceans species use these areas as feeding grounds (for overview see Wolff, 1972). Given the intense use of these areas, the first studies on mobile epibenthic predators carried out a few decades ago already suggested that competition for food, and hence reduced growth rates might occur, at least during parts of the season (Pihl 1985).

However, these suggestions were based on indirect evidence only: the dietary overlap in prey items of the main abundant epibenthic species from stomach content analysis. Direct observations are hampered by the fact that, for most epibenthic species such as crustaceans and to a lesser extent gobies, growth is difficult to follow due to an almost continuous influx of settlement larvae and migration movements (Kuipers and Dapper 1981). This might be the reason why, despite the indication that some areas might have an intrinsic carrying capacity for mobile invertebrates (Pihl and Rosenberg 1982), clear indications of the presence or absence of food limitation is not available. In this respect, juvenile flatfish species have the advantage of presenting in general only a single cohort of settling larvae in spring thereby allowing population growth estimates. In addition, flatfishes are also resilient under laboratory conditions allowing the analysis of growth in controlled environments. Therefore, over the years flatfish species have become model species for the analysis of growth condition in coastal nurseries as an indicator of nursery quality.

The classical approach has been the comparison of observed field growth with predictions from a laboratory-based relationship of maximum growth in relation to water temperature (see for instance Zijlstra et al. 1982; Van der Veer 1986; Van der Veer et al. 1991, 2001; Amara 2004; Freitas et al., 2010a). The overall picture emerging from these studies with various species in different areas was rather consistent: in most cases, maximum possible growth directly after settlement, but an increasing discrepancy between observed field and maximum growth measured in the laboratory, in summer over a large latitudinal range from Bodø in northern Norway (Freitas et al. 2010a), to the Irish Sea (Nash et al. 1994),

and at Balgzand (Teal et al. 2008). Although this discrepancy suggested food limitation, an experimental bias could not be excluded since in summer fish size has outgrown the range where the maximum growth model could be applied (Van der Veer et al. 2009).

Recently, this impasse was solved by the introduction of a mechanistic model based on the Dynamic Energy Budget (DEB) theory (Kooijman 1993, 2000, 2010). This theoretical approach describes quantitatively the energy flows of individual organisms and has been applied to model growth and reproduction in several flatfish (Van der Veer et al. 2001) and bivalve (Cardoso et al. 2006, Pouvreau et al. 2006) species. DEB models do not suffer from size limitation and provide a benchmark that allows analysing growth for the whole growing season including the summer -autumn period. This approach was recently applied to re-investigate 0-group plaice *Pleuronectes platessa* growth conditions in the Balgzand intertidal area (Van der Veer et al. 2010). The comparison of observed growth with DEB predicted maximum growth for prevailing local temperatures showed that field growth was lower than maximum possible and that the difference increased over time until about the end of July, indicating reduced growth conditions and hence reduced nursery quality in summer (Van der Veer et al. 2010).

It is unclear to what extent these results for 0-group plaice at Balgzand are a general phenomena. Nursery quality in terms of growth conditions are affected not only by prevailing food and temperature conditions, but they might also be species-specific depending on feeding mode and environmental preferences. This means on the one hand, the analysis of flatfish growth must be extended to other nursery areas, preferably along a latitudinal gradient and also other flatfish species with a contrasting life cycle should be incorporated.

In this paper we include two other flatfish species with contrasting elements in their life cycles: sole (*Solea solea* L.) and flounder (*Platichthys flesus* L.). Both species are also important components of the demersal flatfish communities and overlap with plaice in the use of coastal nursery grounds (Zijlstra 1972). The three species occur in sympatry from Bay of Biscay to Western Scotland (Nielsen 1986; Quéro et al. 1986). Up north, until the White Sea (Nielsen 1986), only plaice and flounder can be found while, further south, sole and flounder co-occur in Portuguese estuaries up to a latitude of about 40°N (Vinagre et al. 2005). Although presenting similar general life history features, the timing of spawning and settlement events differ among the species (Van der Veer et al. 1991; Van der Veer et al. 2001). The most dissimilar patterns are expected to occur between plaice and flounder which differ the most in the arrival time to the nurseries (Van der Veer et al. 2001; Amara et al. 2001) and between plaice and sole which show distinct
feeding behaviours (Beyst et al. 1999) and depth distributions (Amara et al. 2001). Various nursery areas from northern Norway to Portugal are examined reflecting a latitudinal gradient in seasonal timing of immigration of the various species and in the length of the growing season. The specific aims of this study are to investigate whether there are species-specific latitudinal trends in nursery quality of temperate coastal areas.

2. Materials and Methods

2.1. Field data

Datasets for areas along the Northeast Atlantic coast including both growth data and local temperature conditions were collected from different sources varying from published and other (un)published sources. Studies providing information for more than one of the flatfish species studied were particularly targeted. Information presented in graphical form was scanned and digitalized using the software Grabit![™] XP 10 (Datatrend software). Details on the sampling procedures of published datasets can be found in the original papers (for references see legend of Table 1). Temperature data were as much as possible taken from the original publications; however, in some cases other temperature sources were used to complement the local temperature datasets. These included published studies reporting seasonal temperature patterns or oceanographic summaries available in internet databases (see Results section for more information).

For all species, growth was estimated based on patterns in size distribution of the entire population or specific age classes (or cohorts) sampled over time. Mean length of the population was estimated for each survey and growth rates were calculated as the daily increase in mean length (cm d⁻¹) between two successive sampling dates. To avoid the confounding effects of migration movements on growth estimates, a data selection was carried out prior to the analysis: preferably, changes in mean length were only considered from the end of settlement onwards which generally coincided with a peak in maximum abundance until the end of September (or end of October, for southern areas) before the start of the autumn migration to deeper waters.

2.2. DEB model description

The standard model of the DEB theory (Kooijman 2000, 2010) describes the rate at which an individual organism assimilates and uses energy for maintenance,

growth and reproduction, and how these fluxes change as a function of its state (body size and stored energy) and its environment (food, temperature). An individual is described by three state variables: structural volume V (cm³), reserve energy E (J) and reproductive reserves E_R (J). In terms of dynamics, assimilated energy is first incorporated into a reserve pool from where energy is mobilized to the various metabolic processes following the so-called "k-rule": a fixed fraction (κ) of energy from reserves is allocated to growth plus somatic maintenance, with priority for maintenance processes, while the remainder fraction (1- κ) is directed to maturity maintenance and maturation (embryos and juveniles) or reproduction (adults).

Growth does not depend directly on food density but rather on reserve density (i.e. the ratio between amount of reserve and structure) and body size. To remove the "energy" dimension, we scaled the reserve density [E] by the maximum reserve density $[E_m]$ (J cm⁻³). The change in scaled reserve density $e = [E]/[E_m]$) and in volumetric length $L = V^{1/3}$ (cm) are given as follows:

$$\frac{d}{dt}e = \frac{v}{L}(f - e) \tag{1}$$

$$\frac{d}{dt}L = \frac{v}{3}\frac{e - L/L_m}{e + g}$$
(2)

where f is the scaled functional response (-), L_m the maximum volumetric length an individual can reach (cm), v is the energy conductance (cm d⁻¹), a parameter related to reserve dynamics, g is the investment ratio (-), that stands for the costs of new biovolume relative to the maximum potentially available energy for growth and maintenance. Maximum volumetric length is a compound parameter $L_m = v/(k_M g)$ where $k_M = [p_M]/[E_G]$ is the somatic maintenance rate coefficient (d⁻¹) which stands for the ratio of the costs of maintenance to structural volume synthesis.

The scaled functional response defines the ingestion rate as a fraction of the maximum for an individual of a certain size. This parameter links to food density in the environment by a Holling's type II function, and varies from 0 (representing starvation) and 1 (representing food *ad libitum*).

At constant or abundant food conditions ($f \approx 1$), the reserves are in equilibrium with the environment (e = f) and body size follows the Von Bertalanffy growth curve (Kooijman 2010).

In the DEB model, the temperature effect on physiological rates within a

species-specific tolerance range is based on an Arrhenius-type relation (Kooijman 2010). To account for the reduction in rates outside the optimal temperature range an extended formulation is used in this paper as follows:

$$\dot{k}(T) = k_1 e^{\left(\frac{T_A}{T_1} - T\right)} \frac{1 + e^{\left(\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_1}\right)}}{1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_H}\right)}}$$
(3)

where $\vec{k}(T)$ is the rate at ambient temperature T(K), k_1 is the rate at the reference temperature $T_1(K)$, T_A is the Arrhenius temperature (K), T_{AL} and T_{AH} are the Arrhenius temperatures (K) for the rate of decrease at respectively the lower T_L and upper T_H boundaries.

2.3. Growth predictions

DEB predictions of growth rates require a set of species-specific DEB parameters. Data sets were taken from Van der Veer et al. (2001), Van der Veer et al (2009) and Freitas et al. (2010b). As a first step the reliability of the DEB parameters was validated by comparing growth rates predictions under constant and maximum possible food conditions (f = 1), at different temperatures, with published experimental data on maximum growth. For plaice and flounder, experimental growth data by Fonds et al. (1992) were used, while for sole, data was taken from Fonds and Rijnsdorp (1988).

Temperature parameters used to correct the growth rates according to equation 3 were based on previous estimates (Freitas et al. 2010b) and in some further fine-tuning by comparing the shape of the growth curve predicted by the DEB model with the ones derived from experimental observations.

Due to differences in energy participation and food intake between sexes (Freitas et al. 2010b) maximum growth has been predicted for each sex separately.

Observed field growth was compared with the DEB-based prediction of maximum growth by calculating the ratio of observed to DEB predicted maximum growth (*Realized growth* as defined in Hurst and Abookire 2006) for each species and location. Patterns in realized growth were analyzed over time and compared among areas to assess trends with latitude. To help visualizing patterns in data, smoothing curves were added using the LOESS function in R (R Development Core Team 2009).

3. Results

In total, reliable information could be collected from eleven areas ranging from northern Norway to the Portuguese coast (Table 1). Datasets varied from a single year to a 17-year long dataset. Since interannual comparisons were outside the scope of this paper, data from different years were pooled.

DEB parameter values and additional temperature parameters are summarized in Table 2. The DEB parameter set appeared to be reliable for all flatfish species: estimated maximum growth rates corresponded well to available experimental growth models. For plaice and flounder, DEB simulations for males were close to experimental growth, while for females, DEB predictions were higher (Fig. 1).

