

Reports

Ecology, 91(2), 2010, pp. 311–318
© 2010 by the Ecological Society of America

Seasonal plankton–fish interactions: light regime, prey phenology, and herring foraging

ØYSTEIN VARPE^{1,2,3} AND ØYVIND FIKSEN²

¹University Centre in Svalbard, PB 156, N-9171 Longyearbyen, Norway

²Department of Biology, University of Bergen, PB 7803, N-5020 Bergen, Norway

Abstract. When prey and predator are seasonal migrants, encounters depend on migration phenologies and environmental constraints on predation. Here we investigate the relative contribution of seasonality in irradiance and prey abundance in shaping the rapid seasonal body condition increase of a migrating predator searching visually for its prey: the Norwegian spring-spawning herring, *Clupea harengus*, feeding on the copepod *Calanus finmarchicus*. Two main seasonal pulses of prey are available to herring: (1) the parent generation of *C. finmarchicus*, with peak abundance in March–April, which appear too early to cause the main increase in herring condition; and (2) the abundant offspring generation of *C. finmarchicus*, with peak abundance in June–July, too late to explain the main increase in body condition. However, a mechanistic model of ingestion rate, including both solar irradiance and prey abundance, predicted seasonal food intake in good accordance with observed herring body condition. This suggests that the seasonality in herring foraging and energy storage is closely linked to the return of longer days in spring, and less dependent on a match or mismatch with seasonal peaks in abundance of their zooplankton prey. Consequently, light related constraints on foraging may make visually searching predators at high latitudes resilient to changes and fluctuations in prey phenology and abundance, but vulnerable to changes in the light regime, such as water clarity.

Key words: annual routine; climate change; encounter rate; fish migration; Holling type II model; lipid storage; match–mismatch hypothesis; pelagic ecology; photoperiod; predator–prey interactions.

INTRODUCTION

Recent climate-driven phenology changes and their ecological implications—often differing between species, functional groups, or trophic levels—accentuate the importance of temporal processes in shaping trophic interactions (Stenseth and Mysterud 2002, Edwards and Richardson 2004, Both et al. 2009). The complexities of predator–prey interactions increase when both predator and prey have annual routines involving seasonal migrations, foraging, or reproduction: common in high-latitude ecosystems. To predict changes in food web structure and subsequent ecosystem changes, we must understand how sensitive seasonal predator–prey interactions are to changes in prey or predator phenology.

The trophic coupling between zooplankton and planktivorous fish is often seen as a top-down process, where fish have large influence on zooplankton populations (e.g., McQueen et al. 1989). The effects of zooplankton productivity on planktivores, particularly in marine environments, are not as obvious (but see Arrhenius and Hansson 1999, Beaugrand et al. 2003, Möllmann et al. 2003). Nevertheless, zooplankton are an important link between primary production and pelagic fish stocks, such as for the Norwegian spring-spawning herring (Varpe et al. 2005), the largest stock of Atlantic herring *Clupea harengus*, and currently one of the world's largest fish populations. The feeding migration of herring in the Norwegian Sea generates a fat conveyor belt from ocean to coast: lipid rich zooplankton are converted to herring energy reserves during the oceanic feeding migration and brought to the coast where fasting herring spend reserves during overwintering, the following southward spawning–migration, and finally on egg production (Sløte 1999, Varpe et al. 2005). The fuels for

Manuscript received 1 October 2008; revised 17 April 2009; accepted 1 September 2009. Corresponding Editor: M. H. Carr.

³E-mail: oystein.varpe@unis.no

this capital breeder strategy are gained rapidly, mostly during two months of the feeding migration (Varpe et al. 2005). The main prey of herring are large individuals of the copepod *Calanus finmarchicus*, mainly copepodite stage 5 (C5) and adult (C6) females (Dalpadado et al. 2000, Gislason and Astthorsson 2002). Because of the seasonal vertical migration of *Calanus*, these stages are available in two pulses: when the parent generation (G0) returns from the deep water diapause in early spring, and when the large stages of the next generation (G1) have developed some two to three months later (Heath et al. 2000). This is a common annual pattern in many herbivorous copepods (Varpe et al. 2009).

To understand the timing of the rapid body mass increase of herring, we must assess the extent to which prey are limiting, and how prey density varies over the season. In addition to prey abundance, predator feeding may be regulated by constraints on localization and capture of prey. For a predator relying on vision to detect its prey, the light regime is one such constraint (Eggers 1977, Aksnes and Giske 1993), and at high latitudes, such as the Norwegian Sea, irradiance varies markedly through the year creating seasonal constraints for visually searching predators, such as planktivorous fish including herring (Blaxter 1966).

The timing of the herring body condition increase may be mainly related to (1) the presence of the parent generation of *Calanus*; (2) the presence of the lipid-rich copepodite stages of the offspring generation; or (3) less coupled to peaks in prey abundance, but rather to how light conditions influence prey search efficiency. We refer to these three potential relations as the G0 hypothesis, the G1 hypothesis, and the light hypothesis, respectively. To evaluate them we compiled seasonal data on prey availability (*C. finmarchicus* abundance) and herring body condition, and we developed a Holling type II model of daily prey consumption as a function of irradiance and prey abundance.

