Smaller predator–prey body size ratios in longer food chains

Simon Jennings* and Karema J. Warr

Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK

Maximum food-chain length has been correlated with resource availability, ecosystem size, environmental stability and colonization history. Some of these correlations may result from environmental effects on predator–prey body size ratios. We investigate relationships between maximum food-chain length, predator–prey mass ratios, primary production and environmental stability in marine food webs with a natural history of community assembly. Our analyses provide empirical evidence that smaller mean predator–prey body size ratios are characteristic of more stable environments and that food chains are longer when mean predator–prey body size ratios are small. We conclude that environmental effects on predator–prey body size ratios contribute to observed differences in maximum food-chain length.

Keywords: food web; predator–prey interactions; food chain length

1. INTRODUCTION

Maximum food-chain length, the number of prey to predator transfers of energy or nutrients from the base to the top of a food web, is a key characteristic of any community and affects the rate and efficiency of energy transfer from primary producers to top predators. Maximum food-chain length is correlated with many interacting factors, including resource availability, environmental stability, ecosystem size and colonization history (Ryther 1969; Pimm 1982; Briand & Cohen 1987; Lawton 1989; Pimm *et al.* 1991; Post 2002a).

In aquatic food webs, many species grow in mass by five or more orders of magnitude (Cushing 1975; Cohen *et al.* 2003) and cannibalism, cross-predation and transient predator–prey relationships are common (Steele 1974; Hall & Raffaelli 1993; Pope *et al.* 1994). Such observations provided compelling reasons to develop size-based analyses of food webs (Dickie *et al.* 1987; Kerr & Dickie 2001). In a food web of given body-size composition, a reduction in the predator–prey body size ratio must result in an increase in food-chain length (Cousins 1987). Thus, correlations between maximum food-chain length and variables such as environmental stability may result from changes in predator–prey mass ratios. In food webs that vary in species and size composition, environments that favour smaller predator–prey body size ratios may permit animals feeding at high trophic levels to persist or colonize.

Empirical relationships between the environment, predator–prey body size ratios and food-chain length have not been explored, partly because mean predator–prey body size ratios could not be measured in complex food webs. However, a recently developed method allows mean predator–prey mass ratios to be estimated in aquatic food webs, and such explorations are now possible (Jennings *et al.* 2002a). We use size-based food-web analysis to explore the relationships between mean predator–prey body mass ratios and environmental stability. Having shown that

predator–prey body mass ratios are smaller in more stable environments, we suggest that smaller mean predator–prey body mass ratios allow the persistence of longer food chains.

2. MATERIAL AND METHODS

Food webs were compared at 74 sites in the North Sea (figure 1). Maximum food-chain length and predator–prey body mass ratios were estimated for all fishes of greater than 16 g wet weight, since fishes account for almost all the biomass and production of larger animals in these marine food webs (Jennings *et al.* 2002a). To estimate mean predator–prey body mass ratios we calculated the slope of the relationship between trophic level (from nitrogen stable isotope analysis) by $\log_2$ body-mass class and $\log_2$ body-mass class. The $\log_2$ transformation results in a linear relationship between trophic level and body size (Jennings *et al.* 2002a,b). We assumed that the top predators were the top predators in the fish community, and did not consider the roles of wide-ranging marine mammals, birds or human fishers.

Fishes were caught with an otter trawl net, towed for 30 min at 4 knots (Knijn *et al.* 1993). The catch was divided into species groups and the total weight of each species was measured. All individuals in species groups or sub-samples of species groups were measured to produce raised length–frequency distributions for all species. All fishes weighing more than 512 g were individually weighed and assigned to $\log_2$ body-mass classes. Fishes weighing 512 g or less were randomly subsampled before weighing and then assigned to $\log_2$ body-mass classes. Samples of white muscle tissue, set at a fixed proportion of body weight, were dissected from 20–25 individuals in each body-mass class (or all the fishes in the body-mass class if fewer than 20; Jennings *et al.* 2001). Tissue samples in each class were then combined and homogenized to produce a smooth paste. Samples of paste, ca. 4 g, were retained, frozen at -30°C and subsequently freeze-dried.

The freeze-dried fish tissue was ground to a fine powder (particles less than $60\ \mu\text{m}$), thoroughly mixed, and 1.0 mg was put into a tin capsule for nitrogen stable isotope analysis. The ^{15}N composition of the samples was determined using continuous flow isotope ratio mass spectrometry (Preston & Owens 1983). Samples were oxidized and the N_2 was passed to a single-

* Author for correspondence (S.Jennings@cefas.co.uk).