3.1. Field growth

Observed field growth rates showed a high variability in all areas and for every species (Fig. 2, left panel). Among the three flatfish species, sole showed highest growth rates reflecting faster growth potential (Fig. 2c). Sole maximum growth rates were between 0.15 and 0.2 cm d⁻¹, while for flounder and plaice growth rates were mostly up to 0.1 cm d⁻¹ with the exception of a few individual data points up to 0.13 cm d⁻¹ for plaice in Swedish waters (Fig. 2a). In all species, combined growth rates declined throughout the season with the exception of Mondego estuary (southern Europe) where sole autumn growth rates seemed relatively higher compared to spring/summer period.

3.2. Realized growth

Maximum growth rates predicted by the DEB model for males and females differ due to different parameter values. This difference reflects on the absolute values of the realized growth but the overall pattern is the same for both sexes. Therefore, to simplify the graphical presentation of the results, realized growth patterns are only shown for females (Fig. 2, right panel).

In general, realized growth (RG) showed a decreasing trend over time indicating an increasing discrepancy between field growth and model predictions. For plaice, most areas had a similar pattern in RG with relatively higher values in the beginning of the season, followed by a continuous decrease over time or stabilization, as observed in the Balgzand (Fig. 2d). The only exception referred to France where RG, despite some variability in the beginning of the season, increased in course of time. On average, and considering both sexes, realized growth was

around 0.5-0.6 for most areas with the exception of Icelandic waters for which the mean ratio was above 1 (Fig. 3a).

In flounder, for most areas, realized growth in the beginning of the season was high, in some areas around 1 (Fig. 2e). In most areas except Balgzand, the ratio decreased steeply during the season but stabilized at about the same time, around the end of July. Average ratios were higher in the Balgzand (about 0.7) compared to the other areas. For southern European estuaries average ratios were lower (0.4 in Minho and 0.3 in Mondego) suggesting a latitudinal gradient (Fig. 3b).

Sole showed a more variable pattern compared to the other two species (Fig. 2f). Tagus estuary was the only site with a clear and continuous decrease in realized growth over time. In contrast, in the French Eastern Channel, realized growth increased over a one month period. In the remaining areas, dome-shaped patterns were observed with higher deviances in observed relative to maximum expected growth rates at both beginning and end of the season. In Mondego estuary, there was an additional increase in RG in early autumn reflecting the observed increase in field growth rates. On average, and considering both sexes, realized growth was similar across areas ranging from 0.6 (Minho, France) to 0.8 (in the Dollard) and with no clear latitudinal trend (Fig. 3c).

4. Discussion

4.1. The realized growth approach

The reliability and accuracy of the approach used in this study depends on the quality of the underlying cornerstones: the estimates of field growth and the quality of the DEB parameter set.

Field growth estimates are based on changes in mean population length over time rather than on individual growth trajectories such as otolith microstructure analysis (Modin and Pihl 1994). Accurate and reliable population estimates depend not only on sampling gear designed for catching flatfishes but also on insight in the catch efficiency of the gear (see for instance Kuipers et al. 1992). In most cases a type of beam trawl was used which have generally been considered as welldesigned for catching juvenile flatfishes (Kuipers et al. 1992). However, hardly any information is available on the size selective catch efficiency of the various trawls. In most cases, an average selectivity for all size classes is assumed and only for the 2-m Dutch beam trawl applied in the Balgzand area, insight in the size selective catch efficiency of the gear is available from extensive especially designed field experiments, but only for plaice (Kuipers 1975). This means that in most other areas and maybe for the other flatfish species, population estimates will most likely be biased. Since catch efficiency in general decreases with increasing size, estimates of the mean length assumed to represent growth of the whole population over time, might have been underestimated in most areas. In addition to size selective catch efficiency, seasonal migration patterns might affect population estimates: in spring, due to settlement of small larvae and in autumn by a sizedependent emigration starting with the largest individuals. Therefore, the present analysis was restricted to the period after settlement and before autumn emigration. This timing differed, however, depending on the location of the nursery ground since, in southern areas there is evidence for a prolonged staying in the nursery grounds (Martinho et al. 2008).

Recently, biological indices have been searched to quantify the condition of aquatic organisms (RNA:DNA indices, caloric content) as a proxy for growth rates and individual nutritional condition (Gilliers et al. 2004; Amara et al. 2009; Vasconcelos et al. 2009). Based on nucleid acid analyses applied to several Portuguese nursery grounds, a lack of food limitation has been suggested for *S. solea* (Vasconcelos et al. 2009); nevertheless, the study was restricted to a limited time frame (May and July) and thus the overall picture throughout the season was insufficiently captured.

The DEB parameter set used to predict maximum growth is the other cornerstone of the realized growth approach. Throughout the years, a lot of effort has been put into the estimation of the DEB parameters mostly from independent laboratory experiments (Van der Veer et al. 2001, 2006; Van der Meer 2006). However, in general, there is a lack of experimental data. Furthermore, because the various ecophysiological processes are interlinked, biological quantities measured under experimental conditions do not reflect single processes. Powerful auxiliary theory has therefore been developed to make a better link between measurements available in literature and DEB parameters (Kooijman et al. 2008; Kooijman 2010) but the paucity of appropriate data remains the weakest link of the chain. For the various flatfish species, the DEB parameters were first estimated in Van der Veer et al. (2001) and later modified by Freitas et al. (2010b) as a result of a validation procedure including a comparison of DEB simulations with experimental juvenile growth data under ad libitum food conditions (Van der Veer et al. 2009). While for plaice the model specific parameter values have been reasonably calibrated (Van der Veer et al. 2009), for the other flatfish species, some uncertainty still remains and more data is desirable to validate and refine the parameter set.

Recently, Eichinger et al. (2010) re-estimated the main DEB parameters for juvenile sole using a combination of experimental and literature data. Despite a

good agreement between model simulations and *in situ* growth, maximum growth rates at unlimited food (f=1) calculated using this parameter set are far too low compared to experimental observations of juvenile sole maximum growth (Fonds and Rijnsdorp 1988). In other studies, sensitivity analyses showed that the parameters governing food consumption and the fraction of energy allocated to somatic maintenance and growth (k) are the most influencing on growth (Bodiguel et al 2009). Changing these parameters would affect the absolute values but the overall pattern and shape of the growth curve remains unaltered. The fact that, in general, estimates for the realized growth were in the range between 1 or lower, supports the view that the DEB parameter set seems to be valid and reliable.

Another aspect of the methodological approach concerns potential variability in model parameter values. DEB model parameter values are individual-specific to allow for evolutionary change (Kooijman 2010) and differences between species are thus considered as a natural amplification of individual variability in mean parameter values (Sousa et al. 2008). For widely-distributed populations covering large latitudinal gradients, specific phenotypic and/or genetic adaptations on physiological rates cannot be excluded. In cod *Gadus morhua* (Svånsand et al. 1996), Atlantic halibut *Hippoglossus hippoglossus* (Jonassen et al. 2000) and turbot *Scophthalmus maximus* (Imsland et al. 2000), differences in growth performance of different populations have been demonstrated. In turbot, there is even evidence for counter-gradient variation with high latitude populations showing higher growth performance compared to low latitude ones (Imsland et al. 2000, Imsland et al. 2001). However, how much of this intraspecific variability translates into model parameters, which parameters are more likely to be affected and to what extent overall growth response is affected are questions that still need to be clarified.

4.2. Nursery ground quality

Shallow soft bottom areas are assumed to provide abundant food supply to epibenthic assemblages (Evans 1983). This is supported by an enhanced diversity and abundance of macrobenthic fauna in flatfish nursery grounds compared to adjacent non-nursery areas (Wouters and Cabral 2009).

The generally observed opportunistic feeding behaviour and low dietary selectivity of the various flatfish species (De Vlas 1979, Beyst et al 1999, Amara et al 2001), has reinforced the idea that the potential for competition in highly productive systems is reduced due to abundant food supply (Evans 1983, Cabral et al., 2007). However, the assumption of stability in food conditions for flatfishes after settlement (Van der Veer et al. 1994) has been challenged by several

observations for plaice reporting non-maximal field growth in summer (Nash et al. 1994, Jager et al. 1995, Amara 2004, Freitas et al. 2010a). Using a different approach, the present study supports previous indications that habitat quality in terms of growth conditions changes over the season, especially in plaice and flounder. The range of available resources can be affected by exploitative competition between individuals, either of the same of different species. At present, studies with plaice point to a lack of unequivocal evidence for density-dependent regulation of growth (Van der Veer et al. 2010) and for Irish Sea populations, it is even suggested that the carrying capacity of nursery grounds for plaice is rarely approached (Nash et al. 2007). However, interactions within the benthic-feeder assemblage (other fish and invertebrates) can modify the carrying capacity and trajectories for individual species (Nash et al. 2007) requiring that the whole epibenthic predator functional group has to be considered in analyses of food conditions (Gibson 1994).

Despite the variability in the individual estimates, the combined data revealed different species-specific patterns. For plaice, the results for a wide variety of areas supported a previous study in the Balgzand area: a decrease in habitat quality over time especially from summer onwards (Van der Veer et al. 2010). Increased interspecies competition probably with crustaceans appeared to be the underlying mechanism (Van der Veer et al. 2010). For flounder, settling later in spring in most areas, a similar pattern was observed with a decrease in habitat quality over time, but with slightly lower realized growth rates in summer compared to plaice. Most likely also interspecies competition with crustaceans is the main determinant of the seasonal pattern, and the lower realized growth might result from a smaller size relative to plaice due to later settlement at a smaller size in flounder (Van der Veer et al., 1991). For sole, realized growth patterns were more variable but at a relatively high level and without a clear change during the growing season. This might reflect differences in prey spectrum compared to plaice and flounder.

0-group plaice in the beginning of the season preys upon small, soft, abundant and easily grazed items whereas bivalve siphons, polychaetes and harpacticoid copepods predominate with varying relative importance (Lockwood 1984). Later in the year a diversification in diet occurs and larger items are taken such as tail tips of the lugworm *Arenicola marina* (De Vlas 1979). Prey spectrum of 0-group flounder in general overlaps with that of plaice and also changes with increasing fish size (De Vlas 1979). Predation upon regenerating body parts, such as bivalve siphons, could potentially represent a continuously available food source for these species. However, it has been shown that this sub-lethal type of predation

can have further negative effects on prey populations by inducing changes in burying behavioural and exposing whole individuals to other predators like probing shorebirds (De Goeij et al. 2001). Other types of behavioural adaptations in bivalves such as tidal migrations have been suggested as a mechanism to avoid epibenthic predation (Hiddink et al. 2002) that could further reduce food availability for bivalve-feeder flatfishes.