METHODS

Herring foraging

The Norwegian spring-spawning herring enter the Norwegian Sea to feed after spawning at the coast in February–March (Fig. 1). Some feeding is observed during the first months after spawning (Sløtte 1999, Dalpadado et al. 2000), but in May–June the feeding activity becomes high (Dalpadado et al. 2000, Olsen et al. 2007) and *C. finmarchicus* is dominant in the diet. From July onwards, feeding activity declines and other prey such as amphipods and krill become more common (Dalpadado et al. 2000, Gislason and Astthorsson 2002). Herring can alternate between particulate and filter feeding (Batty et al. 1990), but the absence of small copepods in the stomachs of Norwegian spring-spawning herring (Dalpadado et al. 2000) suggests that particulate feeding dominates. Selection of the most visible particles, typically the largest prey, results in size-

selective predation, a common observation also in other herring populations (Sandström 1980, Batty et al. 1990).

Data

From oceanic ecosystems, zooplankton data with fine seasonal resolution are in short supply, particularly from systems where predators are monitored simultaneously. Here we used data on *C. finmarchicus* from the Ocean Weather Station M (Station M) in the Norwegian Sea (66° N, 2° E; Fig. 1). We used published data from two years of extensive field campaigns with fine temporal resolution: 1949 (Østvedt 1955); and 1997 data obtained by the Trans Atlantic study of *Calanus* (TASC; e.g., Heath et al. 2000). We used densities from surface waters (100–0 m), for adults (C6; Fig. 2a), and copepodite stage 5 (C5; Fig. 2b). Data from 1949 were digitized based on Figs. 8 and 9 in Østvedt (1955) and converted to densities.

Data on individual Norwegian spring-spawning herring were obtained by the Institute of Marine Research (IMR), Bergen, Norway. We used the condition factor $K = 100 \times W/(L)^3$ as our proxy of body condition, where W is body mass (g) and L is body length (cm). The herring data are from 1990–2003, a period with a consistent seasonal migration (Holst et al. 2004). We used data from the end of spawning, annual low in body mass, and until the start of overwintering, when feeding ceases. The same herring data were previously used as input to a bioenergetics model (Varpe et al. 2005). We present means of annual means, potentially excluding interesting between-year variation, but establishing a robust seasonal proxy. No single year has the continuous sampling needed to obtain similar temporal resolution.

Foraging model

To assess the relative importance of *C. finmarchicus* densities and effects of longer days and increased solar irradiance on daily herring feeding rates i_d , we applied a Holling type II foraging model:

$$i_d = P_c \sum_{t=1}^{24} \frac{\beta_{t,d} N_d}{1 + h\beta_{t,d} N_d} \quad (1)$$

where N_d is the density of prey (prey/m³) at day d of the year, P_c is the capture success or reduced food intake due to overlapping search fields in schools, assumed to be 0.5 (Link 1996), and h is the handling time of each prey item set to 1 s (Walton et al. 1992). Prey densities are taken from the time series of *C. finmarchicus* (sum of C5s and adults; Fig. 2c). Values for days without prey sampling were estimated by linear interpolation between days. The search or clearance rate, $\beta_{t,d}$ (m³/s), varies over the diel cycle depending on surface irradiance:

