

Lack of spatial coherence of predators with prey: a bioenergetic explanation for Atlantic cod feeding on capelin

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We tested two biologically based predictions that potentially influence scales of spatial association between Atlantic cod, *Gadus morhua*, and prey populations of capelin, *Mallotus villosus*. If cod aggregate in response to concentrations of prey, then spatial association (coherence) between capelin and cod was predicted to peak at the scale of maximum capelin spatial variance. If capelin–cod coherence did not match the scale of maximum prey spatial variability, then capelin–cod coherence was predicted to peak at the spatial scale that maximizes net energetic benefit to the predator. Contrary to predictions, we found no evidence of aggregative responses of cod to capelin over resolution scales of 20 m to 10 km. This result was observed consistently at the temporal scale of a single transect (c. 1 h duration) and at the scale of averaged transects (c. 2 weeks duration). Estimates of cod foraging energetics showed that they were not constrained by physiology to aggregate relative to capelin at any scale less than 10 km. A net energetic gain of 478 to 784 kJ would result if a 44 cm, 752 g cod consumed a ration of eight to 12 capelin over a period of 58 h. Energetic calculations included costs of egestion and excretion (317 to 476 kJ), maintenance (58 kJ), digestion (125 to 188 kJ), and continuous swimming during ration assimilation (79 kJ). During this period, a 44 cm cod could travel over 38 km swimming at 1 v.l. s⁻¹. Foraging cod are virtually certain to encounter capelin over this distance based on the abundance of pre-spawning capelin present in coastal bays during the spawning season. This study illustrates that aggregative responses of predators do not occur at all scales and possibly occur over a very limited range of scales.

Key words: foraging energetics; Newfoundland; predator–prey interaction; scale-dependence.

INTRODUCTION

Quantifying interactions between predators and prey continues as a dominant theme in ecology. Theoretical models of this interaction have been limited largely to either the spatial scale of an individual organism or to that of the population (for reviews see Levin, 1976; Chesson, 1978; Taylor, 1988; Taylor, 1990; Hastings, 1990; Reeve, 1990; Kareiva, 1990; Berryman, 1992). At these two spatial scales the dependence of observed patterns on measurement scale has been identified (Waage, 1979; Morrison & Strong, 1980; Heads & Lawton, 1983; Hanski, 1991) and the necessity of multiscale quantification of predator–prey theory is expressed regularly in the literature (e.g. Hassell & May, 1973; Anderson & May, 1985; Holdbrook & Schmitt, 1988; Kareiva, 1990; Aronson, 1992; Schneider, 1993). Quantifying the scale-dependence of predator–prey interactions requires comparison of results over a wide range of spatial scales.

Several recent studies have examined whether mobile, aquatic predators are associated with prey at characteristic spatial scales (Table I). Scales of maximum

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TABLE I. Spatial scales of maximum covariation among mobile, aquatic predators and their prey

Predator	Prey	Scale of maximum covariation					Source
		>100 km	100 to 10 km	10 to 1 km	1 km to 100 m	<100 m	
Zooplankton	Phytoplankton			1 km			Mackas & Boyd (1979)
Zooplankton	Phytoplankton		10 km	1 km	<1 km		Star & Mullin (1981)
Krill	Phytoplankton			2.5 km			Weber <i>et al.</i> (1986)
Krill	Phytoplankton	500 km					Miller & Monteiro (1988)
Birds	Zooplankton		10 to 100 km				Heinemann <i>et al.</i> (1989)
Birds	Zooplankton			>5 km			Hunt <i>et al.</i> (1990)
Fish	Fish		10 to 20 km	<5 km		3.5 m	Rose & Leggett (1990)
Birds	Fish			>1 km			Safina & Burger (1985)
Birds	Fish			2 to 6 km	0.25 km		Schneider & Platt (1986)
Birds	Fish			>1 km			Safina & Burger (1988)
Birds	Fish			5 km			Schneider (1989)
Birds	Fish			>1 km			Erikstad <i>et al.</i> (1990)
Birds	Fish			5 km			Platt (1990)

predator-prey association were then matched to dominant physical processes to explain observed patterns of biological variance. This approach assumes that biological pattern is created by physical processes at the same scale (Horne & Schneider, 1994). Direct coupling between biological and physical processes at the same scale is hypothesized often when prey organisms, such as phytoplankton, move passively with the surrounding fluid (e.g. Legendre & Demers, 1984; Mackas *et al.*, 1985). Spatial variance patterns of organisms that move independently of the fluid commonly do not match those of physical quantities (e.g. Weber *et al.*, 1986; Levin *et al.*, 1989; Horne, 1994; Schneider, 1994).