Sole, on the other hand, feeds on sessile or barely mobile organisms like polychaetes (Beyst et al. 1999, Vinagre et al. 2005, Martinho et al. 2008) which might be related to its small mouth gape and limited vision (Piet et al. 1998). Besides, the observed intense nocturnal peak in feeding activity for sole (Vinagre and Cabral 2008) may offer an advantage compared to plaice and flounder which are active daytime feeders (De Groot 1971).

4.3. Latitudinal trends

Latitude is a complicating factor when studying nursery ground quality. An extensive thermal gradient exists across latitudes which can potentially affect growth. However, latitude is a surrogate for other primary environmental gradients such as seasonality and insolation which interact and are cross-correlated (Willig et al., 2003). It is not clear whether food availability in the growing season also varies with latitude. Pauly (1994), in a review of the latitudinal implications for flatfish recruitment, states that benthic and epibenthic food sources decline towards lower latitudes raising the importance of food limitation with decreasing latitude. Although a linear relationship between primary production and macrobenthic biomass has been reported in several shallow temperate estuarine systems (Herman et al. 1999), no suggestion for large spatial scale trends in benthic biomass has been noted.

Studies reporting benthic biomass in flatfish nursery grounds are scarce. A few individual studies, however, seem to support the indication of no trend in potential benthic food availability. In a Mauritanian tidal flat, macrobenthic biomass amounted to 17 g AFDM m⁻² (Wolff et al. 1993) while a compilation for Portuguese nurseries resulted in values of 14.6 AFDM m⁻² (after conversion from dry weight, Wouters and Cabral 2009). In a cold-water nursery ground, macrobenthos biomass in the order of 24 g AFDM m⁻² has been reported (Freitas et al. 2010a), compared to about 30 – 40 g AFDM m⁻² at Balgzand (Beukema et al. 2002). However, the harvestable food supply will be smaller since not all of the macrozoobenthic biomass is preferred, accessible or digestible (c.f. Zwarts and Wanink 1993).

Under the assumption of similar food conditions along species geographic

range, and in the absence of specific growth adaptations, populations at higher latitudes are expected to show a relatively better performance compared to southern ones, as higher temperatures lead to increased maintenance demands with a concomitant need of food resources. Therefore, is food conditions are limiting, this would be reflected in a downward shift in realized growth patterns from northern to southern areas. From the three flatfishes, flounder and to a lesser extent plaice seem to present a latitudinal trend in growth conditions for the areas analyzed. For plaice, realized growth seems to be about 60% of the maximum possible in nurseries ranging from southern North Sea coastal areas to a cold-water Norwegian area. Growth rates reported for Icelandic waters were systematically higher than maximum growth predicted based on local water temperatures. This might also indicate that the thermal conditions were not accurately captured. Temperature measurements at the time of sampling are typically easy to obtain but these provide only snapshots of the prevailing conditions and may not accurately reflect the thermal environment that individuals have been subjected to.

For S. solea there was a large variability in growth conditions without a clear trend across its geographical area, maybe due to the restricted latitudinal range covered by the present analysis (only up to 53°N). Sole shows a latitudinal trend in spawning period with earlier spawning at lower latitudes (Vinagre et al. 2008). In combination with a shorter pelagic phase due to higher winter temperatures in southern areas, an earlier colonization of the estuary is expected. In fact, in Portuguese estuaries, sole juveniles are the first marine species to colonize the area, appearing in April-May (Cabral 2003; Dolbeth et al. 2010) and in Mondego, young-of-the-year can even be observed from late January onwards (Martinho et al. 2008). This could confer an advantage to sole by occupying an empty niche with ample food resources which combined to high summer temperatures would allow high growth rates. However, despite the longer growing seasons resulting in larger sizes by the end of the first year (Martinho et al. 2008), southern areas do not allow for maximum growth. Thermal stress has been suggested as a possible cause for hampering growth rates in Tagus estuary as summer temperatures largely exceeds metabolic optimum temperatures (Vinagre et al. 2008).

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Location	Latitude	Species	Reference
Bodø, Norway	67°N	P. platessa	Freitas et al. 2010a
Faxaflói*, Pálsson 2001 SW Iceland	64°N	P. platessa	Hjörleifsson and
Gullmar Fjord**, Sweden	58°N	P. platessa	L. Pihl, unpub. data Modin and Pihl 1994
Loch Ewe, Scotland	57°50′N	P. platessa	Steele and Edwards 1970
Mariager Fjord, Denmark	56°N	P. flesus	Andersen et al. 2005
Dollard estuary, Wadden Sea	53°N	P. platessa P. flesus S. solea	Jager et al. 1995
Balgzand, Dutch Wadden Sea	53°N	P. platessa P. flesus S. solea	this study
Bay of Canche,	50°30N	P. platessa	Amara and Paul
NW France		S. solea	Amara 2004
Minho estuary, Portugal	41°N	P. flesus S. solea	Dolbeth et al. 2010; Own data
Mondego estuary, Portugal	40°N	P. flesus S. solea	Martinho et al. 2008, Dolbeth et al. 2010
Tagus estuary, Portugal	39°N	S. solea	Cabral 2003

* <u>http://www.hafro.is/Sjora/;</u> Station Reijkjavik ** <u>http://www.smhi.se/;</u> Station Alsbäck, Släggö

Table 2. DEB parameters at a species-specific reference temperature, temperature tolerance and sensitivity parameters for three flatfish species. Whenever parameters differ between sexes, values for males are shown between brackets.

Parameter symbol	Units	Interpretation	Plaice	Flounder	Sole
<i>T</i> ₁	Κ	Reference temperature	283	283	293
V	cm d⁻¹	¹ Energy conductance	0.156	0.156	0.435
g	_	Energy investment ratio	2.635	3.590	3.111
			(3.930)	(4.211)	(3.684)
<i>k</i> _M	d⁻¹	Maintenance rate coefficient	0.0035	0.0035	0.0097
$\delta_{\scriptscriptstyle M}$	_	Shape coefficient	0.219	0.224	0.192
T _A	К	Arrhenius temperature	7000	7500	6500
T_L	К	Lower boundary of tolerance range	277	277	283
T _H	Κ	Upper boundary of tolerance range	295	296	301
T _{AL}	К	Rate of decrease at lower boundary	50000	35000	35000
T _{AH}	К	Rate of decrease at upper boundary	75000	75000	50000

Figure 1. Maximum daily growth (cm d⁻¹) of juvenile a) plaice *P. platessa*, b) flounder *P. flesus*, and c) sole *S. Solea*, under optimal food conditions in relation to water temperature (°C). Growth predictions based on laboratory-derived models (see text for references) are indicated by closed circles; DEB model predictions are indicated by lines for females (solid) and males (dashed) separately.



Figure 2. Field growth rates (cm d⁻¹) (left panel, a-c) and Realized growth (right panel, d-f) for plaice *P. platessa* (a,d), flounder *P. flesus* (b,e), and sole *S. Solea* (c,f). Smoothing curves were added for each area to capture patterns in realized growth over time.



Figure 3. Relationship between Realized growth and latitude for juvenile a) plaice *P. platessa*, b) flounder *P. flesus*, and c) sole *S. Solea*. Values refer to females only (see text).



Chapter 8

Applicability of dynamic energy budgets for analysing growth conditions in multi-cohort temperate epibenthic species

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Abstract

Large numbers of several epibenthic species aggregate in shallow waters during summer feeding on the available benthic meio-and macrofauna. Whether this concentration leads to periods of food limitation affecting habitat quality for some of these species is not clear at present. In the present work we apply the Dynamic Energy Budgets (DEB) theory as a framework to analyse growth, in order to investigate the food conditions of common epibenthic crustaceans (*Crangon crangon* and *Carcinus maenas*) and small gobiidae (*Pomatoschistus minutus* and *P. microps*) in intertidal and shallow Atlantic estuaries. While for some of the species the applicability of the DEB model is prevented by the lack of accurate model parameters, for others, available parameter sets allowed applying the DEB model for reconstructing growth patterns in the field. It is suggested that gobies are not food limited across their distributional range. For crustaceans, conclusions are hampered by the specificities of their life cycles (migrations, protracted periods of settlement) complicating growth estimates in the field.

1. Introduction

Intertidal estuarine systems are characterized by extreme variations in environmental conditions such as temperature and salinity (Kinne et al., 1966), which are thought to be responsible for the observed relative low species richness of the intertidal macrozoobenthos. However, despite the low number of species, those that persist can build large populations that form an important food source for wading birds at low water and tidally migrating fish and crustacean species at high water (Wolff, 1983). In a similar way, the shallow-water epibenthic community is dominated by also a few common species, most of them occurring over a large latitudinal range and reaching high numbers and biomass such as various flatfish species (plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, sole *Solea solea*), gobies (*Pomatoschistus* spp.) and mobile epibenthic crustaceans (shore crab *Carcinus maenas*, and brown shrimp *Crangon crangon*) (Pihl and Rosenberg, 1982; Evans, 1983; Gibson et al., 1993). Given the intense use of these areas combined with similar prey spectra (Evans, 1983; Pihl, 1985) it is questionable whether periods of food limitation affecting habitat quality for some of these species occur in the field.

Over the years, various studies have tried to address the growth conditions in shallowwater habitats, particularly for flatfish species. In general, flatfish in temperate areas present a single cohort that settles in the area during a restricted time period in spring, grows up and leaves the area in autumn. Since sampling of juvenile flatfish can be done quantitatively by small beam trawls with a known and high efficiency (Kuipers, 1975; Kuipers et al., 1992) growth in these species can be analysed from trends and shifts in size-frequency distributions over time. Studies with 0-group plaice P. platessa and flounder P. flesus revealed that growth after settlement seemed to be maximal and only determined by prevailing water temperature (Zijlstra et al., 1982; Van der Veer 1986; Van der Veer et al., 1991; Amara et al., 2001), but during the summer season an increased discrepancy between field growth and expected growth occurred in a wide range of areas (Nash et al., 1994; Jager et al., 1995; Amara, 2004; Teal et al., 2008; Freitas et al., 2010a). This discrepancy could be due to an experimental bias in the growth model or caused by food limitation in summer (Van der Veer et al., 2010). This impasse was recently solved with the application of a modelling approach based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2010), showing that interspecies competition for food is the underlying mechanism responsible for observed growth reduction in plaice in summer (Van der Veer et al., 2010). This conclusion could be confirmed also for 0-group plaice and flounder in other areas along the Northeast Atlantic coast (Freitas et al., 2011).

