

Øystein Varpe · Øyvind Fiksen · Aril Slotte

Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration

Received: 6 January 2005 / Accepted: 13 July 2005 / Published online: 30 September 2005
© Springer-Verlag 2005

Abstract Ecosystems are not closed, but receive resource subsidies from other ecosystems. Energy, material and organisms are moved between systems by physical vectors, but migrating animals also transport resources between systems. We report on large scale energy transport from ocean to coast by a migrating fish population, the Norwegian spring-spawning (NSS) herring *Clupea harengus*. We observe a rapid body mass increase during parts of the annual, oceanic feeding migration and we use a bioenergetics model to quantify energy consumption. The model predicts strong seasonal variation in food consumption with a marked peak in late May to July. The copepod *Calanus finmarchicus* is the most important prey and 23×10^6 tonnes (wet weight) of *C. finmarchicus* is consumed annually. The annual consumption-biomass ratio is 5.2. During the feeding migration 17% of consumed energy is converted to body mass. The biomass transported to the coast and left as reproductive output is estimated from gonad weight and is about 1.3×10^6 tonnes for the current population. This transport is to our knowledge the world's largest flux of energy caused by a single population. We demonstrate marked temporal variation in transport during the last century and discuss the effects of NSS herring in the ocean, as a major consumer, and at the coast, where eggs and larvae are important for coastal predators. In particular, we suggest that the rapid decline of lobster *Homarus gammarus* landings in Western Norway during

the 1960s was related to the collapse of NSS herring. We also discuss spatial variation in energy transport caused by changed migration patterns. Both climate and fisheries probably triggered historical changes in the migration patterns of NSS herring. New migration routes emerge at the level of individuals, which in turn determines where resources are gathered and delivered, and therefore, how meta-ecosystems function.

Keywords Body condition · Capital breeder · Individual behaviour · Norwegian Sea · Salmon

Introduction

Ecosystems are not closed, but receive resource subsidies from other ecosystems (Loreau and Holt 2004; Loreau et al. 2003; Polis et al. 1997). On large spatial scales, subsidies are commonly transported by physical vectors such as ocean currents, rivers or winds. However, migrating organisms are also such vectors (Polis et al. 1997), particularly animals that feed in one area and rest, reproduce or die in other areas. For instance, Pacific salmon *Oncorhynchus* spp. carry resources from ocean to freshwater when migrating from oceanic feeding grounds to rivers and lakes where they reproduce and die (Naiman et al. 2002; Willson et al. 1998). Consequently, large scale ecosystem coupling emerge from life-histories and individual behaviour, and abundant migrating species that transport prey and nutrients between ecosystems are ecological cornerstones in the receiving system (Marston et al. 2002; Willson et al. 1998). The influx of resources to a system affects species abundance, diversity, trophic cascades and community structure (Polis et al. 1997). Even large scale influx of pollutants can result from animal migration (Krümmel et al. 2003). Similarly, the consequences of transport can be large also in the source system (Polis et al. 1997) and the dynamics created require a meta-ecosystem approach to be understood (Loreau et al. 2003). The meta-ecosystem concept is recently proposed and defined as a

Communicated by Wolf Mooij

Ø. Varpe (✉) · Ø. Fiksen
Department of Biology, University of Bergen,
5020 Bergen, Norway
E-mail: oystein.varpe@bio.uib.no
Tel.: +47-55584453
Fax: +47-55584450
E-mail: oyvind.fiksen@bio.uib.no

A. Slotte
Institute of Marine Research, 5817 Bergen, Norway
E-mail: aril.slotte@imr.no

set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries (Loreau et al. 2003). Behaviourally driven flows between systems have received increasing attention during the last decade (Polis et al. 1997; Willson et al. 1998), but quantification of fluxes is rare.

Although less conspicuous than predators feasting on salmon at river mouths (Willson et al. 1998), the resource transport of Norwegian spring-spawning (NSS) herring *Clupea harengus* is impressive by its magnitude and impact. NSS herring is one of the world's largest fish stocks, currently with a spawning stock biomass of about 6×10^6 tonnes, or about 25×10^9 individuals. The population size has fluctuated during the last century, with peak size in the mid 1940s (16×10^6 tonnes in 1945)

and a record low after the collapse in the late 1960s and early 1970s (2×10^3 tonnes in 1972) (Torensen and Østvedt 2000). The life cycle of NSS herring is spatially complex (Holst et al. 2002; Huse et al. 2002). The mature part of the population perform a yearly loop-like migration throughout the Norwegian Sea and along the Norwegian coast; feeding in the ocean during summer, overwintering in fjords in northern Norway, and spawning at coastal banks further south in February–March (Fig. 1). Feeding takes place during a short pulse of intensive zooplankton production in spring and summer (Dalpadado et al. 2000; Østvedt 1955), and the copepod *Calanus finmarchicus* is by far the most important prey (Dalpadado et al. 2000). After the feeding period food is sparse in this high latitude system