$$\beta_{t,d} = \frac{1}{2} \pi R_{t,d}^2 v. \quad (2)$$

Here v is cruising velocity (m/s) and $R_{t,d}$ is prey detection

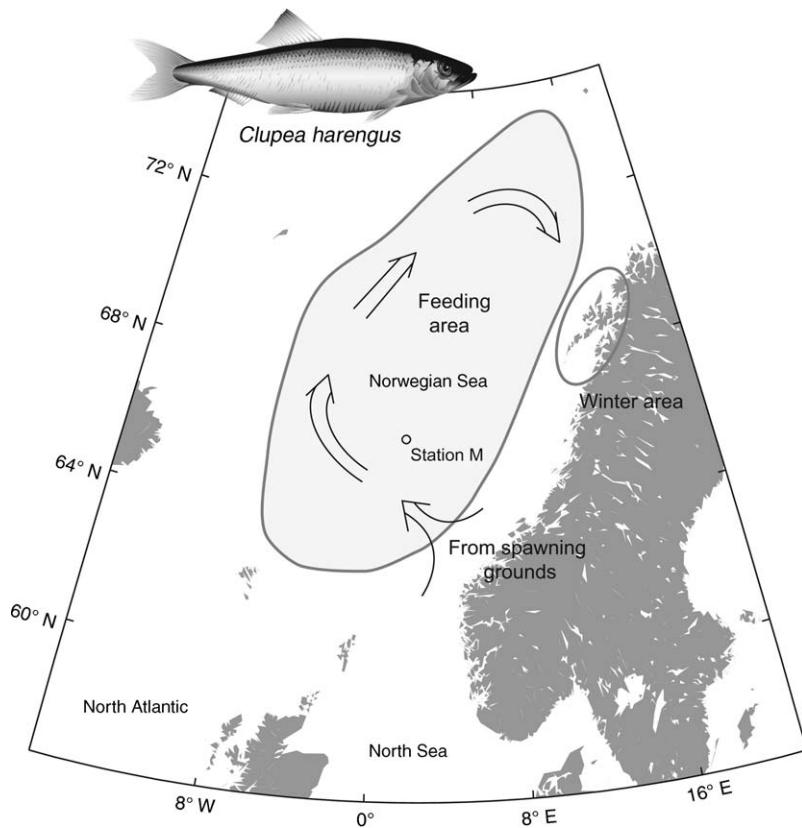


FIG. 1. The Norwegian Sea and the feeding migration of Norwegian spring-spawning herring, based on the 1990–2002 situation presented by Holst et al. (2004). The herring typically leave the coastal spawning grounds in March and return to the wintering area in early fall. *Calanus finmarchicus* data used in the study were from Station M. The herring drawing appears by courtesy of the Gulf of Main Research Institute.

distance (m), assuming that only half of the visual area is effectively scanned (Blaxter 1966). Visual detection range depends on prey size and contrast, optical properties of the water, the visual acuity of the planktivore and most important here, the ambient availability of light that varies on a diel t (hourly) and seasonal d (daily) scale. We applied the model developed by Aksnes and Utne (1997):

$$R_{t,d}^2 \exp(cR_{t,d}) = C_{\text{Cf}} A_{\text{Cf}} E' \frac{I_{t,d}}{K_e + I_{t,d}},$$

or if $R < \sim 0.05$ m,

$$R_{t,d} \approx \sqrt{C_{\text{Cf}} A_{\text{Cf}} E' \frac{I_{t,d}}{K_e + I_{t,d}}} \quad (3)$$

where C_{Cf} is the contrast (0.3; Utne-Palm 1999) and A_{Cf} is the image area (3×10^{-6} m 2) of *C. finmarchicus* and c (m $^{-1}$) is the beam attenuation coefficient (0.3; see Mobley 1994). The model is parameterized for herring, $v = 2$ BL/s and E' and K_e scaled such that R is one herring body length (BL) when light is not limiting and prey is *C. finmarchicus* (Blaxter 1966). Irradiance at the surface, $I_0(t, d)$ (Fig. 3a), is a function of latitude, time

within each day t , and day of the year d and is modeled as by Rosland and Giske (1994), except that maximum irradiance within each day is modeled as by Drange and Simonsen (1996). Ambient irradiance for herring $I_{t,d}$ at a typical foraging depth of 30 m depth is then $I_{t,d} = I_0(t, d) \exp(-k \times 30)$, where $k = 0.1$ is the diffuse attenuation coefficient (m $^{-1}$). The latter value is reasonable in oceanic water at low chlorophyll a levels for 550 nm (see Mobley 1994), the spectral range where fish eyes are most sensitive (e.g., *Gobiusculus flavescens* [Utne-Palm and Bowmaker 2006]).

The actual foraging efficiency may shift up or down depending on variables such as prey depth distribution (assumed to be 30 m), light attenuation coefficients, and the capture or local competition coefficient P_c . However, we are interested in the seasonality in foraging efficiency, and the relative feeding efficiency over the season will be equally sensitive to choice of the scaling parameters. The model allows us to explore the relative importance of changes in prey availability and day length for feeding efficiency and energy intake of herring over a season. The resulting clearance and ingestion rates appear reasonable with the parameterization justified above. We have not included digestion limitations as prey