Characteristic scales of interaction between predators and prey may be influenced also by biological processes such as the aggregative response of predators to concentrations of prey (Holling, 1965, 1966; Murdoch & Oaten, 1975). Concentrations of prey influence potentially the spatial variance patterns of predators and the scale of maximum spatial association between predators and prey. The influence of aggregative responses on the spatial variance of mobile predator-prey interactions has not been examined over a wide range of scales.

We predicted two different scales of maximum spatial association between Atlantic cod *Gadus morhua* (L.) and capelin *Mallotus villosus* (Müller) at the temporal scale of a foraging bout. Spatial association between predator and prey could peak at the scale of maximum prey spatial variance (Fig. 1) which maximizes potential contact rate of predator with prey. If the scale of maximum predator-prey spatial association does not match that of maximum prey spatial variance, then we predicted spatial association between predators and prey to peak at an alternative scale that maximizes net energetic benefit to the predator (Fig. 1).

We used relative density estimates of capelin and Atlantic cod to examine scale-dependent spatial associations between a mobile aquatic predator and its prey. During June and July adult capelin, age 3 years and older, migrate from offshore to Newfoundland coastal waters to spawn on gravel beaches (Templeman, 1948; Carscadden, 1983). During this period Atlantic cod, a demersal species, complete a post-spawning migration to coastal waters to forage on capelin (Akenhead *et al.*, 1982; Lilly, 1987). We compared scale-dependent patterns of capelin spatial variance to measures of spatial association (coherence) between capelin and Atlantic cod. Low coherence values between predator and prey prompted an examination of the bioenergetics of cod foraging to see if cod were obliged to track capelin during this period.

METHODS

SPATIAL VARIANCE PATTERNS

Hydroacoustic surveys were conducted along the western coast of Conception Bay, Newfoundland during the latter half of July and the first week of August, 1991. Linear transects were oriented parallel to the coast within the 100 m depth contour when possible. Stationary fishing gear adjacent to the coast restricted proximity of transects to shore. The majority of transects were run during the day but collectively transects spanned all 24 h in a day. Transect length among the 19 transects used in the analysis varied from 5.5 to 22.7 km (Table II). Capelin and cod relative density distributions

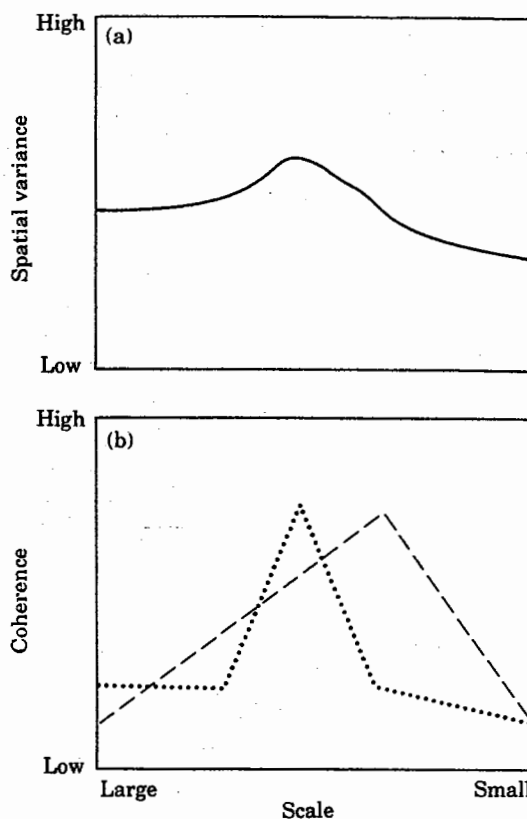


FIG. 1. (a) Schematic diagram of prey spatial variance. (b) Coherence between predator and prey as a function of scale. Dotted line (· · ·) shows peak in coherence between predator and prey matches the scale of maximum prey spatial variance in (a). Dashed line (---) shows peak occurs at another scale that potentially maximizes net energetic gain to the predator.

were surveyed acoustically using a 120 kHz echosounder (Model 105, Biosonics, Seattle, Washington U.S.A.) with a single-beam 22° transducer mounted in a towed V-fin. Pulse width was set at 0.8 ms and generated at a rate of 2 pulses s^{-1} . Data were heterodyned to 10 kHz using a Biosonics model 171 interface and stored on digital audio tapes for echo integration processing. A calibration tone was recorded at the beginning of each day to standardize playback amplitude levels. The V-fin was towed at a depth of approximately 1.5 m, at a speed of 2.5 $m s^{-1}$. A pair of 95 N expansion springs were used to decouple motions of the boat from that of the towed body in order to enhance transducer stability. Acoustic data were integrated using a Biosonics 221 echo integrator which digitally samples voltages at 25 kHz. Relative fish density estimates were calculated from $20 \log R$ amplified target voltages (Burczynski, 1982). Data were stratified in 10 m horizontal by 5 m vertical bins to a maximum depth of 112 m. To prevent integration of surface noise or bottom echoes the top 2 m and bottom 1 m of the water column were not included. Fish relative densities in each bin were classified as cod or capelin on the basis of: (a) classification of targets viewed on an oscilloscope based on signal properties (Rose & Leggett, 1988); (b) simultaneous viewing of near-surface capelin aggregations in the water and traces on oscilloscope and echograms; (c) capture of capelin and cod using hook and line while recording traces on echogram; (d) the observation that capelin and cod were the overwhelmingly dominant species in commercial traps in the sampling area; and (e) similarity of echogram traces with those of capelin and cod reported in northwest Atlantic waters (Atkinson & Carscadden, 1979; Whitehead, 1981; Piatt, 1990; Rose, 1992). Relative fish densities were integrated over