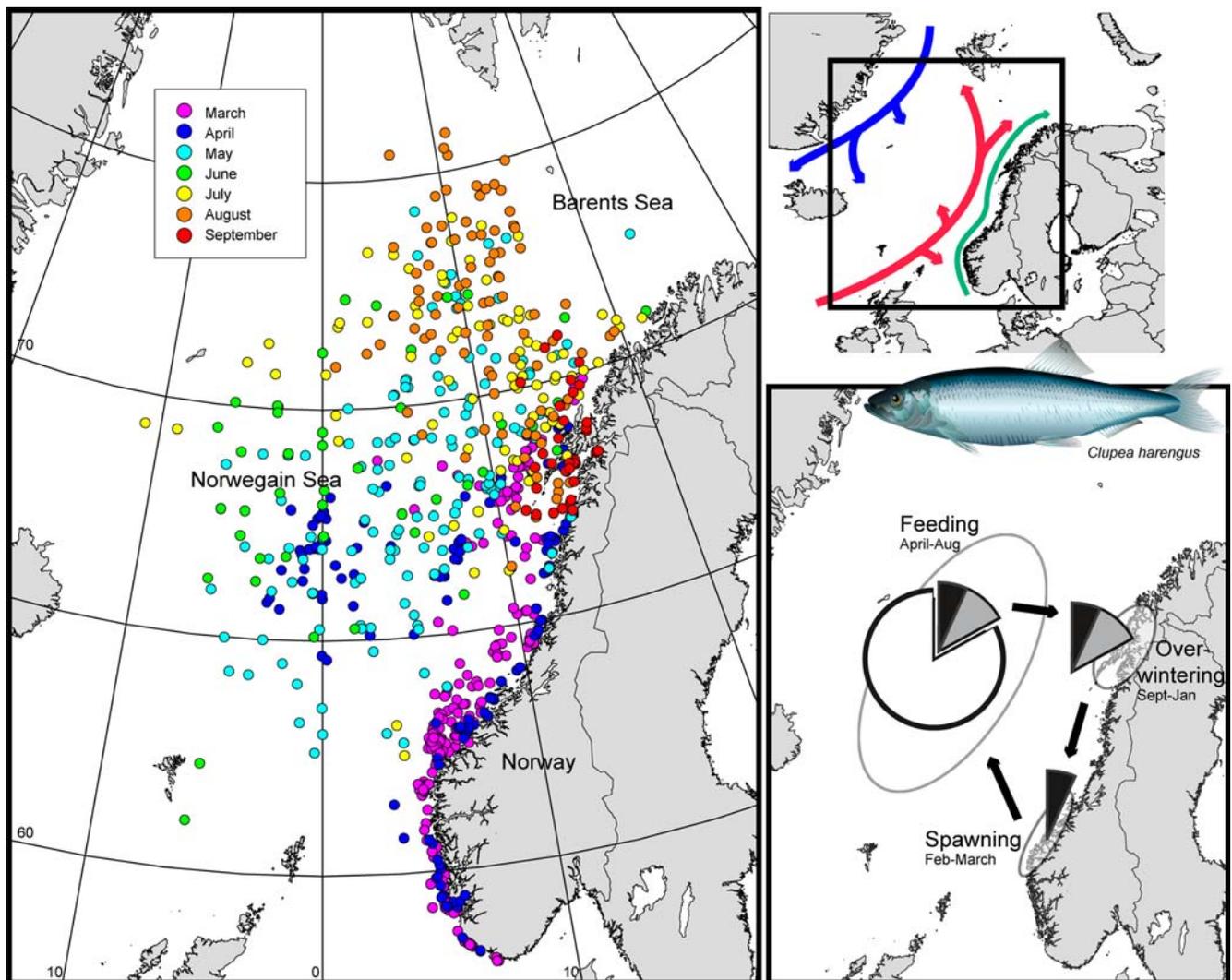


Fig. 1 The distribution, migration, and energy transport by Norwegian spring-spawning herring. *Left*: catches from the Norwegian Sea and the Norwegian Coast (1990–2003) included in the study. Catches are presented for the feeding period (March–September) with a separate colour for each month. *Lower right*: the main feeding, overwintering and spawning area accompanied by the energy transport caused by NSS herring. The cake in the feeding area is energy consumed during the

feeding period from which 17% (grey and black) is transported to the coast, and 7% (black) is left as reproductive output at the spawning grounds. *Black arrows* indicate migration direction. *Upper right*: outline of Northern Europe and the main ocean currents of the study area: Norwegian Atlantic Current (red), Norwegian Coastal Current (green) and East Greenland Current (blue). Gulf of Maine Research Institute made the herring drawing

and NSS herring fasts for about half a year; while overwintering and until spawning is completed (Nøttestad et al. 1996; Slotte 1999). Eggs are spawned on rocky bottom, mainly between 20 and 80 m depth, and hatch after about 3 weeks (Runnström 1941). The larvae drift northwards with the Norwegian Coastal Current and immature NSS herring spend the first 3–4 years in the Barents Sea. Adults, eggs and larvae of NSS herring are important food for many species at the coast (Durant et al. 2003; Høines and Bergstad 1999; Simila et al. 1996; Toresen 1991), and immature NSS herring are important prey in the Barents Sea (Bogstad et al. 2000).

We analysed body mass data for NSS herring, and used the body mass changes during the feeding season as input to a bioenergetics model. From this model we estimated energy consumption during the oceanic feeding migration, which approximates the annual energy consumption. Energy consumption is converted to prey consumption and these results are discussed, particularly in relation to the strong interaction between NSS herring and its main prey, *C. finmarchicus*. Based on the proportion of consumption used for growth, we also estimated the fraction of consumed energy that is brought from oceanic feeding areas to coastal overwintering areas. Furthermore, we used data on gonad weight to estimate the biomass of reproductive output (eggs and milt) spawned at the coast; an index of energy transported from oceanic feeding areas to coastal spawning grounds. We illustrate the temporal variation of this transport during the last century, and discuss the importance of NSS herring as a food source for several coastal species. In particular, we suggest that landings of lobster *Homarus gammarus* at the coast of Norway covary with the biomass of reproductive output left at the coast by NSS herring. Lobsters are opportunistic benthic feeders (Conklin 1995) that could benefit by NSS herring eggs. Finally, we discuss effects and likelihood of changed migration patterns and thereby spatial variation in this large energy flux. New migration routes evolve at the level of individuals (Berthold et al. 1992; Huse et al. 2002), which in turn determines where resources are gathered and delivered, and therefore, how meta-ecosystems function.