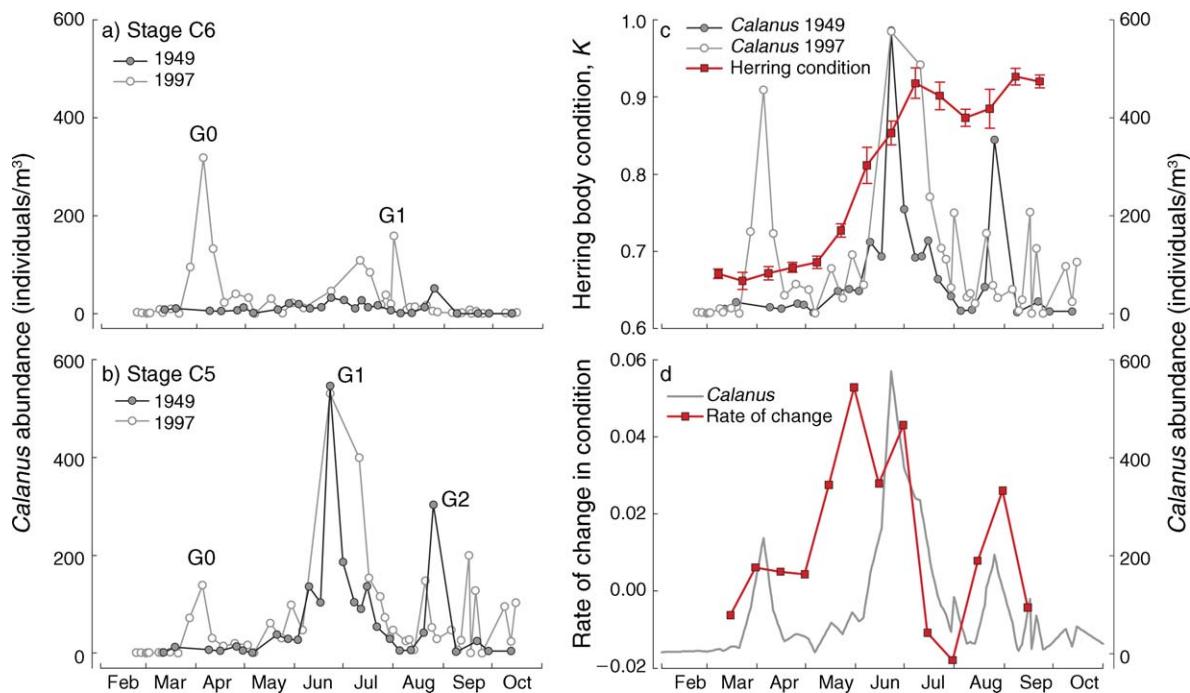


FIG. 2. Seasonal abundance of *Calanus finmarchicus* at Station M in the Norwegian Sea and the body condition development of Norwegian spring-spawning herring during its summer feeding migration. Abundance of (a) adult stage (C6), mainly females, and (b) copepodite stage 5 (C5), the developmental stage preceding maturity. Data are from 1949 (solid) and 1997 (open) and are averages for the upper water column (0–100 m). The parent generation (G0), the offspring generation (G1), and what is most likely a second generation (G2), are indicated. (c) The condition factor *K* (mean of annual means, 1990–2003, with standard error; shown in red) in relation to *C. finmarchicus* abundance (sum of C5 and C6 for each year separately) and (d) rate of change in body condition, for each fortnight (two-week period) in relation to *C. finmarchicus* abundance (stage C5 + C6, and averaged for the two years 1949 and 1997).

handling time will saturate ingestion rate at high prey encounter rates.

RESULTS

The seasonal migrations and the development of cohorts create a highly seasonal presence of *C. finmarchicus* in surface waters (Fig. 2), with the strongest signal provided by peak abundance of C5s from the offspring generation in June/July (Fig. 2b). This peak of G1 occurred at the same time for the two years. The parents of this generation, the G0, had peak abundance in March–April in 1997, but no marked peak in the upper 100 m in 1949 (Fig. 2a) although the seasonal signal from ascending G0s were seen at greater depths (Østvedt 1955). The later and less pronounced peaks of C5s (Fig. 2b) suggest a second generation.

The herring body condition (Fig. 2c) reaches its annual low in March–April followed by a rapid increase during May and June, when large amounts of lipids are stored. The condition factor *K* remains high from July and until the end of the feeding season. From the end of spawning until peak body condition in early July, *Calanus* abundance is a poor predictor of rate of change in herring condition (Fig. 2d; Pearson product-moment correlation coefficient: $r = 0.4$, and if assuming a two week lag in the herring response, $r = -0.2$).

The foraging model predicts a gradual seasonal increase in *Calanus* intake, reaching maximum values in June (Fig. 3b). Predicted intake rates are similar for the two years, although lower during early parts of 1949 due to the absence of G0 from those data. The daily volume scanned for prey (the search or clearance rate) peaks at about 4000 m³/d (at midsummer and 30 m depth). Maximum clearance rate is a bit lower than the 7000 m³/d suggested by Blaxter (1966) for 30 cm long herring. Note that Blaxter based his estimate on a minimum light threshold for feeding, while we model clearance as a gradually satiating function of light.

At prey abundances above 50 individuals/m³, foraging efficiency is sensitive to the seasonal light regime but not to prey abundance (Fig. 4). Herring food intake is sensitive to prey abundance at low (<50 individuals/m³) prey densities (Fig. 4), also seen from the marked but temporary dips in predicted foraging intake for some days with particularly low *Calanus* concentrations (Fig. 3b). For a given prey concentration, food intake increases with day of year until the summer solstice (day 173, Fig. 4).