TABLE II. Date, start time, end time, and distance of hydroacoustic transects in Conception Bay, Newfoundland

Transect	Date (day/month)	Start time	End time	Distance (m)
9101	19/7	10:47	12:04	11 668
9105	20/7	12:47	13:27	5 556
9106	20/7	13:43	14:36	7 223
9107	20/7	15:05	15:59	8 159
9109	23/7	10:17	11:12	8 334
9110	23/7	11:39	14:04	19 631
9112	23/7	17:22	19:53	23 335
9113	24/7	10:36	13:51	20 742
9115	24/7	14:04	16:10	19 816
9122	25/7	21:03	23:47	22 780
9123	25/7	23:59	02:35	20 372
9124	26/7	02:44	04:37	14 631
9125	01/8	11:26	12:43	10 927
9129	02/8	07:43	09:20	10 742
9130	02/8	09:34	10:33	8 519
9131	02/8	10:44	11:47	6 667
3132	02/8	12:32	13:54	9 075
9133	02/8	18:00	20:01	9 445
9134	02/8	20:08	21:02	8 890

the water column to analyse horizontal variation of capelin relative to cod. Relative fish densities were integrated vertically to a maximum depth of 112 m and then summed for each 10 m horizontal distance.

Uni- and bivariate spectral analyses (Jenkins & Watts, 1968; Chatfield, 1980) were used to examine the spatial variance patterns of capelin and the scales of spatial association between capelin and Atlantic cod. This technique estimates scale-dependent variance of a continuously recorded variable over a range of frequency bands. The range of frequency bands is determined by the length of the series and the sampling resolution. The observational window for any series extends from half the length of the series to twice the sample resolution. Coherence measures the strength of association between two variables as a function of frequency and is analogous to a squared correlation, with potential values ranging from 0 to 1. Phase indicates the sign of correlation between two series. Two series that are less than 90° out of phase are positively correlated and termed in phase. Two series that are greater than 90° out of phase are negatively correlated and termed out of phase. A smoothing window of 0.01 cycles m⁻¹ was used in comparative analyses to provide the best compromise between accuracy and smoothness. All spectral density estimates were standardized to permit direct comparison of survey transects (Denman, 1975). The analytic window extends from 20 m to 10 km. Spectral density estimates of capelin and cod were averaged over 0.0001 cycle bins to produce average spectral density plots.

BIOENERGETIC CALCULATIONS

Estimates of daily ration from cod feeding models were compared to surplus energy calculations based on glut foraging on capelin at approximately 4° C. Glut foraging is defined as feeding to repletion. Mean cod length was used to estimate weight of a predator using the weight-length relationship from Bishop *et al.* (1993):

$$\log W = 3.0879 \log L - 5.2106 \quad (1)$$

where $\log W$ is the common logarithm of fish weight (kg) and $\log L$ is the common

logarithm of fish length (cm). Estimated daily ration as a function of temperature was calculated using (Jobling, 1988):

$$\ln FI = (0.104T - 0.000112T^3 - 1.5) + 0.802 \ln W \quad (2)$$

where FI is food intake (kJ day^{-1}), T is temperature ($^{\circ}\text{C}$), and W is mass of fish (g). This estimate was compared to the average amount of food eaten \hat{y}_i (g day^{-1}) by the i th fish using (Waiwood *et al.*, 1991):

$$\hat{y}_i = \hat{P}_j e^{(-1.66 + 0.6547x_i)} \quad (3)$$

where \hat{P}_j represents the probability of feeding (Table 5, Waiwood *et al.*, 1991) at temperature j and x_i is the natural logarithm of fish mass (g).

