Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency

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Abstract. Predator–prey body size relationships influence food chain length, trophic structure, transfer efficiency, interaction strength, and the bioaccumulation of contaminants. Improved quantification of these relationships and their response to the environment is needed to parameterize food web models and describe food web structure and function. A compiled data set comprising 29 582 records of individual prey eaten at 21 locations by individual predators that spanned 10 orders of magnitude in mass and lived in marine environments ranging from the poles to the tropics was used to investigate the influence of predator size and environment on predator and prey size relationships. Linear mixed effects models demonstrated that predator–prey mass ratios (PPMR) increased with predator mass. The amount of the increase varied among locations and predator species and individuals but was not significantly influenced by temperature, latitude, depth, or primary production. Increases in PPMR with predator mass implied nonlinear relationships between log body mass and trophic level and reductions in transfer efficiency with increasing body size. The results suggest that very general rules determine dominant trends in PPMR in diverse marine ecosystems, leading to the ubiquity of size-based trophic structuring and the consistency of observed relationships between the relative abundance of individuals and their body size.

Key words: body mass; consumer–resource; feeding interaction; fish; food web; predator–prey; size spectra; transfer efficiency; trophic level.

Introduction

Body size has a profound influence on the biology and ecology of any animal, accounting for much of the variation in rates of metabolism, energy use, production, and mortality (Dickie et al. 1987, Brown et al. 2004, Marquet et al. 2005, Woodward et al. 2005, Hildrew et al. 2007). Plants and animals in marine food webs span many orders of magnitude in body mass, from small phytoplankton weighing $<10^{-15}$ g wet mass (Agawin et al. 2000) to large predatory sharks of $>10^6$ g (Compagno 1984). Size-based predation is predominantly responsible for the transfer of energy from phytoplankton to progressively larger animals and total production falls with body mass as trophic level rises (Sheldon et al. 1972). Many marine animals grow by five to six orders of magnitude in mass during their life cycle and fulfill a number of trophic roles; thus individual body mass is often a better indicator of trophic level than species identity (Jennings et al. 2001). Knowledge of relationships between the sizes of predators and their prey can be used to predict the strength of predatory interactions, the length of food chains (Reuman and Cohen 2004),

and the pathways of energy transfer in the food web. The role of the predator–prey mass ratio (PPMR) in describing the passage of energy in marine food webs has long been recognized (Sheldon et al. 1972, Silvert and Platt 1980, Moloney et al. 1991); and thus estimates of mean PPMR and variability around the mean PPMR are necessary as inputs to, or for validation of, models of the structure and function of marine food webs (Sheldon et al. 1972, Dickie et al. 1987, Andersen and Beyer 2006, Blanchard et al. 2008) and subsets of those webs (Duplisea and Kerr 1995, Hallowed et al. 2000, Shin and Cury 2001, Hall et al. 2006, Pope et al. 2006).

PPMR determines the length of food chains, with smaller PPMR leading to longer food chain length in a community of given size composition. Thus PPMR can be one way by which many interacting factors such as resource availability, environmental stability, ecosystem size, and colonization history (e.g., Briand and Cohen 1987, Pimm et al. 1991, Post 2002) might affect food chain length (Jennings and Warr 2003) and therefore permit animals feeding at high trophic levels to persist or colonize. Changes in food chain length also affect the efficiency of energy transfer from phytoplankton to higher trophic levels and the bioaccumulation of contaminants (Cabana and Rasmussen 1994).

Measurement of mean PPMR in entire food webs is challenging, and estimates are usually based on dietary studies for a small number of species in a relatively

narrow size range. These estimates may or may not be representative of values for other groups of species and body sizes, or in other locations. For size windows in the food web, typically of three to four orders of magnitude in body mass, mean PPMR has been measured using size-based nitrogen stable isotope analysis (Jennings et al. 2008a). However, this approach is less easily applied to smaller size classes with very variable dynamics and has only been used in a few locations. To improve our capacity to generalize about PPMR in marine food webs, and its relationship with body size and the environment, a complementary approach is to compile information on PPMR from many studies in many locations. Such attempts to generalize may be successful since, within groups that have been intensively studied, there can be remarkable consistency in prey size selection among years (Rice et al. 1991).

Here, we analyze data from a published marine data set (Barnes et al. 2008) to identify relationships between predator size, prey size, environment (latitude, longitude, primary production, temperature, depth, and ecosystem), PPMR, trophic level and transfer efficiency. Body sizes of predators span ten orders of magnitude and environments range from the poles to the tropics.