The G0 hypothesis would be supported if the peak in G0 abundance during March–April occurred during or shortly prior to the increase in herring body condition. However, the G0 peak has short duration and is, at least

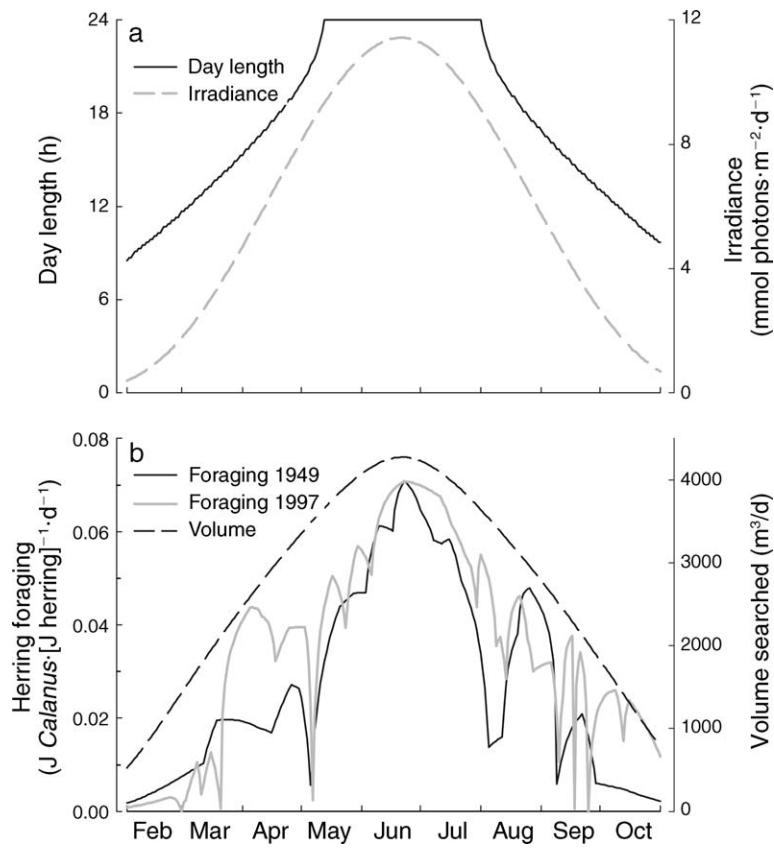


FIG. 3. A foraging model for herring. (a) Seasonal variation in day length (solid line) and irradiance (broken line) at 66° N (latitude of Station M). Day length (hours when surface irradiance > 0.1 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) is for illustration whereas irradiance is input to the foraging model. (b) Clearance efficiency (volume searched; broken line) and herring foraging (energy-specific daily feeding rates) predicted from the Holling functional response model (Eq. 1) for each time series of prey abundance (1949 and 1997). We assumed wet masses of 1.15 mg and 225 g (for a 30-cm fish) and energy densities of 3.5 and 10 kJ/g wet mass for *Calanus finmarchicus* and herring, respectively (see Varpe et al. 2005).

for this nonspatial analysis, too early to cause the main increase in herring condition (May to early June), but may be important for the slow initial increase in condition (Fig. 5). The G1 hypothesis is not supported. The peak in G1 during June and July is too late to contribute to the increase in herring condition (Fig. 5). Finally, the light hypothesis is supported. Despite the temporarily low prey abundance between the peaks in G0 and G1, the foraging model predicts a steady seasonal increase in food intake preceding the body condition increase (Fig. 5).

DISCUSSION

We have related seasonality in prey abundance, *Calanus finmarchicus*, to the rapid and highly seasonal body condition increase of the predator, the Norwegian spring-spawning herring, and we have used a foraging model to predict herring food intake during the feeding season. Our main finding is that light-related constraints on foraging are likely to play a major role in determining the timing of body condition increase in herring. The central role of the light regime has consequences for how

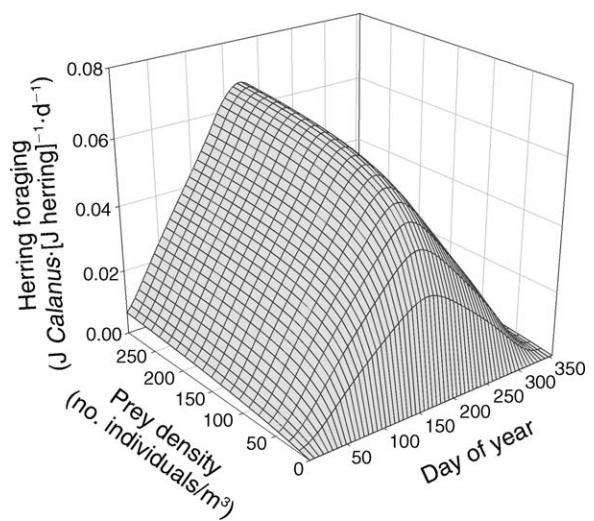


FIG. 4. Modeled herring foraging (energy-specific daily feeding rates; Eq. 1) as a function of prey density and day of year for herring feeding on the copepod *Calanus finmarchicus*.