Calculated estimates of cod daily ration were compared to estimates of surplus energy Δw kJ available to cod from a glut feeding on capelin. Bioenergetic calculations were based on Winberg (1956):

$$\Delta w = pR - T \quad (4)$$

where p is a dimensionless coefficient correcting for the unassimilated proportion of ration R (kJ) and T (kJ) is metabolic dissipation. In these calculations p was set at 30% (Brett & Groves, 1979). Following Kerr (1971), the metabolic component T was separated into maintenance T_s , digestion T_c , and external activities T_F (i.e. swimming).

$$T = T_s + T_c + T_F \quad (5)$$

Maintenance costs $T_s = R_{\text{maint}}$ (kcal day^{-1}) were estimated using an equation from Jobling (1982):

$$R_{\text{maint}} = 0.017 W^{0.879} \quad (6)$$

where W is fish mass (g). Calorific estimates were converted to SI units using 4.184 J cal^{-1} . Digestion costs T_c were set at 11.85% of ingested energy based on laboratory experiments conducted with juvenile cod at 7°C (Soofiani & Hawkins, 1982). Gastric emptying of a full cod stomach at 5°C was set at 58 h or 2.42 days (Tyler, 1970). Mean body lengths of capelin and cod were used to estimate swimming speeds using an equation from Okubo (1987):

$$u = 2.69L^{0.86} \quad (7)$$

where u is speed (cm s^{-1}) and L is total length of fish (cm). Maximum potential range of foraging cod was calculated by multiplying swimming speed by the number of seconds in a day. Swimming costs for cod T_F were estimated using results from respirometer experiments. Amount of oxygen consumed VO_2 ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) at a given temperature was calculated using fish swimming speed (U) in body lengths per second (Soofiani & Priede, 1985):

$$\log_{10} VO_2 = 1.992 + 0.12U \quad (8)$$

Oxygen consumed was converted to energy using an oxycalorific coefficient of $3.36 \text{ cal kg}^{-1} (\text{mg O}_2)^{-1}$ (Brett, 1973).

RESULTS

SPATIAL VARIANCE PATTERNS

At the temporal resolution of an individual transect (*c.* 1 h), a characteristic pattern of capelin spatial variance was not present among the 19 transects surveyed in Conception Bay. Concentrations of spatial variance were observed in individual transects [Fig. 2(a)] but frequencies of maximum spectral density were not consistent among spatially or temporally separated transects. Peaks in spectral density plots occurred throughout the 20 m to 10 km range of analysed spatial scales. Strong concentrations of spatial variance were observed in five of

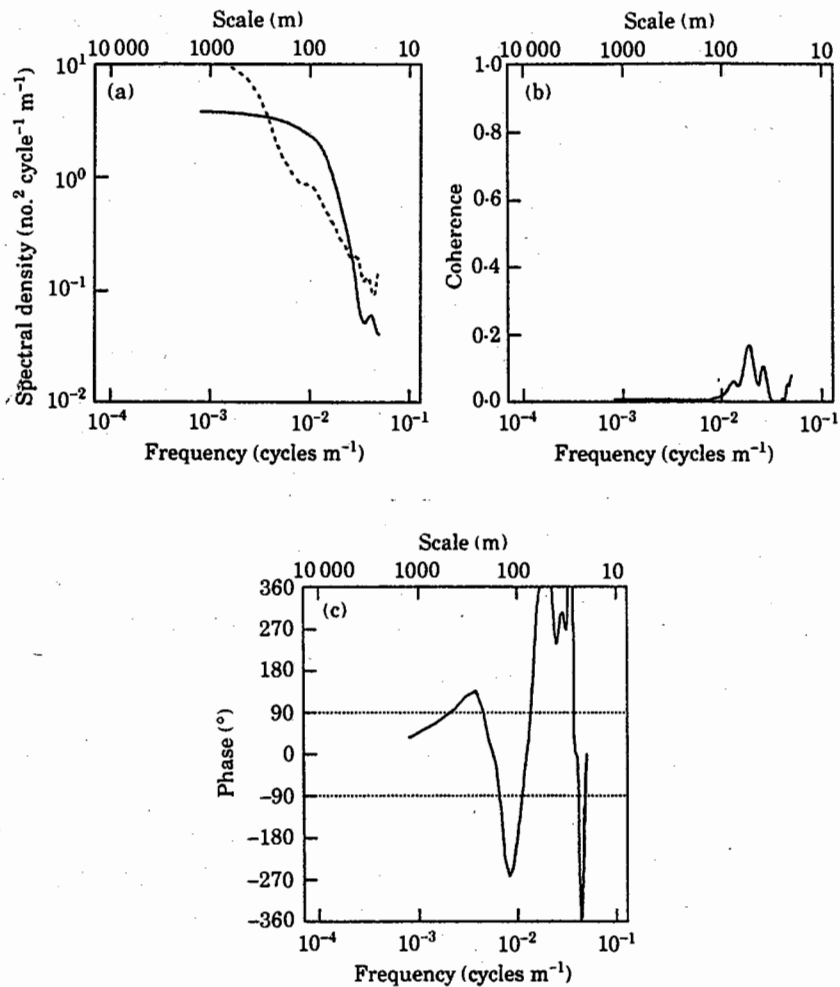


FIG. 2. (a) Spectral density estimates of capelin (---) and Atlantic cod (—) plotted as a function of frequency (bandwidth 0.01, centred, normalized). Periods (m) are shown on upper X axis. (b) Coherence of capelin and Atlantic cod plotted as a function of frequency. (c) Phase estimates of capelin and Atlantic cod plotted as a function of frequency.