Materials and methods

Body mass estimates

We use trawl and seine data from the NSS herring database of the Institute of Marine Research in Bergen. Data from 1990 to 2003 are used due to the stable migration pattern of this period (Holst et al. 2002). Body mass changes are estimated for the feeding period; March–September. Average body mass was calculated for the first and last period of each month and for body length (total length) intervals of 1 cm. The length groups (28–38 cm) included correspond to the migrating and mature fraction of the population (Engelhard and Heino

2004). To eliminate confounding effects related to small samples, we omitted catches represented by less than 50 individuals. Based on inspection of the gonads, we omitted immature individuals and fish that spawned later than April. The resulting sample size is 40,533 individuals. Length-growth during the feeding migration was not accounted for, but the pattern of body mass change was similar if analysed for age- instead of length-groups. However, consumption estimates are conservative because some length-growth occurs during the feeding season.

Bioenergetics model for NSS herring

Bioenergetics models describe how organisms use consumed energy for respiration (including activity costs and specific dynamic action), waste losses (egestion and excretion) and growth (Adams and Breck 1990; Hanson et al. 1997; Rudstam 1988; Stewart and Binkowski 1986; Stewart et al. 1983). We used observed growth to predict daily energy consumption (Rice and Cochran 1984), and in our model, growth is synonymous with body mass change. We estimated consumption from the functions

Table 1 Equations, variables and parameters of the bioenergetics model

Description	Equations	Variables and parameters
Consumption ^a	$C = R + F + U + S + G$	
Respiration ^{b,c}	$R(W, T, V) = \alpha \cdot W^\beta \cdot e^{(\rho \cdot T)} \cdot e^{(\mu \cdot V)}$	$\alpha = 0.0033 \text{ gO}_2 \text{ g}^{-1} \text{ day}^{-1}$ $W = \text{body mass (g)}$ $\beta = -0.227$ $\rho = 0.0548^\circ\text{C}^{-1}$, $T = 5^\circ\text{C}$ $\mu = 0.03 \text{ cm}^{-1} \text{ s}$ $V = \text{swimming speed}$
Egestion	$F(C) = \theta \cdot C$	$\theta = 0.16$
Excretion	$U(F) = \epsilon \cdot F$	$\epsilon = 0.10$
Specific dynamic action	$S(C, F) = \omega \cdot (C - F)$	$\omega = 0.175$
Growth	$G = \text{body mass change}^d$	

Equations and parameters are from Hanson et al. (1997) and Rudstam (1988)

^aConsumption is modelled as g prey g herring⁻¹ day⁻¹. We use wet weight, and we correct for the relative densities of prey and predator (e.g. Stewart et al. 1983). The energy density of NSS herring vary with time (Fig. 2) and the energy density of prey is 3,500 J g⁻¹
^b α is converted to g g⁻¹ day⁻¹ by multiplying with 13,560 J gO₂⁻¹ (Elliott and Davison 1975) and dividing by the energy density of NSS herring (J g⁻¹) (e.g. Stewart et al. 1983)

^cSwimming speed is one body length per second (cm s⁻¹)

^dGrowth was estimated from body mass data. Body mass of an individual of given body length was predicted based on the linear relationship (for each period of half a month) between ln (yearly body mass averages) and ln (body length). To get daily estimates of body mass for individuals of a given body length, we used linear interpolation between the predicted body masses. We could then calculate daily changes in body mass

in Table 1 and assumed that maximum consumption rate did not limit modelled consumption during any day.

The model was parameterized as for Baltic herring (Rudstam 1988), but our approach deviates in the following three aspects. (1) We use a higher swimming speed to account for the feeding migration of NSS herring. Migration distance for large individuals estimated from Misund et al. (1998) is about 2,500 km, and to cover this distance in six months the minimum constant swimming speed must be 16 cm/s. We let swimming speed be one body length per second. This accounts for the longer migration by larger individuals (Misund et al. 1998; Nøttestad et al. 1999), and it is conservative because frequent turning and depth changes occur during migration (Misund et al. 1997, 1998). (2) The energy density of NSS herring is higher and has stronger seasonal variation compared to herring from the Baltic population (Rudstam 1988). We estimated seasonal variation in energy density (Fig. 2) based on data from Slotte (1999), and used the daily estimates in the bioenergetics model. Seasonal cycles in the energy density of the predator can strongly influence seasonal consumption patterns (Stewart and Binkowski 1986). (3) Water temperature in the feeding area vary both spatially and temporally, but we used a constant water temperature of 5°C (Dale et al. 1999; Misund et al. 1998).

Consumption was modelled daily from 15 March to 15 September for each length group, and scaled to population level based on the length distribution in the population. The length distribution was obtained by combining data on spawning stock numbers by age (Anon 2004b) and observed age and length of the mature individuals caught at the spawning grounds in January–April. Length distributions were estimated for each year, 1990–2003, and we used the average length distribution for these years. We assumed no mortality during the feeding season. The body mass average for

each length group observed on 15 March was used to estimate spawning stock biomass by length post spawning. Average yearly spawning stock biomasses post spawning for 1990–2003 was 6.1×10^6 tonnes.