For crustaceans and gobies in the intertidal, information about growth conditions and the occurrence of food limitation is unclear and contradictory. On the one hand, there are indications that food in shallow-soft bottoms is not limiting (Evans, 1983; Evans and Tallmark, 1985; Möller et al., 1985; Doornbos and Twisk, 1987) and that absolute food shortage should be a rare experience (Healey, 1972). On the other hand, suboptimal growth due to food limitation in the brown shrimp C. crangon is suggested (Amara and Paul, 2003; Hufnagel et al., 2010). Analyses of field growth conditions have been hampered by the fact that both gobies and crustaceans have long breeding seasons showing successive influx of small individuals to the demersal population over longer time periods (Evans and Tallmark, 1985), and the shore crab and the brown shrimp present even more or less continuous immigration and settlement of successive brood cohorts during the whole growing season (Klein Breteler, 1976; Kuipers and Dapper, 1981; Pihl and Rosenberg, 1982). Furthermore, in most areas these species have not been sampled quantitatively and therefore growth estimates based on catches of size-selective sampling equipment will be biased to some extent. Only for small beam trawls, information on size selective net and catch efficiency of gobies and crustaceans is present (Van Lissa, 1977; Van der Gaag, 1977). These trawls have extensively been used from the late 1970-ties for monitoring epibenthic fauna at the Balgzand intertidal in the western Dutch Wadden Sea, and more recently in Valosen, northern Norway (Freitas et al., 2010a).

The aim of this paper is to test to what extent the DEB model can be applied to investigate growth, and hence food conditions, of the multi-cohort species gobies and crustaceans in the intertidal, focussing on the two areas with quantitative information, Balgzand and Valosen. In contrast to juvenile flatfish, gobies and crustaceans complete their whole life cycle in shallow waters, allowing a comparison of maximum observed size with the theoretical maximum size possible under no food limitation, as an indicator of the overall average life time growth and food conditions (Freitas et al., 2009). In addition, growth will be analysed in more detail based on shifts in peaks of incidental abundant cohorts, c.f. the method applied in flatfish based on the shift in population mean length over time (Van der

Veer et al., 2010; Freitas et al., 2011). This method is adapted for multi-cohort gobies and crustaceans by generating growth curves for various settlement cohorts separately assuming a settlement event once every month (see Kuipers and Dapper, 1984). A pre-requirement for applying the DEB theory is the presence of reliable parameter sets for the various species (Kooijman, 2010). Parameters for gobies and crustaceans are present, however they are considered to be preliminary requiring some further fine-tuning (Freitas et al., 2010b). Therefore, as a first step, the reliability of the available DEB parameters will be validated.

2. DEB model description

The standard model of the DEB theory (Kooijman, 2000, 2010) describes the rate at which an individual organism assimilates and uses energy for various processes, and how energy fluxes change as a function of its state (body size and stored energy) and its environment (food, temperature). The organism is characterized by three state variables: structural volume V (cm³), reserve energy E (J) and reproductive reserves E_R (J). Energy is extracted from food and added to a reserve pool from where energy is mobilized to the various metabolic processes following the so-called " κ -rule": a fixed fraction (κ) of energy from reserves is allocated to growth plus somatic maintenance, with priority for maintenance and maturation (embryos and juveniles) or reproduction (adults).

The dynamics of growth is defined by two coupled differential equations describing changes in energy density and structural volume (Van der Meer, 2006). To simplify the equation for reserve dynamics, we use the dimensionless variable scaled energy density $e = [E]/[E_m]$. The change in e and in volumetric length $L = V^{1/3}$ (cm) is given as follows:

$$\frac{d}{dt}e = \frac{v}{L}(f - e) \tag{1}$$

and

$$\frac{d}{dt}L = \frac{v}{3}\frac{e-L/L_m}{e+g}$$
(2)

where f is the scaled functional response (-), L_m the maximum volumetric length an individual can reach (cm), v is the energy conductance (cm d⁻¹), a parameter related to reserve dynamics, g is the investment ratio (-), that stands for the costs of new biovolume relative to the maximum potentially available energy for growth and maintenance. Maximum volumetric length is a compound parameter $L_m = v/(k_M g)$ where $k_M = [p_M]/[E_G]$ is the somatic maintenance rate coefficient (d⁻¹) which stands for the ratio of the costs of maintenance to structural volume synthesis. The shape coefficient δ_M is used to convert specific length measurements L_w (total length, standard length, body width) to volumetric length: $L = \delta_M L_w$.

The scaled functional response f links ingestion rate to food density in the environment and varies from 0 (representing starvation) and 1 (representing food *ad libitum*). A particular property of the model is that at constant or abundant food conditions ($f \approx 1$), the

reserves are in equilibrium with the environment (e = f) and body size follows the Von Bertalanffy growth curve (Kooijman, 2010). Ultimate size is only dependent on food availability while the time it takes to approach final size is also dependent on temperature.

The temperature effect on physiological rates such as assimilation, maintenance and structural growth, within a species-specific tolerance range, is described by an Arrhenius-type relationship (Kooijman, 2010). Temperature effects outside the optimal temperature range are discussed in Kooijman (2010) and require an extended formulation which is followed in this paper:

$$\dot{k}(T) = k_1 e^{\left(\frac{T_A - T_A}{T_1 - T}\right)} \frac{1 + e^{\left(\frac{T_{AL} - T_{AL}}{T_1 - T_L}\right)} + e^{\left(\frac{T_{AH} - T_{AH}}{T_H - T_1}\right)}}{1 + e^{\left(\frac{T_{AL} - T_{AL}}{T - T_L}\right)} + e^{\left(\frac{T_{AH} - T_{AH}}{T_H - T_1}\right)}}$$
(3)

where k(T) is the rate at ambient temperature T (K), k_1 is the rate at the reference temperature T_1 (K), T_A is the Arrhenius temperature (K), T_{AL} and T_{AH} are the Arrhenius temperatures (K) for the rate of decrease at respectively the lower T_L and upper T_H boundaries.

The notation and symbols follow those in Kooijman (2010), whereby the following main rules apply:

1. variables are indicated by symbols and lowercase symbols frequently relate to uppercase ones via scaling;

2. quantities are expressed per unit of structural volume with square brackets []; per unit of structural surface area with braces { }; and per unit of weight with angles < >;

3. rates have dots, indicating the dimension per time.

3. Material and methods

3.1. Field data

Growth data (in length) for the various species reported at Balgzand in the Wadden Sea area were used. Information consisted on published and unpublished data and varied from seasonal growth patterns of specific age classes, to maximum lengths reached by the end of different growing seasons. Information was available for the common goby *Pomatoschistus microps*, the sand goby *P. minutus*, the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon*. Since the four species all have a relatively short lifespan (gobies: maximum 2 y; shrimps: 2-5 y; crabs: 3-4 y), records of maximum size observed in the area were included as an indication of the overall life time growth conditions.

Published growth curves for the gobies, covering most of the species lifespan were obtained from Van der Gaag (1977) and for sand goby, a reference of maximum size reached in the area was taken from Fonds (1973). For *C. maenas*, maximum lengths over the growing season were obtained from Klein Breteler (1975) combined with personal observations of the largest size class (7-7.5 cm) found in the area (H.W. van der Veer, unpublished data NIOZ Balgzand database) and a life span of 3-4 y (Klein Breteler, 1976). For *C. crangon*, the maximum size reported by Tiews (1970) and Hufnagel et al. (2010) was taken as an index of maximum possible growth in the area.

Unpublished data from a shallow estuary in northern Norway (Valosen) and from the Balgzand intertidal in the Dutch Wadden Sea were also used. Sampling protocols have been described by Van der Veer et al. (1999) for Balgzand, and Freitas et al. (2010a) for Valosen. Sampling occurred in different years between 1975-2009 in Balgzand and in 2005-2006 in Valosen. In both areas, numbers caught were corrected for net efficiency (Van Lissa, 1977; Van der Gaag, 1977). Growth was estimated based on changes over time in the mean length of single cohorts of the population. Whenever the length-frequency distributions and the population mean length did not show a clear trend in the course of time (as in case of crustaceans), an approximate growth curve for abundant cohorts could occasionally be derived from shifts of peaks in length-frequency distributions.

Additional datasets for other areas including both growth and temperature measurements were collected from the literature. Information presented in graphical form was scanned and digitalized using the software Grab-it!TM XP 10 (Datatrend software). References are included in figure legends.

3.2. DEB model simulations

The DEB model was applied in two steps: first, in a validation of available parameter sets by comparing growth predictions with field growth data from a single area (Balgzand); secondly, if validation was successful (see below), model simulations were run to analyse growth trajectories in the field under prevailing temperature conditions.

3.2.1. Parameter validation

For the various species, DEB parameters have been previously estimated. Parameters have been published for the brown shrimp *C. crangon* in Campos et al. (2009) and for the shore crab *C. maenas* and the two gobies species in Freitas et al. (2010b). For the sand goby, *P. minutus*, another parameter set has become available from Lika et al. (2011, this issue) (set 2). These two sets for *P. minutus* were obtained with different methodologies, the first (Freitas et al., 2010b) is based on independent datasets in combination with a calibration procedure to get consistency among parameters, and the later (Lika et al., 2011, this issue) is based on the co-variation method, involving the simultaneous estimation of parameters from various observations on feeding, growth and reproduction in a single-step procedure. For *C. crangon*, the data set was calibrated assuming an ultimate size of 9.5 cm for females (set 1) (Campos et al., 2009). However, this might be an underestimation since individuals up to 11 cm have been reported (German Demersal Young Fish Survey 2005). Therefore the DEB parameter set for *C. crangon* was adjusted (set 2) by increasing ultimate size and, as a consequence, changing assimilation rate and maximum storage.

To check the reliability of the parameter sets, growth simulations at maximum food conditions were generated and the order of magnitude of predictions compared to length and maximum size reported in the field. Standard DEB model equations and the species-specific parameter values were coded in Octave (v. 3.0.3). Constant and *ad libitum* food conditions were included in the model by setting the scaled functional response f to 1. Simulations were performed using the average monthly water temperatures in cold (1996) and warm (2000)

years from a long-term sea-surface temperature series in a tidal inlet (Marsdiep Time Series, Van Aken, 2010) to capture the range of conditions experienced by the individuals in the field.

The present study considered only the growth from the juvenile (after settlement) to adult stage ignoring embryonic and larval stages. Therefore, initial length in gobies was set to 1.6 cm corresponding to the mean size at which goby larvae changes to a demersal life (12-20 mm; Fonds, 1973); an initial size of 0.5 cm was chosen for *C. crangon* (Criales and Anger, 1986) and of 0.15 cm for *C. maenas* representing the size at which crabs settle in Dutch Wadden Sea intertidal areas (Klein Breteler, 1975). Initial scaled reserve density was taken to be equal to the scaled functional response $e(t_0)=f(t_0)$ which is 1 for simulations at the maximum food level. Start of the simulations was set to different dates depending on the species and in accordance to reports of juvenile arrival to the intertidal flats. Simulations were run for a maximum period according to the maximum life span reported for the various species.