Figure 1. The locations of sample sites.

inlet dual-collector mass spectrometer (Automated Nitrogen Carbon Analysis (ANCA) Integra system, PDZ Europa, UK). Two samples of reference material (a standard mix of ammonium sulphate and beet sugar) were analysed after every five tissue samples to calibrate the system and compensate for drift. The ^{15}N composition was expressed in conventional delta notation ($\delta^{15}\text{N}$), relative to the level of ^{15}N in atmospheric N_2 . Experimental precision was $\pm 0.1\text{‰}$ (standard deviation of $\delta^{15}\text{N}$ for replicates of the reference material).

Trophic level can be estimated using nitrogen stable isotope analysis because the $\delta^{15}\text{N}$ of predators is enriched by 3.4‰ relative to their prey (Minagawa & Wada 1984; Post 2002b). Nitrogen stable isotope analysis is often preferable to diet analysis for estimating trophic levels because many species in a food web switch diet frequently, prey on species that are digested at different rates and have gut contents that cannot be identified (Peterson & Fry 1987; Pinnegar & Polunin 2000; Polunin *et al.* 2001). Moreover, the $\delta^{15}\text{N}$ of a predator reflects the composition of assimilated diet and integrates differences in assimilated diet over time (Owens 1987; Peterson & Fry 1987; Post 2002b).

All $\delta^{15}\text{N}$ estimates were converted to estimates of site-specific trophic level based on the assumptions that the fractionation of $\delta^{15}\text{N}$ was $+3.4\text{‰}$ per trophic level (Minagawa & Wada 1984; Post 2002b) and that the $\delta^{15}\text{N}$ of animals close to the base of the food chain was known (Owens 1987; Post 2002b). Trophic level was calculated as

$$\text{TL}_i = \left(\frac{(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{ref}})}{3.4} \right) + 2.5,$$

where TL_i is the trophic level of species or weight class i , $\delta^{15}\text{N}_i$ is the mean $\delta^{15}\text{N}$ of species or weight class i and $\delta^{15}\text{N}_{\text{ref}}$ is the $\delta^{15}\text{N}$ in an animal close to the base of the food chain, which was assigned a trophic level of 2.5 (Post 2002b). The $\delta^{15}\text{N}$ of this animal, a queen scallop *Aequipecten opercularis* of 55 mm

shell height sampled on 1 September 2001, was predicted from the empirical relationship of Jennings & Warr (2003):

$$\begin{aligned} \delta^{15}\text{N}_{\text{ref}} = & 208.51 - (0.009617 \times D) + (6.7729 \times T_s) \\ & - (0.31562 \times T_s^2) + (1.888 \times T_b) - (0.06505 \times T_b^2) \\ & - (13.7488 \times S) + (0.18969 \times S^2), \end{aligned}$$

where D is the depth (m), T_s is the annual mean surface temperature ($^{\circ}\text{C}$), T_b is the annual mean bottom temperature ($^{\circ}\text{C}$) and S is the mean salinity in August (‰). Depth was recorded at the time of sampling. All other oceanographic data were obtained from the International Council for the Exploration of the Sea (ICES, Copenhagen, Denmark, unpublished data) and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) (unpublished data). $\delta^{15}\text{N}_{\text{ref}}$ had to be calculated rather than determined from empirical data since no single species at the base of the food chain could be sampled at every site and $\delta^{15}\text{N}$ is species and size specific (Jennings & Warr 2003).

The mean predator–prey body mass ratio at each site was expressed as the slope b of the linear relationship $\text{TL} = a + b \log_2 M$, where TL is trophic level and M is body mass. Actual predator–prey mass ratios were calculated as $2^{1/b}$, following Jennings *et al.* (2002a).

Maximum food-chain length was defined as the maximum trophic level of any fish recorded in each trawl sample. As each trawl sample contained 10^3 – 10^5 fishes it was impossible to determine $\delta^{15}\text{N}$ for all individuals that may have fed at the highest trophic level, although all fishes were identified and measured. Moreover, because very small numbers of larger individuals in each species were sampled and the distribution of trophic level within body-size classes is assumed to be similar in all size classes, there is a higher probability of sampling an individual with a high trophic level in intermediate than in large size classes. To negate these concerns, we used cross-site species-specific $\delta^{15}\text{N}$ versus length relationships (Jennings *et al.* 2002c), rebased to $\delta^{15}\text{N}_{\text{ref}}$ at each site, to calculate the trophic levels of all species of all lengths in the sample. Since the relationships give mean trophic level at body size, our calculated among-site differences in maximum food-chain length depend on species identity, body size and $\delta^{15}\text{N}_{\text{ref}}$ rather than site-specific differences in the feeding strategy of individuals.