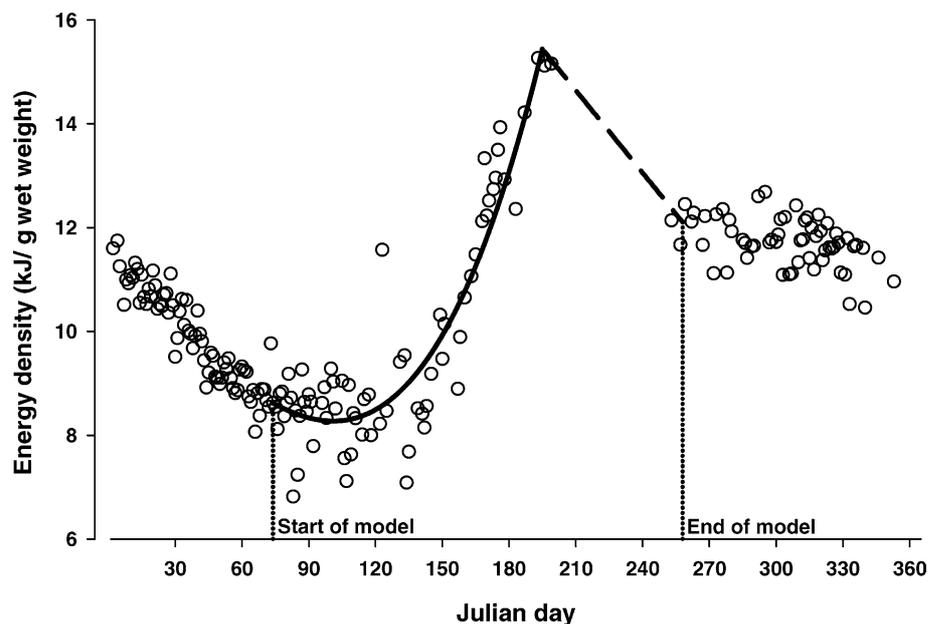
We investigated the sensitivity of the consumption estimate using individual parameter perturbations (Bartell et al. 1986). Alterations of single model variables and parameters, with a 10% positive or negative change always resulted in a smaller relative change in consumption. Among the field based variables and parameters the consumption estimate is most sensitive to changes in body mass and swimming speed. Swimming speed throughout the feeding migration is a poorly known variable, and if we increase swimming speed from 1 to 2 body lengths per second, the model predicts that energy consumption increase by 115%.

About 62% of the diet (wet weight) of NSS herring is copepods, mainly *C. finmarchicus* (Dommasnes et al. 2004). We assumed that this estimate also holds by energy, although compared to other copepods *C. finmarchicus* has high energy content (Laurence 1976). Consequently, we assumed that *C. finmarchicus* account for 60% of the energy requirements of NSS herring. An energy density of 3,500 J/g wet weight (Comita et al. 1966; Laurence 1976) was used to convert consumption from joule to *C. finmarchicus* biomass. To establish this energy density, we assumed that dry weight = $0.13 \times$ wet weight (Mullin 1969).

Gonad mass estimates

To estimate the energy content of spawning products, we used data on gonad mass for males and females with ripe gonads, maturity stage five, in January–March ($n = 8899$). For these individuals, the average proportion of body mass consisting of gonads was 0.19 (SD = 0.04)

Fig. 2 Daily energy density averages for NSS herring using data from Slotte (1999). A cubic curve (solid line) is fitted to the data from day 74 (15 March) to day 195 ($y = 11.067 - 0.027x - 2.807 \cdot 10^{-4}x^2 + 2.749 \cdot 10^{-6}x^3$). For the remaining feeding period, few energy density samples were available. For simplicity, we assumed a linear reduction (dashed line) until day 259 (15 September) ($y = 25.771 - 0.053x$). Daily energy densities y (kJ/g wet weight) are predicted for each day x and used in the bioenergetics model



for males and 0.20 (SD = 0.04) for females. We regressed $\ln(\text{gonad mass})$ on $\ln(\text{body length})$ by sex, to estimate average gonad mass for each sex and length group. The same length distribution as in the bioenergetics model was used to estimate gonad mass for the whole spawning population. We assumed a 50:50 sex ratio. The energy density of gonads was set to 8,000 J/g wet weight for ovaries and 6,000 J/g wet weight for testes (McGurk et al. 1980).

Lobster landings

We used data on lobster landings for the period 1932–2003, and the data are based on landings reported by local marketing co-operatives to the Norwegian Directorate of Fisheries. There has been an overall decrease in lobster landings during this period. We grouped the data into two: Western Norway, Rogaland–Møre og Romsdal, counties where spawning by NSS herring takes place, and Southern Norway, Østfold–Vest Agder, counties where NSS herring do not spawn. Then we examined if the pattern of decrease was different between the two regions, and if the pattern observed for Western Norway was related to the variation in biomass of reproductive output transported to the coast by NSS herring.

Results

Consumption

The body mass of NSS herring increases quickly during a few summer months, particularly from the second half of May until the first half of July (Fig. 3a). The marked body mass increase during the feeding season, 34–37% depending on body length, is capital needed for successful survival and reproduction the following winter and spring.

We used the body mass changes as input to a bioenergetics model and estimated food consumption by NSS herring during the annual feeding migration. Food consumption is low and increases slowly during the first two months after spawning, but it is high during the second half of May and in June. Thereafter, food consumption declines in July, while a second but smaller peak appears in the first half of August (Fig. 3b). For the average NSS herring population (1990–2003) annual energy consumption is 1.3×10^{17} J. To better illustrate the scale of this estimate, one may say that this energy would sustain the citizens of London for about 6 years (London population: 7.2×10^6 individuals, daily energy requirement per individual: 2,000 kcal = 8.4×10^6 J).

Assuming that 60% of the diet of NSS herring is *C. finmarchicus* (see Materials and methods), 23×10^6 tonnes (wet weight) of *C. finmarchicus* is consumed by NSS herring. This estimate is the average for 1990–2003, but