3.2.2. Simulations

For those species with a good match (judged by eye) between observations and simulations, a second round of simulations was performed whereby predicted maximum growth trajectories were compared to field growth from different datasets. For the two crustacean species with a large period of settlement, multiple simulations were performed starting the 1st day of each month during a 4-5 months period. Starting conditions were the same as in the validation section and in addition, some of the parameters from the temperature correction expression (see eq. 3) were manipulated to reproduce a metabolic arrest in winter and/or avoidance of high temperatures in summer.

4. Results

4.1. DEB parameter validation

Differences between cold and warm years in the Marsdiep area were largest in the first months of the year decreasing until June. From August onwards, the effect of a warm year was visible with, on average, a 1°C higher mean temperature (Fig. 1).

The validation of the parameter sets based on the comparison with field growth data of Balgzand intertidal for the various species is presented in Fig. 2. In *P. minutus* (Fig. 2A), with parameter set 1, gobies would only reach a total length of 5.6 cm by the end of the second year, far from the modal length observed in the field (7-9 cm in the second year of life). Maximum length predicted by DEB model using parameter set 2 was much more in line with the size range reached in the field. Growth rates also seemed to be more accurately captured with set 2 particularly during summer in the first year of life. In *P. microps*, the parameter set resulted in very low growth compared to the average size of 4.7 cm attained by the common goby population at the end of their second year of life (Fig. 2B). Therefore, no further model simulations were carried out for this species.

With respect to the crustaceans, the model parameters available for *C. maenas* seemed to be in the correct order of magnitude (Fig. 2C). Not only the growth trajectory was correctly reproduced but also the size of 7-7.5 cm observed in the field was reached at the end of the third year of life which fits into the species lifespan described. For the brown shrimp, *C. crangon*, simulations with the parameter set (set 1) resulted in a maximum length of 8.8 cm after 5 years (Fig. 2D). The adjustments of the parameter set for a maximum size of 11 cm (set 2) resulted in more adequate simulations with respect to maximum size and therefore, set 2 was applied in the simulations.

4.2. Growth simulations

The growth simulations in gobies assuming constant and abundant food conditions (f=1) were slightly lower or at the same level as growth in length observed in the various areas (Figs. 3-7). To simulate a growth arrest in winter as has been observed in the field, T_L was set to 5°C for all areas.

The seasonal growth patterns in the various areas were fairly well represented. In Valosen (Norway), model simulations matched observed growth of both age classes in summer but underestimated autumn growth (Fig. 3). Growth rates in the field seemed slightly higher compared to model predictions at the local water temperatures. For the Balgzand, model simulations using the average temperatures in the various years of sampling from the long-term series resulted in a slightly lower growth than observed mean growth of all years pooled (Fig. 4a). In Lake Grevelingen, an enclosed Dutch saline lake, simulations matched observed growth of the 0-group in one of the studied years (1980) but overestimated growth of the new recruits in another year as well as the growth of the adults (I-group) in both years (Fig. 5). Growth patterns in a small sandy beach in inner Oslofjord (Norway) were the most difficult to reproduce (Fig. 6). The extremely high growth rates of the 0-group observed in 1975 were much higher that predicted by the model at abundant food and at the described water temperatures. The model however, was able to capture the seasonal pattern in mean length for both year classes. Using growth data from the same area but for 1976 resulted in a good match between observations and model simulations. Finally, in Mondego estuary (Portugal), good correspondence between model simulations and average field growth was observed (Fig. 7), especially after setting the upper thermal tolerance limit (T_H) to 20°C which caused a slowing down of growth during summer.

For the crustaceans, information is only available for Balgzand (both species) and Valosen (only *C. crangon*). In the Balgzand, settlement of shrimps started in April (Beukema, 1992) and the growth simulations indicated that initial differences in size due to differences in settlement decreased during the growing season (Fig 8; top panel). In combination with field data (Fig 8; middle panel), it seemed that the first data points (encircled) in January-February referred to individuals that had settled in the year before. All observations of mean length peaks fitted within the range of the various growth trajectories. In two years (1996 and 2000) it was possible to follow the changes in peaks over a short time period (Fig 8; bottom panel). These few estimates of field growth fitted with the growth simulations assuming maximum growth. In Valosen, shrimp settlement started in June (Fig. 9) and there seems to be a second settlement by the end of August indicated by an increase in the abundance of smaller size

classes (not shown). Simulated maximum growth trajectories using average temperatures around high tide were far too low compared to field growth derived from shifts in length peaks (Fig. 9). However, simulations with temperatures around low water (Fig. 10) corresponded nicely with the observed growth patterns.

For the shore crab *C. maenas*, only data from Balgzand is available (Fig. 11). Two main age groups could be distinguished: the 0-group which first appeared in fishing samples by the end of July and the I-group appearing at the tidal flats in May. Growth trajectories assuming settlement from July- October (Beukema, 1991) indicated that the various estimates of field growth felt within the range of predicted maximum growth (Fig. 11).

5. Discussion

5.1. The applicability of DEB for multi-cohort species

The applicability of the DEB model to investigate food conditions depends on the reliability of both growth data and of the DEB parameter set used to predict maximum growth. In addition, accurate measurements of water temperature are crucial for a proper representation of the environmental conditions experienced by the population (juveniles and adults).

Growth in crustaceans is particularly difficult to study. The discontinuous nature of growth by moulting, together with an almost continuous spawning (see Boddeke, 1982 for shrimps) and long recruitment make distinction and following of separate cohorts complicated. Although some software tools for tracking cohorts are available, this type of analysis requires frequent sampling and results can still be biased by size-, gender-, and temperature-dependent migrations (Hufnagel, 2009), size-dependent mortality and environmental conditions. Gobies also show extended breeding seasons (Healey, 1972; Fouda and Miller, 1981; Leitão et al., 2006) which combined with a fast growth in the first year of life determines that just about one month after the first appearance of recruits there is a mixing with older individuals and the different year classes become difficult to recognize (Evans and Tallmark, 1985). In contrast to crustaceans, age in gobies can, to some extent, be assessed by reading hard structures (otoliths, scales) (Fouda and Miller, 1981; Moreira, 1991). Improvements would probably arise from using individual growth rates derived from otolith microstructure analysis instead of considering population averages only.

Growth estimates from length-frequency data are related to how abundances are calculated. Reliable estimates of abundances as a basis for growth estimates can only be obtained from surveys once gear efficiency is known (Evans and Tallmark, 1979; Rogers and Lockwood, 1989; Wennhage et al., 1997). Small beam trawls are typically used in shallow areas for the quantitative sampling of flatfishes and epibenthic species (Wennhage et al., 1997). For Balgzand and Valosen datasets, numbers have been corrected for gear efficiency according to published gear efficiencies. However, even after introducing a correction it is likely that due to mesh selectivity, smaller size classes (< 20 mm) are still not caught quantitatively.

The quality of the model parameters is another cornerstone of the approach. The estimation of parameters on the basis of published data has been considered a challenge

(Sousa et al., 2010) and a systematic method is undoubtedly needed. For both gobies and crustaceans, the parameter values from Freitas et al. (2010b) were the first attempt to estimate parameters in these species. For gobies, however, the parameter sets could not be validated due to a lack of experimental data on maximum growth under controlled temperature and food conditions. Fonds (1970) carried out rearing experiments with sand goby larvae to juvenile stage but the results are not very conclusive. Although larvae were fed daily it is difficult to assess whether fish experienced *ad libitum* food conditions over the whole period and, in addition, antibiotics were added to improve survival which could affect growth. The new co-variation method by Lika et al. (2011; this volume) is a step forward improving parameters estimation. Several different datasets can be used in a single-step procedure allowing estimating parameters that typically can only be accessed indirectly. In addition, it makes use of the co-variation rules of parameter values among species implied by the DEB model. This approach should also be applied to improve the available estimates for crustaceans.

Besides the need for fine-tuning of the DEB parameters, some of the discrepancy between field growth data and simulations, especially cases where observed growth is larger than predictions of maximum growth, can be related to an inaccurate representation of the temperature conditions in the field. Despite their mobility, organisms using intertidal areas are exposed to much fluctuating conditions compared to marine species inhabiting subtidal habitats. In both the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas*, young stages can be found during the whole tidal cycle at the intertidal, either active at high water or buried in the sediment at low water (Klein Breteler, 1976; Beukema 1991, 1992). In autumn and winter, migration to deeper and relatively warmer waters takes place. A similar pattern is shared by gobies inhabiting very shallow tidal pools during most of the year and moving to sublittoral areas in winter (Jones and Miller, 1966). Most likely, using sea-surface temperatures or bottom temperatures at high water, might result in a biased picture of the thermal regime experienced. Moreover, segregation between juvenile intertidal habitats and adult habitats in offshore areas (as shown for crustaceans) further complicate the assessment of prevailing water temperatures.

In the absence of detailed and precise information on growth, the DEB theory offers the possibility of evaluating overall average food conditions over the life span of an organism. It consists in determining an approximate functional response of the population using theoretical ultimate size as a benchmark. The ultimate maximum length L_m is the result of physiological processes (energy uptake and utilization) that are fully determined by model parameters. The asymptotic length L_{∞} an individual can reach in a given food environment (represented by the scale functional response *f*) is given as $L_{\infty} = fL_m$. Therefore, different populations can be compared from the point of view of energy utilization.

In *P. minutus*, anecdotal information on the maximum lengths range from 9.5 cm in Brittany (Swedmark, 1958), to 10.3 cm in Ria de Arosa (Iglesias, 1981) and the greatest report is 11 cm in the North Sea (Muus and Dahlström, 1978 *in* Teal et al. 2009). In most areas however, maximum sizes in the range of 8-9 cm have been observed from the Dutch coastal areas (Fonds, 1973; Doornbos and Twisk, 1987) to southern European estuaries (V. Freitas and Campos unpublished data; Dolbeth et al., 2010). These would result in f in the range of 0.7-0.8 (8 or 9 cm divided by 11 cm) indicating average food conditions in the order

of 70-80% of the maximum possible. In crabs, the largest size ever reported is 10 cm carapace width (P-O.Moksnes, unpublished data) in Sweden and most literature for other European areas reports maximum sizes of 8-9 cm in males (see Baeta et al., 2005 for a review). Following the same approach, these values would indicate an f of 0.8-0.9 in natural conditions. In the brown shrimp, *C. crangon*, estimates of asymptotic length from the southern North Sea for more than 50 years, averaged ca. 8 cm with very little variation during the years (Hufnagel et al., 2010). Considering a theoretical ultimate size of 11 cm, the resulting f is about 0.7.