Relationships between predator–prey body mass ratios and environmental stability, and between maximum food-chain length, predator–prey body mass ratios, primary production and fishing effort were explored with generalized linear models. The standard deviation of the mean monthly bottom temperature ($^{\circ}\text{C}$ by year) was used as an index of environmental stability. Primary production was expressed as the mean primary production ($\text{g C m}^{-2} \text{yr}^{-1}$) in the ICES statistical rectangle (boxes of 0.5° latitude and 1° longitude) surrounding each site (ICES, unpublished data). We also accounted for potential fishing effects, because fishing reduces the abundance of large fishes, which may feed at high trophic levels (Pauly *et al.* 1998; Pinnegar *et al.* 2002). Total fishing effort ($\log_{10}$ combined beam trawl and otter trawl h yr^{-1}) in each ICES rectangle was used as a measure of fishing effects (Callaway *et al.* 2002).

3. RESULTS

The heaviest predator at each site rarely fed at the highest trophic level and the longest food chains supported predators with intermediate body size (figure 2). Among sites, there was a weak but significant correlation between the maximum trophic level of any individual and the

Figure 2. The relationship between the maximum trophic level of any individual and the trophic level of the largest individual shows that top predators in the food web often have intermediate body size.

Figure 3. The relationship between body-mass class and mean trophic level among sites ($\pm$ s.d.).

trophic level of the largest individual ($r = 0.287$, $n = 74$, $p = 0.02$). The range in maximum trophic level of individuals among sites was only 0.5 trophic levels while the range in trophic level of the largest individual exceeded 1.5 trophic levels (figure 2). On average, trophic level rose consistently and significantly with body mass (figure 3), and the mean predator-prey mass ratio among sites was 424 : 1 (figure 3; $b = 0.115$).

Mean predator-prey body mass ratios were smaller when the environment was more stable ($F_{1,72} = 18.08$, $p < 0.001$). There was a highly significant relationship between the maximum trophic level of any individual (maximum food-chain length) and the mean predator-prey body mass ratio. Fishing effort and primary pro-

duction did not have significant effects on maximum food-chain length (table 1).

4. DISCUSSION

Mean predator-prey body size ratios were smaller in more stable environments, and longer food chains were found in food webs where mean predator-prey body size ratios were smaller. In a community of given species and size composition, smaller predator-prey body size ratios must increase food-chain length. However, real communities differ in species and size composition. In these real communities, our results still suggest that environmental factors favouring smaller mean predator-prey body size ratios allow individuals feeding at very high trophic levels to persist. We propose that relationships between environmental variables and food-chain length will often be explained by the effects of the environment on predator-prey body size ratios.

Since our estimates of trophic level are rebased to $\delta^{15}\text{N}_{\text{ref}}$, environmental effects on processes at the base of the food chain (e.g. the microbial food loop; Azam *et al.* 1983) will not confound relationships between environmental variability and predator-prey body size ratios. However, in seeking to avoid sampling errors when estimating maximum food-chain length, we did not account for variation in the feeding strategies of individuals of the same size and species. Therefore, our measure of maximum food-chain length is mean maximum food-chain length based on the composition of the community rather than maximum food-chain length based on differences in the feeding behaviour of individuals. If the difficulties of estimating maxima from small sample sizes could be overcome, it would be desirable to see whether our conclusions apply to measures of maximum food-chain length based on differences in the feeding behaviour of individuals. Such an analysis would provide a basis for disentangling the effects of individual feeding strategies and community assembly on food-chain length, and for assessing the extent to which constraints on trophic structure regulate community assembly.

The trophic level of the largest predator has been used as a measure of maximum food-chain length (e.g. Post *et al.* 2000). While the trophic levels of the largest predators were significantly correlated with maximum food-chain length, the longest food chains actually supported species of intermediate body size. This may explain why the relationship between fishing intensity and maximum trophic level was not significant, even though fishing differentially depletes the largest fishes in the community and reduces mean trophic level (Pauly *et al.* 1998; Pinnegar *et al.* 2002).

