

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 temperature on the response curve appears to be species-specific and hence, predator–prey specific. Therefore, no general 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

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 life-history 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 stomach-content 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

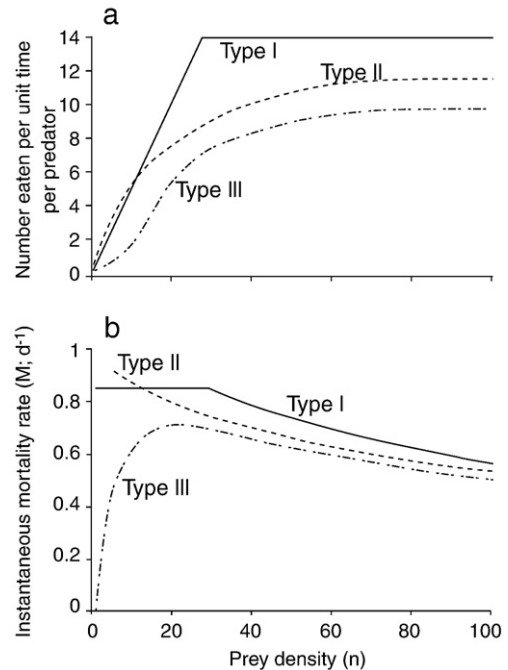


Fig. 1. Types of functional predator–prey response curves (after Bailey, 1994, based on Peterman and Gatto, 1978). a: Shape of different types of hypothetical response curves; b: Corresponding instantaneous mortality (d^{-1}) curves.

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 multi-species 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

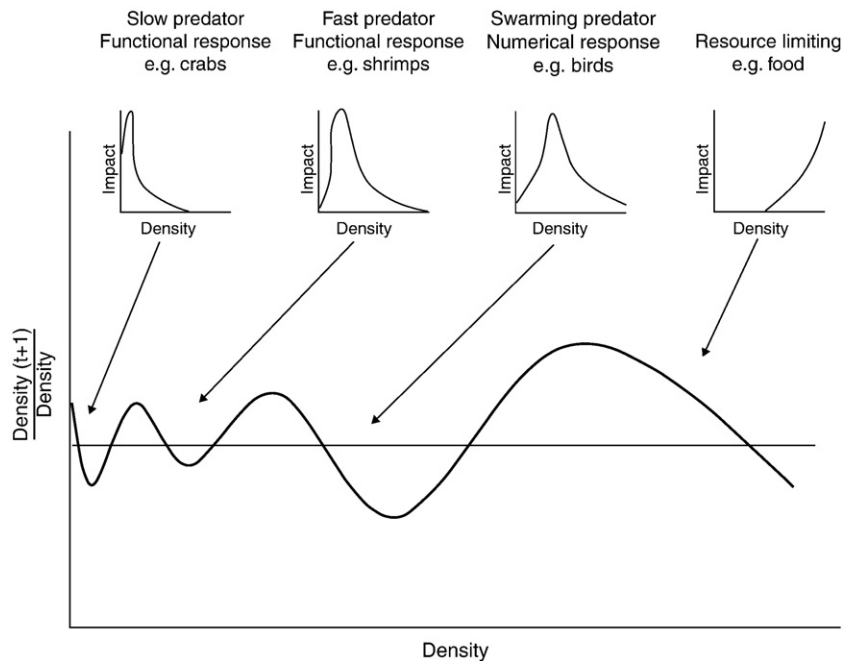


Fig. 2. Illustration of the responses of various predators to different prey densities. Modified from [Holling \(1987\)](#).

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 risk-taking 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 size-dependent 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 preying 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

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 size-selective 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

Table 1
Observed predator–prey interactions for North Atlantic coastal species

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

For more information see text.

(which essentially represents the inverse of a density-dependent 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 prey-switching behavior and functional responses of juvenile flounder *Platichthys flesus* in the laboratory, using the sessile bivalve *M. balthica* and the free-moving 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 density-dependent 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. septempinosus* under laboratory conditions. The Type

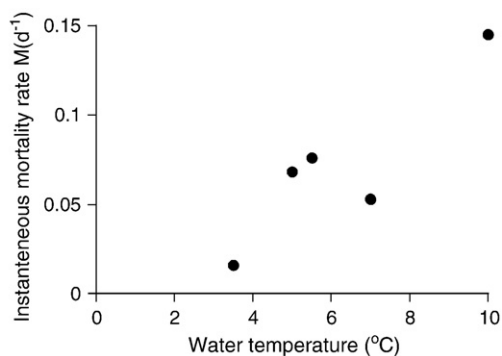


Fig. 3. Relationship between weekly mean temperature (°C) and predation of newly-settled plaice *Pleuronectes platessa* [expressed as instantaneous mortality rate M (d^{-1})] by the brown shrimp *Crangon crangon* at Balgzand in 1980. Data after Van der Veer and Bergman (1987).

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 density-dependent 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 density-dependent 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). Density-dependent 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 species-specific. 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 size-structured 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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