This method is especially suitable for short-lived species because of the higher probabilities of observing asymptotic lengths compared to long-lived species. However, it still requires that survival is high enough to allow observing the typical "plateau" in length-at-age data. In sand gobies, for instance, most adults that survive winter die in their second summer of life after spawning (Fonds, 1973) and only a short percentage (1-2%) of the population can participate in a second spawning in spring (Bouchereau and Guelorget, 1998).

Therefore, in the present study we have tried to go one step further and reconstruct food conditions based on seasonal growth trajectories available despite being aware of the limitations related to the quality of growth data discussed above.

5.2. Growth and food conditions in gobies and crustaceans

The DEB growth simulations using prevailing temperature conditions in the various areas suggest that in the goby *P. minutus*, growth in almost all areas is close to maximum possible. This is in contrast to juvenile flatfishes that seem to suffer from interspecies competition for food in summer (Teal et al., 2008; Van der Veer et al., 2010; Freitas et al., 2011). To what extent this relates to the fact gobies uses a "sit-and-wait" foraging mode (Magnhagen, 1986), laying down on the bottom, until a prey comes across, is unclear. Despite their sedentary nature, this strategy may allow gobies to maximize energy intake rate by reducing disturbance upon potential prey (Jackson et al., 2004). Also the fact that male gobies cannibalize their eggs, in what seems to be a strategy to obtain energy (Kvarnemo et al., 1998) might be an important factor reducing the risk of food limitation.

In crustaceans, the specificities of their life cycles and uncertainties about age constrain the application of the DEB approach. In temperate waters, variability in growth estimates as observed in the Balgzand seems to be the rule and even long-term time series do not solve completely the question about food conditions. A solution, however, seems to be literally "going north", towards higher latitudes, where the marked seasonality in temperatures and possibly food conditions may constrain the number of settlements and make it easier to track growth. This was observed in the Valosen dataset, where growth of a single cohort of *C. crangon* could be easily followed during two years and resulting in similar patterns as expected under no food limitation.

The discrepancy between reconstructed food conditions in juvenile flatfishes (interspecies competition) on the one hand, and gobies and crustaceans, on the other hand (less competition) raises the question to what extent this might be explained by the fact that

both gobies and crustaceans show cannibalistic behaviour, thereby enlarging and buffering their potential food sources.

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Figures and captions



Figure 1. Monthly average water temperature (°C) in the Marsdiep area (Dutch Wadden Sea) in a cold (1996) and warm (2000) year. Data after van Aken (2010).



Figure 2. DEB simulated growth in length (cm) at the Balgzand intertidal, Dutch Wadden Sea in cold (solid line) and warm (dashed line) years, assuming *ad libitum* food conditions (f=1), and using available DEB parameter sets for a) *P. minutus*, b) *P. microps*, c) *C. maenas* and d) *C. crangon*. For *P. minutus* and *C. crangon*, two sets of parameters were tested. See text for further explanations. Dots indicate observed (mean in gobies, maximum in crabs) size in the area for the various species.



Figure 3. *P. minutus*. Simulated growth in length (cm) for Valosen, Norway at maximum food conditions (f=1) and prevailing water temperatures (average for 2005 and 2006). Dots indicate observations of mean length for 0-group and I-group in 2005 and 2006.



Figure 4. *P. minutus*. Simulated growth in length (cm) for Balgzand at maximum food conditions (f=1) and prevailing water temperatures. Dots indicate observations of mean length for 0-group and I-group. Data from various years.



Figure 5. *P. minutus*. Simulated growth in length (cm) for Lake Grevelingen at maximum food conditions (f=1) and prevailing water temperatures (average for 1980-1982). Dots indicate observations of mean length for the 1980 year-class (closed circles) and 1981 year-class (open circles). Data after Doornbos and Twisk (1987).



Figure 6. *P. minutus*. Simulated growth in length (cm) for the inner Oslofjorden, Norway at maximum food conditions (f=1) and prevailing water temperatures. Observations of mean length in 1975 (closed circles) and 1976 year-classes (open circles). Data after Hesthagen (1977).



Figure 7. *P. minutus*. Simulated growth in length (cm) for Mondego estuary at maximum food conditions (f=1) and prevailing water temperatures. Dots indicate observations of mean length for the spring cohort. Data after Dolbeth et al. (2007).



Figure 8. Crangon crangon. Simulated growth in length (cm) at the Balgzand in cold (solid line) and warm (dashed line) years, assuming *ad libitum* food (f=1), for shrimps settling in different months (March-August). Dots indicate mean length of the population over time based on shifts in modes from length-frequency distributions, usually between two sampling dates. In two years it was possible to follow the changes in peaks over a longer time period. Growth is indicated by dots and lines.



Figure 9. *Crangon crangon*. Simulated maximum growth in length (cm) in Valosen (Norway) using average temperatures during low tide (solid line) and high tide (dashed line), assuming *ad libitum* food (f=1), for a cohort settling in June and another late cohort settling in beginning and end of August. Dots indicate the mean length of the population in 2005 and 2006 based on shifts in modes from length-frequency distributions.



Figure 10. Weekly average temperatures (°C) in Valosen estuary (Norway) around low water (open circles) and high water (solid circles).



Figure 11. *Carcinus maenas*. Simulated growth in length (cm) at the Balgzand in cold (solid line) and warm (dashed line) years, assuming *ad libitum* food (f=1), for crabs settling in different months (July-October). Dots indicate the growth of population based on shifts in modes from length-frequency distributions. Data from various years.

Chapter 9. Synthesis: Impact of climate change on epibenthic predation as regulating mechanism on estuarine bivalve recruitment

The main objective of this thesis was to analyse (epibenthic)predator-(benthic)prey relationships in temperate shallow-water systems in relation to temperature, in order to contribute to the debate whether climate-related changes in trophodynamic interactions might have a predictable effect in the fuelling function of these areas. More specifically, the potential impact of temperature changes in the overall epibenthic predation pressure upon bivalves was studied by defining a theoretical framework that takes into account the key mechanisms underlying size-based interactions: physiological response to temperature and prevailing food conditions of prey in relation to predators. First, the major assumptions and pitfalls of the approach followed will be presented and secondly, implications of the main findings of this thesis for bivalve recruitment will be discussed and confronted with observed ecosystem changes suggested by longterm monitoring series in some intertidal systems.

Methodological issues

Latitude as a surrogate for temperature.

The major assumption underlying this research is that the impact of climate change on epibenthic predation could be mimicked by analysing predation over a latitudinal gradient, whereby latitude is considered as a surrogate for temperature. Along the Northeast Atlantic coast, a general latitudinal trend in sea surface temperature is observed, with average temperatures decreasing towards higher latitudes (Campos and Van der Veer 2008). While winter temperatures show a clear gradient with latitude, ranging from about 10°C in Minho (Portugal) to around 0°C with ice cover in Bodø (Norway), summer temperatures across the NW Atlantic region are generally more similar being limited to about 20°C (Campos and Van der Veer 2008). This might reflect a higher contribution of hydrodynamics in more southern areas, due to direct influence of the open ocean by mixing and therefore buffering seawater temperature. Coastal upwelling events due to wind forcing are a recurrent feature in the NW Iberian coast during spring-summer (Smyth et al. 2001) raising cooler waters into the surface. These events have been found to shift the yearly warm period from summer to autumn (Ramos et al. 2009), which might have implications for temperature-dependent biological events. In short, although major temperature gradients can be recognized, local conditions especially hydrodynamics, may overrule general trends and its contribution needs to be considered.

Species-specific physiological response to temperature.

Another assumption is that thermal tolerance window and sensitivity within the preferred range are rigid, allowing generalizations in time and space concerning species thermal response. Temperature has such a pervasive effect on performance that organisms have certainly managed to respond to thermal environment. These responses can vary from short-term organismal-level behavioural and physiological adjustments, to adaptive shifts resulting from acclimation within the lifetime of an individual and usually involving molecular and/or cellular modifications (Angilleta 2002). On the scale of multiple generations, selection may finally alter the parameters of performance windows and their vulnerability to further change. An intriguing but unsolved question is whether widely distributed ectothermic species, showing some degree of genetic subpopulation structuring, exhibit different genetically determined thermal optima, sensitivity and tolerance limits. Elucidation of such patterns requires multiple-generation experiments under common garden conditions to accurately distinguish effects due to developmental plasticity from true genetically based temperature-adaptive differences among populations (Somero 2010).

The variability in sensitivity and temperature tolerance between different life stages is another complicating factor in the analysis of species response to temperature. The ontogenetic change in temperature sensitivity observed in shrimps (Campos and Van der Veer 2008) has also been reported for juvenile cod (Peck and Buckley 2007) and a similar tendency in the range of tolerable temperatures was observed for various other species. Despite the lack of explanations for this phenomenon, available evidence indicate that juveniles are able to exploit larger ranges in temperatures compared to earlier and later life stages pointing to a differential vulnerability that needs to be accounted for when making conjectures about individual species responses to climate change. In relation to bivalves, some differences have been found between juvenile and adult vulnerability to heat stress in *M. balthica* and *M. arenaria* (Kennedy and Mihursky 1971). However, it is not clear whether the optimal range for physiological

performance follows the same tendency as the thermal window for survival. Since epibenthic predation occurs especially upon newly settled bivalve spat, addressing this topic would be valuable in the context of predator-prey interactions.

Scale and population connectivity.

Not many information is available concerning long-term variability and level of bivalve recruitment over a large gradient and most data comes from intermediate latitudes, with a particular emphasis on the temperate Wadden Sea. Therefore, it is difficult to perceive the contribution of epibenthic predation on a large scale. Our review (chapter 2) on population regulation of various epi- and benthic species revealed that because there are numerous local factors potentially affecting the regulating action of predation, the effect of latitude will probably be masked. We surmise that any latitudinal pattern in the overall recruitment variability along species distributional range is more likely to result from a trend in controlling rather than regulating factors.

Further information on bivalve recruitment over a large gradient would be required to test this hypothesis namely of the increased recruitment variability towards the north due to a relatively higher contribution of abiotic factors. Preliminary observations from a cold-water system (Valosen, northern Norway), seem to support a higher contribution of controlling mechanisms. Bivalve spat abundance is extremely high (Fig. 4) compared to the numbers of potential predators, implying that predation will have a small impact on the level of recruitment. Although most individuals grow not larger than 2 mm by autumn (pers. obs.) potentially enlarging the predation window compared to temperate systems, predation does not seem to be the main factor. A limited size means little amount of reserves to survive the rigours of winter. The influence of environmental stressors (storms, hydrodynamic action) and stochastic physical disturbances is hence more likely to be determinant for recruitment variation.