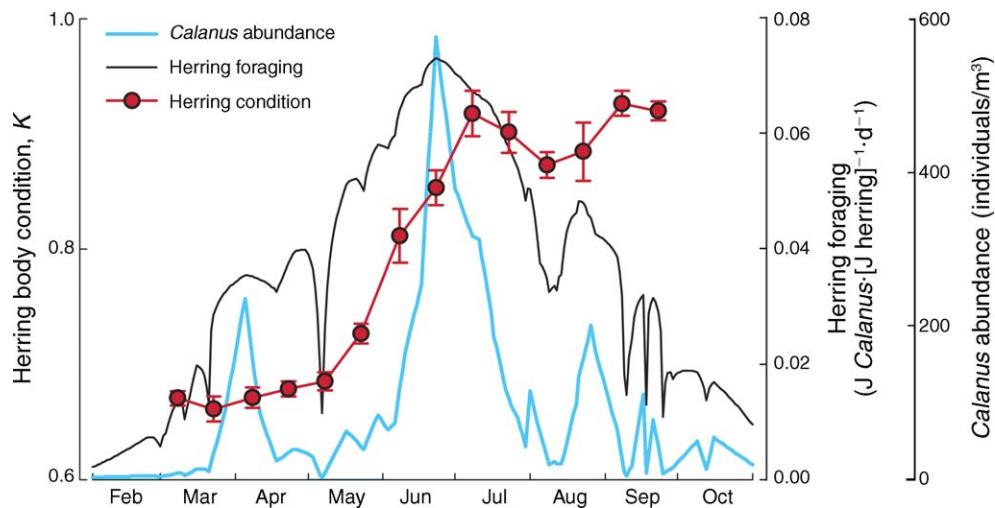


FIG. 5. Seasonal *Calanus*-herring interactions in the Norwegian Sea. The condition factor K (mean of annual means, 1990–2003, with standard error; shown in red) of Norwegian spring-spawning herring, modeled herring foraging (energy-specific daily feeding rates), and *Calanus finmarchicus* abundance (blue line; see also Fig. 2d), the main prey of herring and used as input to the foraging model, are shown.

we understand the long-distance feeding migration of herring and for how sensitive the *Calanus*-herring interaction, and other interactions involving visually searching predators, may be to environmental changes that cause shifts in prey phenology.

Body condition increase and the feeding migration

The foraging model predicted a steady increase in ingestion rates with increasing day length and surface irradiance, despite a marked drop in prey abundance when G0 has died and G1 is developing. Consequently, the seasonal increase in irradiance seems key to explaining herring food intake and the timing of the increase in herring body condition. Although the main increase in herring body condition seems decoupled from the seasonal peaks in *Calanus* abundance, the foraging efficiency was sensitive to changes in prey abundance at low prey densities. Efficient foraging is a driver behind many long-distance migrations (Alerstam et al. 2003), but the feeding migration of Norwegian spring-spawning herring is not necessarily an adaptation to match peaks in prey abundance, but rather to avoid times or areas where prey densities are particularly low.

Predicted herring foraging increases from mid March but there is only a weak increase in herring condition before the rapid increase some two months later. At some point, the food intake can sustain basic metabolic needs and the net gain can be stored as lipids. The model predicts this limit to be around $0.03 \text{ J Calanus} \cdot \text{J herring}^{-1} \cdot \text{d}^{-1}$. Still, the main strength of the model is on predicting seasonal patterns, rather than absolute intake rates.

A herring body condition increase of ~30% during two months marks a well defined foraging season. There has been some support for the hypothesis that herring has adapted its feeding migration to match the spring

ascent and the reproducing generation of *C. finmarchicus* (see Gislason and Astthorsson 2002). Others have focused on the importance of a match with the second pulse of *Calanus*, the developing offspring generation, G1 (Skjoldal et al. 2004). Predation on G0 may be the driver for the onset of the migration, but our analysis suggests that the presence of G0 is too short and too early to serve as an explanation for the increase in herring body condition. The direction of the herring feeding migration, starting in coastal and Atlantic water masses and moving west and northwards towards mixed and Arctic water masses, may however allow herring to feed on G0 for a prolonged period. This requires a spatial delay in the development of spring conditions; the onset of the phytoplankton bloom and the phenology of *C. finmarchicus*. There is some support for such delays (Broms and Melle 2007). These spatial aspects of the *Calanus*-herring interaction may question our use of Station M data as a proxy for *Calanus* seasonality in the Norwegian Sea, particularly because herring have important feeding grounds west of Station M (Holst et al. 2004). However, for several years during the 1990s herring were abundant near Station M also in May (Olsen et al. 2007), at a time when considerable feeding must take place to explain the rapid seasonal body condition increase. Still, we had to trade spatial for temporal resolution and several spatial questions remain to be answered. For instance, to what extent is the northward turn of the feeding migration driven by a latitudinal lag in prey phenology or by longer days at high latitudes (see also Nøttestad et al. 1999)?

The herring migration may also be driven by processes other than a spatially delayed spring development. If herring deplete prey concentrations, and continuously move towards higher prey densities, the

feeding migration may be a density-dependent migratory wave (Fauchald et al. 2006). The absence of an oceanic feeding migration at low population sizes (Holst et al. 2004) supports density dependence as one driver of the feeding migration.