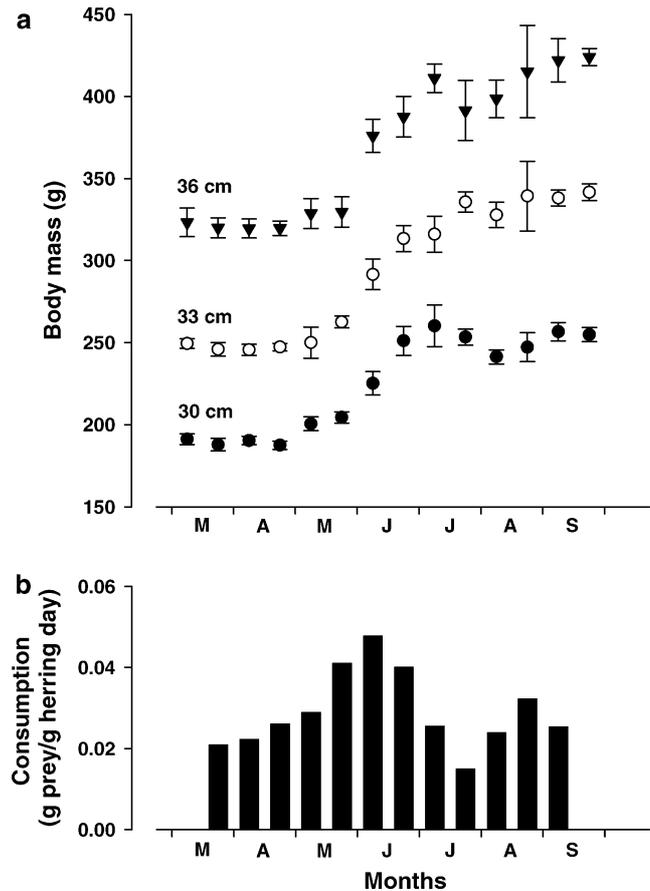


Fig. 3 Average body mass and consumption rate of NSS herring during the feeding migration, from the end of spawning until the start of overwintering. Averages are for periods of half a month. **a** Body mass for three different length groups, and averages are mean of yearly means (1990–2003) with SE. **b** Predicted specific consumption rate as average for all length groups in the bioenergetics model. The consumption estimates are based on an energy density of $3,500 \text{ J g}^{-1}$ wet weight for prey, and varying energy density (Fig. 2) for NSS herring

it could be doubled for the period prior to the collapse of NSS herring. Furthermore, assuming all prey has the same energy density as *C. finmarchicus*, we can estimate the biomass of consumed prey. The annual consumption-biomass ratio ranges from 4.6 to 6.2 depending on when NSS herring biomass is measured (low value: biomass after the feeding season, high value: biomass after spawning). If we sum up daily consumption-biomass ratios, the annual consumption-biomass ratio is 5.2.

Transport

Most of the consumed energy is used during the feeding migration. However, the bioenergetics model predicts that 17% of consumed energy is used for growth (body mass increase) and therefore transported to the coast. Some of this energy is used for metabolic needs while overwintering and for the spawning migration, and the

rest is used for reproduction next spring. Using data on gonad weight prior to spawning, we estimated that NSS herring leave 1.3×10^6 tonnes (9.4×10^{15} J) of reproductive output (eggs and milt) at the coastal banks. Hence, about 7% of the energy consumed at sea is used to produce gonads. The biomass of the spawning population of NSS herring has fluctuated greatly during the last century. We estimate historical transport by assuming that the present day's average for the proportion of body mass consisting of gonads prior to spawning also hold for the past (19% , see Materials and methods for details). The biomass transported to the coast by NSS herring should be doubled at times of high population sizes (Fig. 4). Conversely, the flux of energy from ocean to coast almost ceased after the collapse of the NSS herring stock (Fig. 4).

Lobster landings in Norway have declined since the 1930 s (note the reduced fishing effort during the Second World War), both in areas with spawning by NSS herring (Western Norway) and in areas where NSS herring do not spawn (Southern Norway) (Fig. 4). However, lobster landings decreased steadily in Southern Norway while there was a rapid decline in Western Norway during the 1960 s. This co-occurred with the NSS herring collapse and the cease of energy transport from ocean to coast (Fig. 4).

Discussion

NSS herring is important for the transfer of secondary production to higher trophic levels, but because of its

migration, food consumed in the ocean is transported to higher trophic levels at the coast. Consequently, migrating NSS herring is an important factor in both the oceanic and coastal ecosystem (e.g. Hamre 1994).

Consumption and ecological consequences in the ocean

The Norwegian Sea is a large marine ecosystem influenced by inflow of warm water from the North Atlantic and cold water from the Arctic Ocean (Fig. 1). There is strong seasonality in light conditions and therefore in primary and secondary production (Skjoldal et al. 2004). The Norwegian Sea is one of the principal regions of *C. finmarchicus* in the North Atlantic (Planque and Batten 2000).

The body mass of NSS herring increased rapidly from the second half of May to the beginning of July and the bioenergetics model consequently predicts high levels of food consumption during this period. At this time of the year, NSS herring is feeding in the central Norwegian Sea and the proportion of *C. finmarchicus* in the diet is particularly high (Dalpadado et al. 2000). From June onwards, the new generation of *C. finmarchicus* descend to overwintering depths (Arashkevich et al. 2004; Østvedt 1955) and is less available for NSS herring (Dalpadado et al. 2000). Copepod stage IV and V of *C. finmarchicus* build large fat sacs before they descend to deeper waters (Arashkevich et al. 2004). The seasonal consumption pattern predicted by the bioenergetics model emphasise the peak in energy transfer between zooplankton and NSS herring in the period before