The DEB approach: temperature + growth = food?

The application of the standard DEB model to answer questions about food limitation can be seen as a step forward giving strong mechanistic support to our analyses. For many years, the classical approach for analyzing growth conditions in coastal areas, particularly in those acting as nursery grounds for flatfish, has been the comparison of observed field growth with predictions from a laboratory-based model. This has limited value for making predictions outside the range of sizes where the maximum growth model can be applied.

Although the DEB approach does not suffer from these constraints, there are still some pitfalls that deserve some more thoughts. These are mainly related to: [1] the model parameters, [2] the estimates of field growth and [3] the accuracy of water temperature records.

Despite years of research (see progress made from the early DEBIB project to AquaDEB), the estimation of the DEB parameters still remains a challenging part in the application of the DEB theory. Because these parameters represent physiological processes which have intricate relationships with each other at the individual level, its estimation is not completely straightforward and different procedures have been applied throughout time. This evolution is reflected in this thesis: e.g. the parameters used to model growth in bivalves have been estimated with a different procedure compared to gobies. A systematic procedure has now started to be implemented (add_my_pet program; http://www.bio.vu.nl/thb/deb/deblab) aiming to make a better link between biological quantities measured under experimental conditions (or available in literature) and DEB parameters. Still, the paucity of appropriate data remains a problem which reflects in the accuracy of the parameters and consequently, on the reliability and quality of the model simulation results.

Another gap in our current knowledge that might influence overall results concerns the intraspecific variability in model parameters. For widely-distributed populations covering large latitudinal gradients, the possibility of specific phenotypic and/or genetic adaptations cannot be excluded. In particular, the fraction of energy devoted to reproduction may differ among populations as has been shown in some bivalve species (Van Haren and Kooijman 1993, Drent 2004, Santos et al. 2011) which point out the need for research on the flexibility in energy allocation rules. Also, differences in growth performance among populations and some evidence for latitudinal compensation in growth has been shown in flatfish (Imsland et al. 2000, 2001) and shrimps (Campos et al. 2009). However, how much of this intraspecific variability translates into model parameters, which parameters are more likely to be affected and what is the magnitude of the bias introduced by not accounting for these aspects in populations' comparisons are questions that still need further clarification.

Conclusions about food conditions under the framework presented in this thesis depend on the quality of the field growth estimates. In all cases, changes in modal or mean length within the population were used to distinguish trends in growth. These are correct estimates if the effects of migration, gear efficiency and size-dependent mortality are negligible. Although for flatfish, we were able to diminish these effects by restricting the analysis to a period between settlement and autumn emigration, for crustaceans a lot of uncertainty in growth estimates still remains. Nevertheless, by considering the growth of individual separate cohorts, the DEB model could still be applied. Further improvements are needed and more tools seem necessary to better elucidate the growth conditions of crustaceans in the field. Mark-recapture programs have been applied to track individual growth in *C. maenas* (Yamada et al. 2005) but its applicability depends largely on recovery rates. In flatfish and gobies, it would be interesting to see if the conclusions based in individual growth trajectories derived from otolith microstructure analysis would be the same.

Another factor affecting the results is related to the temperature used in model simulations. In most cases, temperature data available in literature consists of measurements in the water column taken at the time of sampling. These can result in inaccurate representation of the actual temperature conditions experienced in the field, especially for migrating species and for shore crabs and shrimps which can be found buried in the sediment during low water (Beukema 1991, 1992) or gobies which can inhabit shallow tidal pools during long periods (Jones and Miller 1966). Although continuously measurements with temperature loggers can be an improvement, another problem relates to whether these measurements from the environment are a good proxy for body temperature. Studies with terrestrial and intertidal marine organisms have shown that this is not always the case (Kearney et al. 2010) and the use of biomimetic loggers in intertidal rocky systems indicate that body temperature trajectories can differ widely even when predator and prey share identical microhabitats (Broitman et al. 2008). Although it is outside the scope of this thesis to explore the detailed mechanisms of physical ecology of species interactions, these results suggest that reliable forecast of the ecological effects of climate change requires accurate predictions of body temperatures in field conditions.

<u>Basic assumptions.</u>

In this thesis, the theoretical framework for analysing effects of temperature changes on epibenthic predation was based on the following simplifying assumptions:

1. Bivalve recruitment is determined following settlement in the intertidal, after they have outgrown the preferred size window of a chain of potential predators; the overall effect of predation is the product of absolute daily predation (predator-related) and the length of the total period of predation (preyrelated).

2. Tolerance range determines the potential (spatial and temporal) overlap between predators and prey.

3. Temperature sensitivity determines the absolute predation intensity (predator consumption rate) as well as the length of the predation window (prey growth rate).

4. Differences in temperature sensitivity and tolerance windows between predator and prey affect the overall impact on bivalve recruitment.

5. Differences in food conditions between predator and prey affect the predator-prey size ratio and the predation window, and thus the overall impact on bivalve recruitment.

Under the premises above, an increase in temperature within the tolerance range of both prey and predators could result in three different scenarios according to food conditions:

[1] optimal food conditions for both predators and prey: no impact of temperature;

[2] relatively better food conditions for prey: lower prey mortality with higher temperature;

[3] relatively better food conditions for predators: higher prey mortality with increasing temperature.

Temperature sensitivity acts on top of this, as follows:

[1] similar thermal sensitivities of prey and predators: no impact on prey mortality;

[2] higher sensitivity of prey compared to predators: lower prey mortality;

[3] lower sensitivity of prey compared to predators: resulting in higher prey mortalities (Fig. 5).

The impact of temperature on epibenthic predation and ultimate bivalve recruitment

Crustacean-bivalve spat interactions.

Considering the main predator-prey relationship, crustaceans preying upon bivalve spat, DEB-based reconstructions of food conditions showed that bivalve growth is far below maximum possible, irrespectively of latitude, suggesting food limitation and reinforcing previous indications for the Dutch Wadden Sea (Kamermans et al. 2002, Cardoso et al. 2006). Such a scenario indicates that, unless changes in primary productivity occur, bivalves will hardly benefit from rising temperatures. Even though for most bivalve species (except *M. balthica*, see below) future temperature changes would remain within their tolerance range and even in the neighbourhood of their optimal temperature, growth performance would be limited by food resources.

On the other hand, preliminary results with crustaceans suggest their growth is not food-limited. If food conditions remain optimal in such a way that individual maintenance needs can be fully covered, these predators can then take full advantage of higher temperatures to grow maximally. As temperature is a major determinant of foraging, increased food consumption is expected to result from temperature rises.

These contrasting growth conditions of bivalves as prey and crustaceans as predators point to a disadvantageous position of bivalve prey which is expected to intensify under a warming climate scenario: increased predation intensity by crustaceans will not be compensated by a parallel increase in bivalve growth therefore resulting in enlarged size-selective predation window and overall mortality. On top of this, crustaceans have wide thermal windows and higher temperature sensitivity compared to their own potential predators and their bivalve prey. This means that, for the same temperature increase, physiological rates of predator species that depend on temperature (food intake, growth) will change more compared to the reaction of their prey. Converting the Arrhenius temperatures to temperature quotients (Q_{10} s), the various bivalves have a Q_{10} of 2 indicating that, within their preference range, prey reaction roughly doubles with a 10°C temperature change, while in shrimps this value is about 2.4. Considering the juvenile stage only, small shrimps show even higher values in the order of 3

implying a 3-fold effect on physiological rates like food ingestion which translate into higher absolute predation pressure.

Interactions within the epibenthic species complex.

The impact of temperature changes on the epibenthic species complex preying upon crustaceans is less clear.

First, the thermal response of most of the potential predators including larger predatory fish is currently unknown. Also, information on food conditions allowing predators to fill in their growth potential is essential but in general not available. Despite the traditional view that shallow water areas are extremely productive providing enough food resources for the whole epibenthic community (Evans 1983, Evans and Tallmark 1985, Möller et al. 1985), our results indicating food limitation in juvenile flatfish in contrast to optimal food conditions in crustaceans and gobies show that generalizations need some prudence. To what extent these contrasting results can be explained by the cannibalistic behaviour, providing food with optimal nutritional proportions for maximum growth (Moksnes 2004) remains unknown. Cannibalism appears to act as a self-regulating mechanism stabilizing population dynamics of juvenile crabs in nursery grounds (Moksnes 2004). In brown shrimp, cannibalism is also very common (Marchand 1981, Evans 1983) but its importance remains unclear. It raises the question of how do these feedback loops within the community influence prey population dynamics. In the context of predator-prey interactions, the processes determining recruitment in predatory species (crabs, shrimps) and the importance of cannibalistic interactions should also be taken into consideration in future studies.

The fact that flatfish have narrower tolerance ranges compared to gobies and seem to suffer from food restrictions in part of the summer, fit with the observations of recent extensive periods of increase of sand gobies in the Dutch coastal zone (Tulp et al. 2008) in contrast to drastic reductions in plaice in the shallow intertidal area (Van der Veer et al. 2011). The seasonal occurrence pattern of 0-group plaice in the Wadden Sea has also changed: not only has it started leaving the intertidal area in late summer (H. W. van der Veer and J. IJ. Witte pers. obs.), possibly as a result of excessive warm water temperatures (Van der Veer et al. 2010).

Other pieces of a complex puzzle.

Besides changes in the various predator-prey interactions via the mechanisms discussed above, temperature effects on numerical responses may play a role. Unlike immediate predator responses, these refer to comparatively longer time effects, involving reproductive output and population growth rate, and leading to changes in predator abundance.

Long-term monitoring of *C. crangon* abundance in the Marsdiep, near the entrance of the Dutch Wadden Sea has shown an overall increasing trend over the last 34 years (Campos et al. 2010) particularly in numbers of the autumn stock representing adult shrimps leaving the nursery intertidal areas. Similar trends were observed in the tidal flats, where the biomass of small shrimps (<25 mm) has roughly doubled during spring in the last 2-3 decades (Beukema and Dekker 2005). The abundance of shore crabs *C. maenas* also seem to have increased in the last decade based on the high-water beam trawl catches in the Balgzand intertidal area (Fig. 6, H.W. van der Veer, unpublished data).

In the case of *C. crangon*, temperature and fish predation are key factors affecting adult stocks (Campos et al. 2010). The increasing *C. crangon* abundance observed in the Dutch Wadden Sea, both in intertidal and subtidal areas, has been suggested to result from a predation release given that some of the shrimp fish predators have declined since 1985 (Tulp et al. 2008). On the other hand, in the North Sea, warm-water species such as red mullet *Mullus surmuletus* and gurnards which are important predators of *C. crangon* in southern European waters (Costa and Bruxelas 1989) have shown a northward expansion in recent years (Beare et al. 2004, Hofstede et al. 2010) and, in the Wadden Sea, increasing catches of *Dicentrarchus labrax*, another warm-water species and decapod-eater, have also been reported (H. Witte, pers. comm., Tulp et al. 2008).