19 transects. Weaker concentrations of spatial variance were observed in seven of 19 transects. No concentrations of spatial variance at any scale were observed in the remaining seven transects. Among the cod spectral density plots, only two transects contained strong concentrations of spatial variance. An additional seven transects contained concentrations of spatial variance spread over a broader range of frequencies [Fig. 2(a)]. Coherence values between cod and capelin were generally below 0.2 in all transects. Only three of the 19 transects contained recognizable peaks of coherence at any scale [Fig. 2(b)]. In all transects phase spectra of capelin and cod oscillated in and out of phase over the range of analysed spatial scales [Fig. 2(c)].

To examine patterns of spatial variance over longer temporal scales, spectral density estimates of capelin and cod relative densities were averaged over 0.0001 frequency bins and plotted as a function of frequency. Average spatial variance

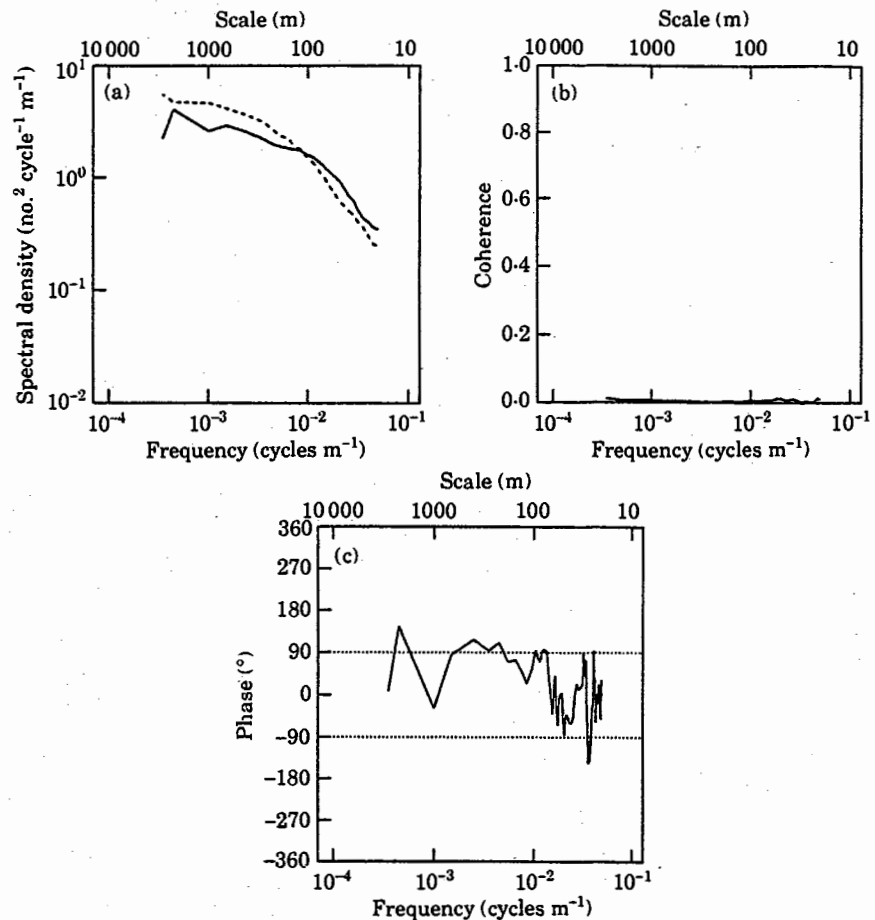


FIG. 3. (a) Average spectral density estimates of capelin (---) and Atlantic cod (—) plotted as a function of frequency (averaged over 0.0001 cycle bins). Periods (m) are shown on upper X axis. (b) Average coherence of capelin and Atlantic cod plotted as a function of frequency. (c) Average phase estimates of capelin and Atlantic cod plotted as a function of frequency. Area between dotted lines marks region of positive spatial association.

plots of capelin and cod [Fig. 3(a)] contained two regions of differing slopes separated by a transition region. A peak in spatial variance indicating a characteristic scale of aggregation was not observed in the average power spectra of either capelin or cod. Coherence between the two species was uniformly near zero [Fig. 3(b)] and oscillated in and out of phase [Fig. 3(c)].