Peak abundances of the offspring generation of *Calanus*, G1, occur after the increase in herring body condition. Feeding during peak G1 abundances can therefore not have caused the rapid seasonal fattening of herring but may be important for maintaining high body condition. Feeding on G1 should be expected for a number of reasons: (1) The last developmental stages of G1 are particularly profitable prey because they store large amounts of lipids before diapause (Jonasdottir 1999). (2) The abundance of large G1 stages is higher than for G0 a few months earlier, and G1 may be available longer than G0. (3) The largest energy demands of Norwegian spring-spawning herring overlap more closely in time with G1 than G0 (Varpe et al. 2005). (4) There is some evidence for a top-down control of *Calanus* abundance caused by herring foraging the year before (Olsen et al. 2007). This is more likely caused by direct predation on G1, which will ascend as mature individuals next year, than via predation on G0 back in spring.

In the Norwegian Sea, the first *C. finmarchicus* descend to the deep diapause habitat as early as June (Østvedt 1955, Speirs et al. 2005). This early retreat, despite seemingly sufficient food for a second generation, may be a predator driven life history adaptation (Kaartvedt 2000) caused by high predation risk also on G1. Similarly, because herring is spawning at the coast at about the same time as *C. finmarchicus* ascend from diapause, the herring may have difficulties arriving in time to feed on G0, whereas *C. finmarchicus* may avoid herring predation by being early (cf. Kaartvedt 2000, Varpe et al. 2007). In turn, herring may have to trade optimal spawning time against profitable foraging time: a parent–offspring conflict. For the last 70 years, the bulk of herring spawning has occurred between early February and late March (Ø. Varpe, E. M. Olsen, and A. Slotte, *unpublished manuscript*), so in most years the herring may reach the *Calanus* ascent in the Norwegian Sea. However, an early ascent and reproduction by *Calanus* would also reduce predation risk from herring due to less irradiance.

Climate change, prey phenology, and visual feeding

Phenology changes reported from both terrestrial (Crick and Sparks 1999, Both et al. 2009) and marine systems (Edwards and Richardson 2004) have been linked to climate change. The classic match–mismatch hypothesis relates recruitment success of fish populations to the degree of match between fish larvae and their food source (Cushing 1990). Matching prey abundance is an issue for all organisms relying on a seasonal food source (Stenseth and Mysterud 2002, Durant et al. 2005). For instance, species with life cycles

involving long-distance migrations may have difficulties adapting to phenology changes in their breeding area, with negative population level consequences from the resulting mismatch (Both et al. 2006). However, the consequences of a mismatch may not always be severe, even in highly seasonal environments. Here we have shown that for plankton–fish interactions seasonality in irradiance and visual constraints on foraging are likely to dampen potentially detrimental effects of a poorer match with peak prey abundance, as long as shifts in prey phenology are not strongly in the direction of lower light levels. Consequently, constraints caused by photoperiod may make visually searching predators at high latitudes resilient to fluctuations in prey phenology, and less sensitive to prey mismatch. On the other hand, small changes in water clarity may lead to changed foraging conditions for pelagic fish such as herring. Differences in water clarity in coastal systems are well known to structure pelagic ecosystems (e.g., Aksnes et al. 2004), and long-term changes in water clarity have been observed for oceanic environments with potential influences on fish foraging (Aksnes 2007). Consequently, we must account for changes in prey abundance, phenology, and the light regime when evaluating the potential for changes in trophic interactions and the robustness of aquatic ecosystems to environmental changes.

ACKNOWLEDGMENTS

This study was supported by grants from the Research Council of Norway. The Institute of Marine Research (IMR) provided herring data, and we are indebted to A. Slotte for introducing Ø. Varpe to these data. We thank C. Broms and K. Leonardsson for comments on an earlier draft. Valuable comments by three anonymous referees helped us improve the paper. *Calanus* data for 1997 were from the Trans-Atlantic Study of *Calanus finmarchicus* (TASC), European Commission contract no. MAS3-CT95-0039.

LITERATURE CITED

- Aksnes, D. L. 2007. Evidence for visual constraints in large marine fish stocks. *Limnology and Oceanography* 52:198–203.
- Aksnes, D. L., and J. Giske. 1993. A theoretical model of aquatic visual feeding. *Ecological Modelling* 67:233–250.
- Aksnes, D. L., J. Nejstgaard, E. Sæberg, and T. Sørnes. 2004. Optical control of fish and zooplankton populations. *Limnology and Oceanography* 49:233–238.
- Aksnes, D. L., and A. C. W. Utne. 1997. A revised model of visual range in fish. *Sarsia* 82:137–147.
- Alerstam, T., A. Hedenstrom, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247–260.
- Arrhenius, F., and S. Hansson. 1999. Growth of Baltic Sea young-of-the-year herring *Clupea harengus* is resource limited. *Marine Ecology Progress Series* 191:295–299.
- Batty, R. S., J. H. S. Blaxter, and J. M. Richard. 1990. Light-intensity and the feeding-behavior of herring, *Clupea harengus*. *Marine Biology* 107:383–388.
- Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664.
- Blaxter, J. H. S. 1966. The effect of light intensity on the feeding ecology of herring. Pages 393–412 in R. Bainbridge, G. C.