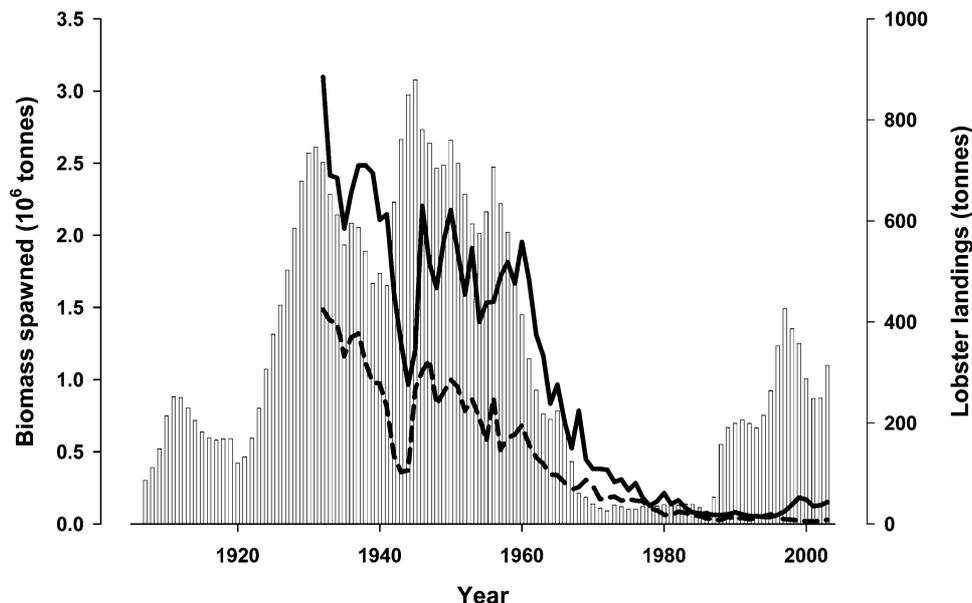


Fig. 4 Variation between years in the biomass of reproductive output for the NSS herring population and landings of lobster in Norway. Bars: estimates of reproductive output are based on yearly spawning stock biomass for 1907–1949 (Torensen and Østvedt 2000) and 1950–2003 (Anon 2004a), and on the observation that 19% (this study) of the spawning stock biomass is left at the coast as

reproductive output (eggs and milt). Solid line: landings of lobster reported in Western Norway, Rogaland–Møre og Romsdal, counties at the coast where spawning by NSS herring takes place. Broken line: Landings of lobster reported in Southern Norway, Østfold–Vest Agder, counties at the coast where spawning by NSS herring do not take place

C. finmarchicus descend. The high abundance of *C. finmarchicus* is one reason for the high consumption rates, but the lipid rich individual is particularly valuable prey and may explain the efficient energy transfer at the time. Future bioenergetics models for NSS herring may therefore improve with better understanding of seasonal variation in prey energy density. It also suggests a strong coupling between the life cycle of *C. finmarchicus* in the Norwegian Sea and the migration and feeding strategies of NSS herring.

The decrease in body mass in late July was unexpected and strongly reduce food consumption for a short period, while food consumption increase again towards the end of the feeding migration. This may reflect the occurrence of a second peak in zooplankton production, possibly the second generation of *C. finmarchicus* observed in some areas of the Norwegian Sea (Østvedt 1955).

We estimated that NSS herring take about 24×10^6 tonnes of *C. finmarchicus* per year at times of a medium-sized NSS population (cf. Dommasnes et al. 2004). Few population-size or production estimates are available for *C. finmarchicus* although this single species dominate the planktonic biomass in the North Atlantic (Planque and Batten 2000). However, for the Nordic Seas (Norwegian, Icelandic and Greenland Seas), an area larger than the feeding area of NSS herring, the annual production of *C. finmarchicus* is estimated to 75×10^6 tonnes (Aksnes and Blindheim 1996), but Skjoldal et al. (2004) estimated higher production. NSS herring mainly feed on the largest copepodite stages (stage IV, V and adults) (Dalpadado et al. 2000), and about half the production consists of these stages (Aksnes and Blindheim 1996). The abundance of the largest copepodite stages of *C. finmarchicus* in the Norwegian Sea could therefore be regulated by predation at times of a large NSS herring population. This may influence the overwintering population of *C. finmarchicus*, and because the reproductive potential of *C. finmarchicus* is low (Aksnes and Blindheim 1996), high predation on *C. finmarchicus* one season may lead to few recruits the next season, and consequently low food availability for NSS herring.

Transport, temporal variation and ecological consequences at the coast

When NSS herring spawn on the bottom in near shore areas on the continental shelf, this is the end station for the energy transported by NSS herring. However, after hatching, the larvae are advected further by the Norwegian Coastal Current, a northbound flow clearly separated from the Norwegian Atlantic Current further offshore (Fig. 1).

The energy transport from ocean to coast varies temporally with the population size of NSS herring (Fig. 4) as elegantly documented also for sockeye salmon *Oncorhynchus nerka* (Finney et al. 2000). At the coast,

predators and decomposers are receivers of these resources. For instance, NSS herring eggs are food for benthic fish predators, particularly haddock *Melanogrammus aeglefinus* (Høines and Bergstad 1999; Toresen 1991), but eggs from demersal spawners may also be important for benthic crustaceans. We suggested a relationship between food availability for lobsters and the landings of lobsters in Western Norway. This was partly motivated by the assertion among fishermen that the decline of the NSS herring population has contributed to poor lobster landings (Ø. Fiksen, personal communication). There has been an overall decline in lobster landings in Norway, most likely due to increased fishing effort (A. L. Agnalt, personal communication). However, the decline in Western Norway was particularly rapid shortly after the collapse of the NSS herring population. The collapse of NSS herring occurred after a period with new technical advances in the herring fishery and a resulting increase in fishing mortality (Dragesund et al. 1997). Therefore, the rapid decline in lobster landings in Western Norway may have been caused by reduced food availability, directly or indirectly caused by the decline in the amount of herring eggs spawned at the coast. We can only speculate on possible causal explanations such as reduced egg-production or reduced offspring survival for lobsters. At times of a large NSS herring population, spawning also takes place outside the main spawning grounds (Dragesund et al. 1997), and this wider spawning distribution makes herring eggs available to a larger proportion of the lobster population. We suggest that future studies test the observed relationship between NSS herring abundance and lobster landings and study the possible mechanisms in more detail.

After hatching, the herring larva grow as they drift northwards. First year NSS herring pass the large colony of Atlantic puffins *Fratercula arctica* at Røst in Lofoten, and it is an important prey fed to the chick. The breeding success of Atlantic puffins in this colony is closely related to the abundance of first year NSS herring and particularly to the body length of first year NSS herring (Durant et al. 2003; Lid 1981). The importance of body length reflects the growth conditions experienced by the herring larva after hatching (Durant et al. 2003). Immature NSS herring are also important prey for several species when reaching the Barents Sea (Bogstad et al. 2000). Additionally, predation by immature NSS herring on capelin larvae *Mallotus villosus* have had indirect effects on cod *Gadus morhua* abundance because capelin is the main prey of cod (Hamre 1994; Hjermann et al. 2004). Consequently, NSS herring dynamics are important, not only in the Norwegian Sea and at the coast, but also in the Barents Sea ecosystem (Hamre 1994).