In summary, a characteristic scale of spatial association between capelin and cod was not observed at the temporal scale of an individual transect (*c.* 1 h) or at the scale of averaged transects (*c.* 2 wk).

BIOENERGETIC CALCULATIONS

One potential explanation for the lack of spatial coherence between capelin and cod is physiological limitations of the predator. To test this we compared energetic estimates from cod consumption models to empirical back-calculations of cod foraging on capelin.

A sample of 132 capelin caught nearshore had a mean length (\pm S.E.) of 15.36 ± 0.15 cm. A sample of 140 cod caught in passive fishing traps located in the sampling area had a mean length of 44.4 ± 0.54 cm. Based on length frequencies of this sample, cod traps catch fish greater than 34 cm in length. Lilly (1987) has shown that cod do not feed on adult capelin until they are greater than 35 cm in length. Using the weight-length relationship from equation (1), we estimated that the mass of a 44.4 cm cod would be 752.2 g. We used Jobling's (1988) food intake model [equation (2)] to calculate that a 752.2 g fish would ingest $68.07 \text{ kJ day}^{-1}$ at 4°C . This is 45% higher than the 11.16 g day^{-1} or $46.87 \text{ kJ day}^{-1}$ calculated from Waiwood *et al.*'s (1991) 'average food eaten' model [equation (3)]. Mass eaten was converted to energy derived from capelin using 1004 calories g^{-1} wet capelin (Jenkins, 1975). If mass eaten was converted to energy using Tyler's (1973) original conversion factor of 4610 calories g^{-1} of dry shrimp *Pandalus montagui* (Leach) and a dry to wet mass ratio of 0.27, the amount of energy required was increased to $58.11 \text{ kJ day}^{-1}$. Consequently, energy requirements for a 752.2 g cod ranged between 58 and 68 kJ per day.

Energy ingested by cod foraging on capelin was calculated by multiplying numbers of fresh capelin observed in cod stomachs by the average energy content of a single capelin. Net energetic gain was calculated by subtracting metabolic costs of egestion, excretion, maintenance, digestion and foraging from total energy ingested. Based on 50 stomach samples from cod caught in cod traps, a glut ration of capelin ranged typically from eight to 12 fish. Capelin calorimetric yields from fresh capelin samples taken during the spawning season ranged from 3.9 kJ g^{-1} (Montevecchi & Piatt, 1984) to 4.2 kJ g^{-1} (Jenkins, 1975). Using an average wet capelin weight of 31 g (Jenkins, 1975) or a combined male and female average of 34 g (Montevecchi & Piatt, 1984), average energy content of capelin was estimated at 131 to 133 kJ per capelin. Setting average caloric content to 132 kJ per capelin and an average ration of eight to 12 capelin, total energy consumption was calculated to range from 1057 to 1585 kJ per glut feeding. Egestion and excretion of an unassimilated portion of the ration was estimated at 317 kJ (eight capelin ration) to 476 kJ (12 capelin ration). Maintenance costs T_m of a 752.2 g fish incorporating a 58 h gastric emptying period were estimated at 58 kJ [equation (6)]. Digestion costs T_d ranged from 125 kJ (eight capelin) to 188 kJ (12 capelin). Estimated swimming speeds [equation (7)] were 28.19 cm s^{-1} for capelin and 70.23 cm s^{-1} for cod. Swimming speeds of cod may be lower in cold water. For example, He (1991) observed maximum sustained swimming speeds of 0.9 to 1 body lengths per second (B.L. s^{-1}); temperatures ranged from -0.3 to 1.4°C . Metabolic costs due to swimming T_F at 1 B.L. s^{-1} were calculated at $129.42 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ [equation (8)] or $1.82 \text{ kJ kg}^{-1} \text{ h}^{-1}$. Therefore if a 44.4 cm, 752.2 g cod swims continuously at 1 B.L. s^{-1} during the 58 h needed to digest the ration, an additional 79.34 kJ of energy would be consumed. During this period a predator could travel a distance of 38.36 km swimming at a speed of 1 B.L. s^{-1} .