Historically, the largest fish predators found in the North Sea were not sampled because their abundance has been greatly depleted by intensive fishing. However, their presence would not have affected the conclusion that predator-prey mass ratios influence maximum food-chain length. This is because most large predators 'feed down the food web' on smaller and more productive size classes of prey. For example, when blue-fin tuna (*Thunnus thynnus*, to 500 kg) were common in the North Sea, they fed predominantly on herring (trophic levels of herring

Table 1. Analysis of variance for a general linear model fitted to the relationship between maximum food-chain length (maximum trophic level of any individual in the samples), predator–prey body mass ratio (slope b in the relationship $TL = a + b \log_2$ body mass), primary production and fishing effort ($\log_{10}$ total hours fishing by ICES rectangle). In the ‘source’ analysis, the effects of each variable were assessed over and above the effects of the other.

	d.f.	SS	MS	F-value	p-value
full model					
model	3	0.236	0.079	6.95	< 0.001
error	70	0.792	0.011		
total	73	1.028			
source					
predator–prey mass ratio	1	0.159	0.159	14.08	< 0.001
primary production	1	0.035	0.035	3.08	0.084
fishing effort	1	0.022	0.022	1.99	0.163

typically 3.5–4.0). Many other large predators also fed down the food web, including basking sharks and whales.

If maximum food-chain length can depend on predator–prey body size ratios, then feeding behaviour, as mediated by the interactions between individuals and their environment, will have a fundamental effect on maximum food-chain length. The life history, morphology and motility of a predator place ultimate constraints on the prey it can eat, but, within these constraints, prey-size selection will depend on the environment, competition, prey availability, prey processing costs, prey population stability and prey production (Stephens & Krebs 1986; Cohen *et al.* 1993; Hughes 1993). Our analyses do not allow us to determine whether the significant relationship between our measure of environmental variability and predator–prey body size ratios demonstrates causality, as annual temperature variation may be a surrogate for many other types of physical and biological variability that could affect predator–prey interactions. For example, at deeper sites with lower annual temperature variation, tide and wave effects are smaller, the water is generally clearer and there are more complex seabed habitats, so predators may be able to track and feed on larger, mobile and patchily distributed prey more easily. Conversely, in turbid shallow sites subject to high levels of physical disturbance, tracking and catching large active prey in the water column may be more difficult, and more fishes, of all body sizes, may feed on smaller but more evenly distributed and more productive benthic animals on the sea-floor.

Primary production did not have a significant effect on food-chain length. Since primary production at all our sites was relatively high (greater than $100 \text{ g C m}^{-2} \text{ yr}^{-1}$), this was consistent with the view that primary production limits food-chain length only in the range $1\text{--}100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Post 2002a).

Food webs do not have clearly defined boundaries in the open marine environment, and a site-based comparison of food webs is one of only a few approaches for identifying the factors that affect the structure of naturally assembled food webs on large spatial scales. The site-based approach relies on the premise that trophic interactions within sites are stronger than those between sites. This is reasonable when most sites are 30–80 km from their nearest neighbours (figure 1), and when there is strong temporal and spatial persistence of fish assemblage structure (Callaway *et al.* 2002). However, the site-based approach will always violate the statistical assumption that

sites are independent and increase the probability of Type II error. We cannot account for the effects of non-independence because the degree of interaction between sites cannot be measured and any interaction will not be a simple function of latitude or site separation.

Several other caveats and concerns apply to large-scale comparisons of food webs (Hall & Raffaelli 1993) and the use of stable isotopes to assess trophic level and predator–prey mass ratios (Jennings *et al.* 2002a; Post 2002b). However, large-scale comparisons of food webs with a natural history of community assembly do provide insights into the structure and function of food webs that could not be obtained from small-scale experiments using artificially assembled communities or from manipulative field experiments.

We conclude that environmental effects on predator–prey body size ratios account for some of the variation in maximum food-chain length between food webs. The potential indirect effects of the environment on food-chain length have largely been ignored in previous studies. Future attempts to account for variation in maximum food-chain length could usefully focus on the relative effects of environmental variables on predator–prey body mass ratios and community assembly.

The authors thank Richard Ayers, Trevor Boon, Grant Course, Tracy Dinmore, Chris Firmin and the officers and crew of RV *Corystes* and RV *Cirolana* for their efforts at sea, Anne Bruce and Rowan White for conducting the stable isotope analyses, Steve Cousins for helpful discussions and the referees for suggestions that improved the manuscript. The authors also thank CEFAS (DP166), DEFRA (MF0731) and the US National Science Foundation (SCOR IOC NMFS WG 119) for funding this research.

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