Finally, adult NSS herring are also preyed upon, e.g. by killer whales *Orcinus orca* aggregating in the fjords hosting the population of NSS herring during autumn and early winter (Simila et al. 1996). NSS herring have used these fjords for overwintering since the mid 1980 s (Holst et al. 2002) and with the whales, tourism and

whale-safaris have become more important for the region. These fjords are also efficient fishing grounds, and a large part of the annual catches of NSS herring is taken in the overwintering area (e.g. Anon 2004b).

Transport and other meta-ecosystems

The NSS herring population is to our knowledge the largest fish population that feed in one distinct area or ecosystem, and spend the rest of the year in another. The resulting biomass transfer is probably also the largest flux of energy caused by a migrating population, although NSS herring has a conservative life history, being long lived with many reproductive attempts. Conversely, semelparous species (which reproduce once, then die) such as capelin and Pacific salmon leave a larger proportion of the mature population in the receiving system. However, although Pacific salmon are known for large transports from ocean to freshwater, the biomass of the annual historical runs of the five salmon species in the northeast Pacific is about the same as the reproductive outputs of the current population of NSS herring (Gresh et al. 2000).

Spatial variation in transport

In addition to the temporal variation in transport discussed above, the energy flow caused by NSS herring varies spatially as migration patterns change. Migration patterns can change quickly through short time evolution (e.g. Berthold et al. 1992) and learning (e.g. Huse et al. 2002), and climatic changes and fisheries have historically led to new migration routes for NSS herring (Dragesund et al. 1997; Holst et al. 2002; Huse et al. 2002).

Climatic variation has influenced the distribution of the cold front and possibly determined the western extent of the feeding migration (Holst et al. 2002). Future climate changes are expected to increase the water temperature in the Norwegian Sea (Hassol 2004), and species-distributions are predicted to shift to the north (Beaugrand et al. 2002; Hassol 2004). In fact, the spawning grounds of NSS herring have shifted northwards during the last century (Devold 1963; Holst et al. 2002). This determines where the transported resources are deposited relative to coastal consumers such as benthic invertebrates, fish and seabirds. The response of these species will vary depending on several constraints. For instance, the Atlantic puffin may adjust timing of reproduction according to its food source (Durant et al. 2004), but responses to spatial changes are constrained by foraging ranges and the position of colonies.

Learning may also change migration patterns and the resulting spatial patterns in energy transport. When strong year-classes are recruited to the spawning stock, there are few older individuals to learn from, due to numerical domination by recruits, and the probability of

new migration routes increase (Huse et al. 2002). This probability is particularly high when the adult stock is small, and this bottleneck-effect probably induced the change of overwintering habitat from Iceland to northern Norway during the recovery of the NSS herring population in the 1980 s (Huse et al. 2002).

Conclusion

Migration and distribution of animals emerge at the level of individuals and belong to the realm of behavioural- and evolutionary-ecology. At the same time, migrating animals affect biogeochemical cycles and flows (Polis et al. 1997), affect how ecosystems are coupled, and remain an integral part of a meta-ecosystem perspective (Loreau et al. 2003). There are current trends towards managing populations with a holistic and ecosystem-based approach (e.g. Pikitch et al. 2004), and as illustrated here, the coupling between ecosystems is also important as are the individuals responsible for the coupling (cf. Ashley et al. 2003).

Acknowledgements We thank Dag L. Aksnes, Sigrunn Eliassen, Jens Christian Holst, and two referees for valuable comments on the manuscript. We thank the Directorate of Fisheries for data on lobster landings and Ann-Lisbeth Agnalt for systematizing some of the data. Ø.V. thanks Ann-Lisbeth Agnalt for discussions on lobster biology and catch statistics, and Christian Jørgensen for valuable discussions on several aspects of this work. Ø.V. and Ø.F. acknowledge the Norwegian Research Council for funding.

References

- Adams SM, Breck JE (1990) Bioenergetics. In: Schreck CB, Moyle PB (eds) Methods for fish biology. American Fisheries Society, Bethesda, pp 389–415
- Aksnes DL, Blindheim J (1996) Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44:7–28
- Anon (2004a) Extract of the report of the advisory committee on fishery management. International Council for the Exploration of the Sea, Copenhagen
- Anon (2004b) Report of the northern pelagic and the blue whiting fisheries working group. International Council for the Exploration of the Sea, Copenhagen
- Arashkevich EG, Tande KSS, Pasternak AF, Ellertsen B (2004) Seasonal moulting patterns and the generation cycle of *Calanus finmarchicus* in the NE Norwegian Sea, as inferred from gnathobase structures, and the size of gonads and oil sacs. *Mar Biol* 146:119–132
- Ashley MV, Willson MF, Pergams ORW, O'Dowd DJ, Gende SM, Brown JS (2003) Evolutionarily enlightened management. *Biol Conserv* 111:115–123
- Bartell SM, Breck JE, Gardner RH, Brenkert AL (1986) Individual parameter perturbation and error analysis of fish bioenergetics models. *Can J Fish Aquat Sci* 43:160–168
- Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Berthold P, Helbig AJ, Mohr G, Querner U (1992) Rapid micro-evolution of migratory behavior in a wild bird species. *Nature* 360:668–670
- Bogstad B, Haug T, Mehl S (2000) Who eats whom in the Barents Sea? *NAMMCO Scient Publ* 2:98–118