In summary, surplus energy Δw following the consumption of eight to 12 capelin was estimated at 478 to 784 kJ (Table III). These estimates include energetic costs of egestion, excretion, maintenance, digestion, and continuous swimming during ration assimilation. This result shows that cod are not

TABLE III. Energetic calculations of cod glut-feeding on capelin based on models from Winberg (1956) and Kerr (1971)

Model component	8 capelin	12 capelin
Ration (R) (kJ)	1057	1585
Egestion and excretion (P) (kJ)	-317	-476
Maintenance (T_m) (kJ)	-58	-58
Digestion (T_d) (kJ)	-125	-188
Swimming (T_s) (kJ)	-79	-79
Surplus energy ($\Delta\omega$) (kJ)	478	784

The predator is assumed to be a 44 cm, 752 g cod with a clearance rate at 5° C of 58 h (Tyler, 1970). Foraging speed is set at 1 B.L. s⁻¹. Energetic content of the ration was calculated at 132 kJ per capelin. Egestion and excretion was set at 30% of ration (Brett & Groves, 1979). Maintenance of a 752 g cod was calculated at 24 kJ day⁻¹ (Jobling, 1982). Digestion at 7° C was estimated as 11.85% of ration (Soofiani & Hawkins, 1982). Swimming costs a 1 B.L. s⁻¹ were calculated at 1.37 kJ h⁻¹ (Soofiani & Pride, 1985).

required to track capelin continuously at any spatial scale less than 10 km. Empirical back-calculations of cod glut feeding on capelin were a minimum of 2.9 times higher than those calculated using cod consumption models. Jobling's model [equation (2)] estimated a consumption of 165 kJ compared to the 140 kJ calculated using Waiwood *et al.*'s model [equation (3)]. Physiological differences between cod used in consumption model experiments and those sampled for the empirical model may limit comparison between the two classes of models.

DISCUSSION

Spatial coherence between capelin and cod was low at all spatial scales within the 19 survey transects. Small concentrations or peaks of coherence occurred in three transects but scales of maximum coherence were not consistent among these transects. When transects were averaged, coherence values were near zero across all sampled spatial scales. A characteristic scale of spatial association between capelin and cod was not observed. In the absence of any consistent spatial association, no attempt was made to determine the form of a functional aggregative response.

The lack of a characteristic scale of spatial association between capelin and cod was an unexpected result. Capelin comprise a major component of cod diet (Popova, 1962; Lilly, 1987; Lilly, 1991), especially during the capelin spawning season (Thompson, 1943; Methven & Piatt, 1989). We expected a characteristic scale of association to fall somewhere within the range of a few body lengths to the spatial scale of a small bay. Coherence between adult capelin and Atlantic cod has been observed at the spatiotemporal scale (length <5 m, duration <1 h) of a foraging bout (Rose & Leggett, 1990). This was observed only once, during a short (185 m) transect in the day when cod were feeding actively on capelin. We have included samples from all hours of the day (Table II) to ensure sampling occurred when cod were feeding actively on capelin.

One possible explanation for the lack of coherence is Type II error, i.e. failure to detect a real effect. This may occur if samples are not taken at the 'right' spatial scale. However, this study analysed mobile predator-prey interactions over four orders of spatial magnitude (20 m to 10 km). A sampling range of this size is rare within a single study. For comparison the 14 predator-prey interaction studies that report 'characteristic' scales of spatial association (Table I) collectively sample 6 orders of spatial magnitude.

Another potential source of Type II error is the vertical integration of relative fish abundance data. Abundance data were integrated over the water column to analyse horizontal variation of cod relative to capelin. Two-dimensional transects were analysed as a one-dimensional data series. School sizes may be increased due to horizontal overlap between aggregations that are separated vertically in the water column. This is more likely among capelin where aggregations form near the surface and near the thermocline (Methven & Piatt, 1991). In spectral analysis the combining of vertically separated shoals to larger aggregations potentially increases the scale of maximum association between the predator and prey. This will not influence the foraging success of a predator but may influence conclusions on spatial interaction at small scales (cf. Rose & Leggett, 1990). The influence of vertically integrating abundance data on spatial variance patterns of predators and prey could be examined by computing the power spectra and coherence in two dimensions (Ford, 1976; Ripley, 1981) and comparing results to the one-dimensional case. A two-dimensional spectral analysis was not conducted because of the requirement of a square data matrix (Ripley, 1981). In any transect longer than 112 m, the padding of the vertical dimension with zeros potentially influences spectral density estimates.

A second procedural step which could contribute to Type II error is the choice of bandwidth used in the analysis. Bandwidth determines the number of adjacent periodograms averaged to estimate spectral density magnitude in each frequency band (Chatfield, 1980). In a series of replicated spectral analyses that differed only in bandwidth, we found that coherence values were lower in replicates that used narrow bandwidths. Bandwidths are not reported commonly for spectral analyses of biological data. We selected a narrow bandwidth (0.01) to minimize bias due to smoothing among frequency bands (Diggle, 1990).