These shifts in predators' species distribution and composition raise the question whether the release of predation previously suggested for *C. crangon* can be to some extent compensated by increased pressure by different predators making the outcome of (fish) predator-(shrimp) prey interactions even more difficult to predict.

While in temperate coastal zones and estuaries gadoids are the typical fish predators, in more southern areas the piscivore community is more diverse (Costa 1988) enlarging the range of potential predators. Increasing predation risk with latitude was observed in some decapod crustaceans in the NW Atlantic coast (Heck

and Wilson 1987) and it might also be the case in the NE coast as suggested by the comparison of *C. crangon* size structure over its geographic range (Fig. 7). Survivorship to larger sizes seems to be negatively related to water temperature possibly reflecting more intense predation pressure; however, more detailed information on population dynamics from the various areas is needed, namely growth rates and migrations in order to fully understand these patterns. Whether future temperature rises may turn temperate systems like the Wadden Sea into more southern-like estuaries and what would be the consequences for shrimp and also shore crab recruitment are unclear but pertinent questions that require long-term monitoring in order to be answered.

Concluding remarks

Over the last 15 years, frequent recruitment failures in the main bivalve species in the western Wadden Sea led to insufficient food supply for some specialised bird species (Beukema and Dekker 2005). Whether such a declining trend may persist requires understanding those processes affecting prey population dynamics itself and of the predatory species. The impact of climate effects on species interactions is a topic that only now starts receiving some attention.

Under field conditions, predator-prey systems are characterized by a continuously changing mosaic of interactions that depend on local habitat structure, on coexistence of other species (alternative prey, multiple predators) and on species-specific temperature responses (Freitas et al. 2008). Analysing the impact of climate-related temperature shifts on species interactions is therefore not a straightforward task but it should build on a mechanistic understanding. This has been attempted in this thesis by developing a framework to analyse the general impact of temperature changes on epibenthic predation and its consequences for bivalve recruitment in temperate systems. This might provide the basis for future modelling studies to test hypothesis and make more accurate predictions.

Recent literature advocating the need to incorporate physiology into model projections of climate change has been rising steeply (Pörtner and Farrel 2008, Rijnsdorp et al. 2009, Pörtner 2010) and this thesis reinforces that this is particularly essential in the outcome of size-dependent predator-prey interactions. For most species, including those with key ecological roles, thermal responses are however not known. In addition, there are several possible complicating factors

(e.g. life history changes in thermal tolerance widths and sensitivity, local adaptation to thermal environment) that need to be considered when examining species responses.

The linkage between thermal tolerance and concurrent energetic costs is an intriguing topic that has only been superficially approached in this thesis due to limited data available. However, understanding whether these physiological responses occur at the expenses of other processes is important to appreciate biological responses to global change at the individual, population and community levels.

Climate change is much more than thermal changes and other potential factors acting at a local smaller scale may make predictions less obvious. The interaction of factors like hypoxia, acidification (Pörtner 2010) or changing salinities due to freshening on the physiology of individuals and on populations' response needs to be considered for the development of realistic scenarios.

Summary

It is generally conceded that the globe is undergoing a period of rapid climate change that includes a substantial warming. A major challenge to ecologists nowadays is to predict possible impacts of such temperature shifts which can only be achieved if there is an understanding of the basic mechanisms underlying climate-driven changes at the individual, population and community levels. One of the key factors that limit predictions is that climate change may not only affect species performances, but also interactions among species, namely predator-prey relationships.

In shallow-water temperate systems, an important interaction is predation on newly-settled bivalve spat by crustaceans. Several studies have highlighted the importance of crustacean predation (mainly by shore crab *Carcinus maenas* and shrimp *Crangon crangon*) as an important source of post-settlement mortality and contributing to the year-to-year recruitment variability typically found. Such variability in bivalve stocks affects the predictability of this food source for other species groups like wading birds which use shallow-water areas as an essential chain of re-fuelling stations on their migratory pathways.

Because of the significance of this interaction to the ecological function of shallowwater systems, the aim of this thesis has been on developing a framework to study the impact of temperature changes on epibenthic predation based on first principles of physiology and available ecological data, in order to gain predictive power to anticipate effects of rising temperatures on bivalve survival. Instead of considering the crustacean-bivalve relationship in isolation, this interaction has been analysed as part of an intricate predator-prey system where crustaceans are simultaneously predators but also prey for other abundant components of shallow-water habitats, including several flatfish, gobies and larger demersal fish.

Such a complex of epibenthic predators is present from the cold-water Norwegian systems to relatively warmer Portuguese estuaries experiencing a wide range of temperature conditions. Assuming that latitude is a good surrogate for temperature, a latitudinal perspective was adopted to examine the impact of temperature on epibenthic predation on a large geographic scale and to capture the main patterns.

The starting hypothesis was that the temperature effect on size-dependent interactions boils down to physiological principles since both growth performance of prey and crustacean predation are temperature-related. In this respect, not only temperature but also food conditions are key factors, since temperature influences the time prey take to escape predation by reaching a size refuge, and food conditions ultimately determine if prey growth potential can be achieved, reducing the predation window. In addition, temperature directly affects metabolic demands influencing predator's ingestion rates.

The specific temperature responses (tolerance range, sensitivity) of prey in relation to predators were determined based on experimental data reported in literature. Clear differences were found between species, with crustaceans showing higher temperature sensitivity and tolerance ranges compared to their potential fish predators and bivalve prey. The overall picture arising pointed out that crustaceans may benefit from temperature increases leading to a higher predation pressure upon bivalves under such a global warming scenario. Nevertheless, because predictions are based on the differential growth responses of prey and predators, and growth is strongly determined by food availability, elucidation of prevailing food situation in the field still needed to be addressed.

In order to tackle questions concerning food conditions in the field, we used the Dynamic Energy Budget (DEB) theory and its modelling tools. The major advantage of this approach was the possibility of describing growth in relation to food and temperature in a consistent way, using a single model for the various species (predators and prey), whereby differences between species are reflected in the values of model parameters only. A major component of this thesis dealt with the estimation of model parameters which is still the most challenging aspect of the theory application. In this respect, several improvements have been made throughout time, which are naturally reflected in this thesis. Since data from different areas was taken, several assumptions had to be made which could potentially create unforeseen pitfalls. These are discussed in the final chapter and provide opportunities for future research.

The DEB-based approach revealed that in bivalves, growth is far below maximum possible irrespectively of latitude, suggesting food limitation. On the other hand, in crustaceans, feeding conditions seem to be optimal and hence, growth appears to be largely determined by prevailing water temperature conditions. These contrasting growth conditions of bivalves as prey and crustaceans as predators point to a disadvantageous position of bivalves which is expected to intensify under a warming climate scenario: increased predation intensity by crustaceans will not be compensated by a parallel increase in bivalve growth therefore resulting in enlarged size-selective predation window and overall mortality. If future temperature shifts approach upper thermal limits of some of the bivalve species,

possible extinctions may occur. This seems to be the case of the balthic clam *Macoma balthica* which in the last decades has progressively declined in the Wadden Sea.

The impact of temperature changes on the epibenthic complex preying upon crustaceans is less clear. Using the same framework as the one applied for analysing crustaceans-bivalve interactions requires that information on thermal responses and food conditions is accessible, which is not the case for most potential predators. For some predators (gobies and flatfish), the fact that flatfish have narrower tolerance ranges and seem to suffer from food restrictions in part of the summer, seem to fit with the observations of recent extensive periods of increase of sand gobies in the Dutch coastal zone as well as drastic reductions in plaice in the shallow intertidal area. Shifts in species composition and abundance within the epibenthic species complex (replacement of cold-water by warm-water species) as well as cannibalistic interactions, common among crustaceans, might make the outcome of these interactions even more difficult to predict.

Has this thesis contributed to increase our understanding on the potential effects of climate change on bivalve recruitment? Although only part of the problem has been tackled, we advocate that physiological-based studies are a cornerstone for assessing climate change impacts on species interactions. The DEB-approach as a tool to analyse growth conditions in the field, including food reconstructions, is promising instrument and although it has been applied for each species individually it could be used to model predator-prey interactions in a more systematic way. However, we still have to deal with complicating and largely unexplored factors like intraspecific variability in model parameters and population-specific adaptations.

Figures (Introduction)



Fig. 1 Example of the main trophic interactions occurring within the epibenthic species complex that influence bivalve survival and food availability for mollusceating birds.



Fig. 2 Basic components of the overall predation pressure: a) growth performance of bivalve prey affecting the duration of the predation period, assuming a size refuge at about 3 mm; b) predation intensity, here indicated by different possible types of functional responses.



Figure. 3 Energy fluxes through an organism in the standard DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake); 2 defecation; 3 assimilation; 4 demobilization of energy into reserves; 5 mobilization of energy from reserves; 6 utilization; 7 growth; 8 somatic maintenance; 9 maturity maintenance; 10 maturity; 11 reproduction. The rounded boxes indicate sources or sinks; the rectangles indicate state variables.

Figures (Synthesis)



Fig. 4 Bivalve spat densities of *Cerastoderma edule* (Cer), *Macoma balthica* (Mac), *Mytilus edulis* (Myt) and *Mya arenaria* (Mya) in a cold-water intertidal system, Valosen (Norway), during 2005-2006.



Fig. 5 Theoretical framework for the effect of temperature and food conditions on overall prey mortality. Temperature sensitivity of physiological rates for prey versus

predators (top panel) and average food conditions (scaled to the maximum possible, range 0 to 1) of prey versus predators (lower panel).



Fig. 6 Long-term trends in the abundance (ind.1000 m⁻²) of shore crabs *Carcinus maenas* in the Balgzand. High-water beam trawl catches in spring-early summer (March-June).



Fig. 7 Differences in the size-frequency distributions of *Crangon crangon* in four shallow-water areas. Left: Relative frequencies for each 5-mm size class (0: 0-4 mm, 1: 5-9 mm, 2: 10-14 mm, etc); Right: a) boxplots of the size-frequency data indicating an overall decrease in the prevalence of larger size classes with latitude; b) relationship between the 75% percentile size class and maximum mean summer temperatures. Data sources: Valosen, Wadden Sea, Minho: unpublished datasets; Port Erin from Oh et al. 1999; Mondego from Viegas et al. 2007.

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