- Comita GW, Marshall SM, Orr AP (1966) On the biology of *Calanus finmarchicus* XIII. Seasonal change in weight, calorific value and organic matter. *J Mar Biol Ass UK* 46:1–17
- Conklin DE (1995) Digestive physiology and nutrition. In: Factor JR (ed) *Biology of the lobster Homarus americanus*. Academic Press, San Diego, pp 441–463
- Dale T, Rey F, Heimdal BR (1999) Seasonal development of phytoplankton at a high latitude oceanic site. *Sarsia* 84:419–435
- Dalpadado P, Ellertsen B, Melle W, Dommasnes A (2000) Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J Mar Sci* 57:843–857
- Devold F (1963) The life history of the Atlanto-scandian herring. *Rapp et Proc Verb Cons Int Explor Mer* 154:98–108
- Dommasnes A, Melle W, Dalpadado P, Ellertsen B (2004) Herring as a major consumer in the Norwegian Sea. *ICES J Mar Sci* 61:739–751
- Dragesund O, Johannessen A, Ulltang O (1997) Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia* 82:97–105
- Durant JM, Anker-Nilssen T, Hjermann DO, Stenseth NC (2004) Regime shifts in the breeding of an Atlantic puffin population. *Ecol Lett* 7:388–394
- Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc R Soc Lond B* 270:1461–1466
- Elliott JM, Davison W (1975) Energy equivalents of oxygen-consumption in animal energetics. *Oecologia* 19:195–201
- Engelhard GH, Heino M (2004) Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. *Fish Res* 66:299–310
- Finney BP, Gregory-Eaves I, Sweetman J, Douglas MSV, Smol JP (2000) Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science* 290:795–799
- Gresh T, Lichatowich J, Schoonmaker P (2000) An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25:15–21
- Hamre J (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodivers Conserv* 3:473–492
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF (1997) *Fish Bioenergetics* 30 University of Wisconsin Sea Grant Institute
- Hassol SJ (2004) *ACIA, Impacts of a warming Arctic: Arctic climate impact assessment*. Cambridge University Press, Cambridge
- Hjermann DO, Ottersen G, Stenseth NC (2004) Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proc Natl Acad Sci USA* 101:11679–11684
- Holst JC, Dragesund O, Hamre J, Misund OA, Østvedt OJ (2002) Fifty years of herring migration in the Norwegian Sea. *ICES Mar Sci Symp* 215:352–360
- Huse G, Railsback S, Fernö A (2002) Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *J Fish Biol* 60:571–582
- Høines AS, Bergstad OA (1999) Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. *J Fish Biol* 55:1233–1257
- Krümmel EM, et al (2003) Delivery of pollutants by spawning salmon: fish dump toxic industrial compounds in Alaskan lakes on their return from the ocean. *Nature* 425:255–256
- Laurence GC (1976) Caloric values of some North Atlantic calanoid copepods. *Fish Bull* 74:218–220
- Lid G (1981) Reproduction of the puffin on Røst in the Lofoten islands in 1964–1980. *Fauna Norv Ser C, Cinclus* 4:30–39
- Loreau M, Holt RD (2004) Spatial flows and the regulation of ecosystems. *Am Nat* 163:606–615
- Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol Lett* 6:673–679
- Marston BH, Willson MF, Gende SM (2002) Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. *Mar Ecol Prog Ser* 231:229–236
- McGurk MD, Green JM, McKone WD, Spencer K (1980) Condition indices, energy density and water and lipid content of Atlantic herring (*Clupea harengus harengus*) of southeastern Newfoundland. *Can Tech Rep Fish Aquat Sci*:1–41
- Misund OA, Melle W, Ferno A (1997) Migration behaviour of Norwegian spring spawning herring when entering the cold front in the Norwegian Sea. *Sarsia* 82:107–112
- Misund OA, et al (1998) Distribution, migration and abundance of Norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in spring and summer 1996. *Sarsia* 83:117–127
- Mullin MM (1969) Production of zooplankton in the ocean: the present status and problems. *Oceanogr Mar Biol Ann Rev* 7:293–314
- Naiman RJ, Bilby RE, Schindler DE, Helfield JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417
- Nøttestad L, Aksland M, Beltestad A, Ferno A, Johannessen A, Misund OA (1996) Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus* L) in a coastal spawning area. *Sarsia* 80:277–284
- Nøttestad L, Giske J, Holst JC, Huse G (1999) A length-based hypothesis for feeding migrations in pelagic fish. *Can J Fish Aquat Sci* 56:26–34
- Pikitch EK, et al (2004) Ecosystem-based fishery management. *Science* 305:346–347
- Planque B, Batten SD (2000) *Calanus finmarchicus* in the North Atlantic: the year of Calanus in the context of interdecadal change. *ICES J Mar Sci* 57:1528–1535
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316
- Rice JA, Cochran PA (1984) Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65:732–739
- Rudstam LG (1988) Exploring the dynamics of herring consumption in the Baltic: applications of an energetic model of fish growth. *Kiel Meeresforsch* 6:312–322
- Runnström S (1941) Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway. *FiskDir Skr Ser HavUnders* 6:1–71
- Simila T, Holst JC, Christensen I (1996) Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Can J Fish Aquat Sci* 53:769–779
- Skjoldal HR, Dalpadado P, Dommasnes A (2004) Food webs and trophic interactions. In: Skjoldal HR (ed) *The Norwegian Sea ecosystem*. Tapir Academic Press, Trondheim, pp 447–506
- Slotte A (1999) Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *J Fish Biol* 54:338–355
- Stewart DJ, Binkowski FP (1986) Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. *Trans Am Fish Soc* 115:643–661
- Stewart DJ, Weininger D, Rottiers DV, Edsall TA (1983) An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Can J Fish Aquat Sci* 40:681–698
- Toresen R (1991) Predation on the eggs of Norwegian spring-spawning herring (*Clupea harengus* L) on a spawning ground on the west-coast of Norway. *ICES J Mar Sci* 48:15–21
- Toresen R, Østvedt OJ (2000) Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish Fisheries* 1:231–256
- Willson MF, Gende SM, Marston BH (1998) Fishes and the forest: expanding perspectives on fish-wildlife interactions. *Bioscience* 48:455–462
- Østvedt OJ (1955) Zooplankton investigations from weathership M in the Norwegian Sea, 1948–1949. *Hvalr Skr* 40:1–93