A simple biological explanation for low coherence between capelin and cod is physiological constraints imposed on cod while foraging. If energetic costs of tracking prey over large distances exceed net energy gained by consuming prey, then the spatial coupling of cod to capelin is restricted potentially to scales smaller than those analysed in this study (20 m). Bioenergetic calculations do not support the hypothesis that foraging cod must track capelin aggregations. Energetic costs of swimming continuously for 58 h were 10 to 14% of the total energy used to obtain and assimilate the ration. This is a conservative estimate of cod foraging activity. Tracking studies of Atlantic cod show that cod do not swim continuously throughout the day (Hawkins *et al.*, 1985; Keats *et al.*, 1987) or after feeding (Clark & Green, 1990). If our assumptions concerning swimming costs are correct, then the energetic cost of digestion was 1.6 to 2.4 times higher than the cost of finding the ration. Our estimate of energetic

costs of swimming (1.37 kJ h^{-1}) agreed well with the 1.33 kJ h^{-1} calculated using Tytler's (1969) oxygen consumption model for haddock *Melanogrammus aeglefinus* (L.), another gadoid. The energetic cost of swimming represents a small proportion of the total energy used when cod forage on capelin. We conclude that the lack of coherence between capelin and cod was not due to physiological constraints imposed on foraging predators.

Differences in energy estimates between food intake models and glut feeding calculations deserve comment. Estimates from food intake models were at least three times smaller than those from glut feeding calculations. The food intake models (Jobling, 1988; Waiwood *et al.*, 1991) were based on laboratory studies of captive fish that were fed daily. Some of the fish used in the laboratory experiments had been held in captivity for a period of up to 4 years (Waiwood *et al.*, 1991). Energetic gains from glut feeding were calculated by estimating the amount of energy consumed in a capelin ration and then subtracting energy required to maintain the animal, to digest and clear ingested material, and to swim continuously while the ration was cleared from the stomach. Feeding efficiency ($\Delta w/R \times 100\%$) during this period ranged from 45 to 49% depending on capelin ration size. This is more than double the 20% observed at 7°C for cod feeding on fish pellets (Hawkins *et al.*, 1985). But our calculations encompass a short, intensive feeding period in the wild. Cod sampled for these calculations had probably completed a post-spawning migration from offshore banks (Rose, 1993). These fish feed on local concentrations of pre-spawning capelin in coastal waters to replenish depleted somatic and reproductive energy reserves (Turuk, 1968). It is also unlikely that activity levels and reproductive cycles of cod used in laboratory experiments would match those of wild-caught fish. Differences in energetic intake and feeding efficiency estimates are attributed to the time of sampling and physiological differences among animals used in the two types of models.

Temporal and spatial scales used in theoretical predator-prey models frequently differ from those used to test predictions in the laboratory or field. The temporal resolution of population-interaction models is set implicitly at the generation time of the predator. But the temporal scale of survey transects is typically short relative to the life span of the predator or even the prey. Field and laboratory observations are conducted commonly at temporal scales equivalent to that of a foraging bout. In addition, the range of spatial scales used to formulate aggregative-response models have also differed from those tested in the field. Theoretical descriptions of aggregative responses by predators are based on changes in prey density at a single spatial scale (e.g. Holling, 1965, 1966; Murdoch & Oaten, 1975). Field studies identify the type of response and range of spatial scales over which aggregative responses occur (e.g. Heads & Lawton, 1983; Piatt, 1990). The temporal scale of these measurements will influence the resulting observed spatial patterns. All field surveys cited in Table I report spatial scales of maximum association between predators and prey. These conclusions are based on single or a limited number of transects which represent short temporal scales implicitly. Among studies that present results from multiple transects (Weber *et al.*, 1986; Schneider & Piatt, 1986; Schneider, 1989; Rose & Leggett, 1990) the scale of maximum spatial association differs among transects. With the exception of the study by Weber

et al. (1986), there has not been a combining of association values from a number of transects to examine spatial scales of association between aquatic predators and prey at larger temporal scales. To ensure compatibility between theoretical and empirical studies we emphasize the need to state the spatial and temporal scale of observation when quantifying interactions between predators and prey.

On average, we did not find a 'characteristic' scale of spatial association between capelin and cod over a measurement window spanning four orders of spatial magnitude. Low coherence between predators and prey across a range of spatial scales has been observed also in zooplankton feeding on phytoplankton (Star & Mullin, 1981), birds preying on leaf miners (Heads & Lawton, 1983), multiple predators feeding on brittle stars (Aronson, 1992), and parasites feeding on chrysomelids (Morrison & Strong, 1980, 1981). For cod, an explanation of this lack of association was derived from energetic calculations. These showed that cod do not need to be coupled spatially with prey at scales less than 10 km. Hence cod can function successfully as 'sit and wait' predators. The physiology of the predator, rather than spatial distribution patterns of the prey, explained the absence of a classic form of population interaction at small scales. This study illustrates that aggregative responses of predators do not occur at all spatial scales. We speculate that aggregative responses may only occur over a small range of scales.

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