- Evans, and O. Rackham, editors. Light as an ecological factor. Blackwell Scientific Publications, Oxford, UK.
- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78:73–83.
- Broms, C., and W. Melle. 2007. Seasonal development of *Calanus finmarchicus* in relation to phytoplankton bloom dynamics in the Norwegian Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 54:2760–2775.
- Crick, H. Q. P., and T. H. Sparks. 1999. Climate change related to egg-laying trends. *Nature* 399:423–424.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Advances in Marine Biology* 26:249–293.
- Dalpadado, P., B. Ellertsen, W. Melle, and A. Dommasnes. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES Journal of Marine Science* 57:843–857.
- Drange, H., and K. Simonsen. 1996. Formulation of air-sea fluxes in the ESOP2 version of MICOM. Nansen Environmental and Remote Sensing Center, Bergen, Norway.
- Durant, J. M., D. O. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N. C. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8:952–958.
- Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884.
- Eggers, D. M. 1977. Nature of prey selection by planktivorous fish. *Ecology* 58:46–59.
- Fauchald, P., M. Mauritzen, and H. Gjøsæter. 2006. Density-dependent migratory waves in the marine pelagic ecosystem. *Ecology* 87:2915–2924.
- Gislason, A., and O. S. Astthorsson. 2002. The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia* 87:236–247.
- Heath, M. R., et al. 2000. Comparative analysis of *Calanus finmarchicus* demography at locations around the Northeast Atlantic. *ICES Journal of Marine Science* 57:1562–1580.
- Holst, J. C., I. Røttingen, and W. Melle. 2004. The herring. Pages 203–226 in H. R. Skjoldal, editor. *The Norwegian Sea ecosystem*. Tapir Academic Press, Trondheim, Norway.
- Jónasdóttir, S. H. 1999. Lipid content of *Calanus finmarchicus* during overwintering in the Faroe-Shetland Channel. *Fisheries Oceanography* 8:61–72.
- Kaartvedt, S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES Journal of Marine Science* 57:1819–1824.
- Link, J. 1996. Capture probabilities of Lake Superior zooplankton by an obligate planktivorous fish: the lake herring. *Transactions of the American Fisheries Society* 125:139–142.
- McQueen, D. J., M. R. S. Johannas, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on fresh water pelagic community structure. *Ecological Monographs* 59:289–309.
- Mobley, C. M. 1994. Light and water: radiative transfer in natural waters. Academic Press, San Diego, California, USA.
- Möllmann, C., G. Kornilovs, M. Fetter, F. W. Koster, and H. H. Hinrichsen. 2003. The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fisheries Oceanography* 12:360–368.
- Nøttestad, L., J. Giske, J. C. Holst, and G. Huse. 1999. A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 56:26–34.
- Olsen, E. M., W. Melle, S. Kaartvedt, J. C. Holst, and K. A. Mørk. 2007. Spatially structured interactions between a migratory pelagic predator, the Norwegian spring-spawning herring *Clupea harengus* L., and its zooplankton prey. *Journal of Fish Biology* 70:799–815.
- Østvedt, O. J. 1955. Zooplankton investigations from weathership M in the Norwegian Sea, 1948–1949. *Hvalrådets Skrifter* 40:1–93.
- Rosland, R., and J. Giske. 1994. A dynamic optimization model of the diel vertical-distribution of a pelagic planktivorous fish. *Progress in Oceanography* 34:1–43.
- Sandström, O. 1980. Selective feeding by Baltic herring. *Hydrobiologia* 69:199–207.
- Skjoldal, H. R., P. Dalpadado, and W. Melle. 2004. Food webs and trophic interactions. Pages 447–506 in H. R. Skjoldal, editor. *The Norwegian Sea ecosystem*. Tapir Academic Press, Trondheim, Norway.
- Sløtte, A. 1999. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology* 54:338–355.
- Speirs, D. C., W. S. C. Gurney, M. R. Heath, and S. N. Wood. 2005. Modelling the basin-scale demography of *Calanus finmarchicus* in the north-east Atlantic. *Fisheries Oceanography* 14:333–358.
- Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. *Proceedings of the National Academy of Sciences (USA)* 99:13379–13381.
- Utne-Palm, A. C. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *Journal of Fish Biology* 54:1244–1258.
- Utne-Palm, A. C., and J. K. Bowmaker. 2006. Spectral sensitivity of the two-spotted goby *Gobiusculus flavescens* (Fabricius): a physiological and behavioural study. *Journal of Experimental Biology* 209:2034–2041.
- Varpe, Ø., Ø. Fiksen, and A. Sløtte. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* 146: 443–451.
- Varpe, Ø., C. Jørgensen, G. A. Tarling, and Ø. Fiksen. 2007. Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos* 116:1331–1342.
- Varpe, Ø., C. Jørgensen, G. A. Tarling, and Ø. Fiksen. 2009. The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos* 118:363–370.
- Walton, W. E., N. G. Hairston, and J. K. Wetterer. 1992. Growth-related constraints on diet selection by sunfish. *Ecology* 73:429–437.