METHODS

The analyses were based on a published consolidated data set of nearly 35 000 predation events from 27 marine locations, with all records linked to studies in the peer-reviewed literature (Barnes et al. 2008). The criteria used to determine which data should be included in this analysis were (1) that predators were sampled in the natural marine environment, (2) that the location of the study was identified, (3) that predators were identified to genus or species, and (4) that predator and prey sizes were measured and reported and, if necessary, could be converted to mass. Records were selected from the data set that included predator and prey mass data of satisfactory quality (mass had either been measured or could be estimated from length measurements using length-mass relationships that were known for the species, genus, family or at least general shape of the organism; for details, see Barnes et al. [2008]).

Latitude and longitude were taken directly from the original publication or determined from charts and descriptions. Estimates of mean annual sea surface temperature (SST) were derived from the moderate-resolution imaging spectroradiometer (MODIS) data collected by NASA terra-satellites. The satellites provide thermal infrared remote sensing of global waters that we analyzed at a resolution of 36 km. Monthly SST averages for each year from 2001 to 2005 were extracted through the Jet Propulsion Laboratory physical ocean-ography DAAC web portal and mean annual SST values calculated (data *available online*).[5] Primary

production estimates were obtained for the years 2001–2004 at a 36×36 km resolution from the outputs of a model that uses the approach of Longhurst et al. (1995) to predict primary production from the surface concentration of chlorophyll *a* pigment as measured by the sea-viewing wide field-of-view sensor (SeaWiFS; Mélin 2003). Depth was estimated using the General Bathymetric Chart of the Oceans (GEBCO) digital atlas (maintained and published by the British Oceanography Data Centre, Proudman Oceanographic Laboratory, Bidson Observatory, Birkenhead, Merseyside, UK). Large Marine Ecosystem boundaries were defined using NOAA shape files (*available online*).[6]

Predator mass and prey mass were $\log_{10}$-transformed for all analyses, as logged values had distributions closer to normal. Predator mass was treated as the independent variable as it is usually measured or calculated with less error than prey mass (prey removed from predator guts are often damaged or deformed and prey may not be identified to species thus requiring that general rather than species-specific relationships are used to convert length measurements to mass) and because prey size choice is made by the predator. Owing to the potential biases introduced by nonindependence of data (multiple records for the same predator, multiple predators of the same species, and multiple predator species at the same site), mixed effects models (Pinheiro and Bates 2000) coded in R (R Development Core Team 2007) were used to investigate relationships between $\log_{10}$(PPMR) and the factors $\log_{10}$(predator mass), predator species, study location, individual predator identifier, ecosystem, depth, mean annual sea surface temperature, mean primary production, and latitude; incorporating them as nested random effects or as fixed effects as appropriate (see results for structures and properties of selected models).

Our analyses are based on diet data and thus describe realized PPMR, a function of the range of prey sizes available in the environment and prey size selection by the predator (Ursin 1973). These two processes are often parameterized independently in food web models but cannot be distinguished here because there is no information on the sizes of prey encountered by individual predators in their environment. Some re-searchers have attempted to predict or measure the range of prey sizes available in the environment to determine prey size selection. However, the efficacy of such approaches is difficult to judge when we do not know how the range of prey sizes encountered by an individual predator reflects the range of prey sizes in the environment. The ideal way of determining prey size selection would be through observation of prey encoun-ters and feeding events by individual predators, a possibility in small experimental systems but not yet

TABLE 1. Data sources for predator and prey mass data with environmental information, for all study locations.

Code	Location	Large marine ecosystem	Latitude	Longitude	Depth (m)
1	Greenland	East Greenland Shelf	60°00′ N	40°00′ W	2686
2	Strait of Georgia	Gulf of Alaska	49°00′ N	123°00′ W	127
3	Apalachicola Bay, Florida	Gulf of Mexico	29°40′ N	85°10′ W	30
4	Gulf of Alaska	Gulf of Alaska	56°50′ N	156°00′ W	209
5	Off the Bay of Biscay	NE Atlantic	44°00′ N	16°00′ W	3798
6	Gulf of Maine, New England, USA	NE US Continental Shelf	42°00′ N	70°00′ W	20
7	Mid Atlantic	Mid Atlantic	39°50′ N	73°00′ W	48
8	Great South Bay, Long Island, New York, USA	NE US Continental Shelf	40°10′ N	73°10′ W	52
9	Antarctic Peninsula	Antarctic	63°00′ S	58°00′ W	881
10	Antarctic Peninsula	Antarctic	62°00′ S	55°00′ W	1752
11	Oxwich Bay, Wales	Celtic-Biscay Shelf	51°52′ N	04°10′ W	8
12	French Polynesian EEZ	Mid Pacific	12°00′ S	144°00′ W	4785
13	Northeast North Sea and Skaggerak	North Sea	57°00′ N	08°00′ E	31
14	Western Greenland	West Greenland Shelf	66°20′ N	56°00′ W	215
15	Andaman Sea (west of south Thailand)	Bay of Bengal	08°24′ N	97°53′ E	371
16	Celtic Sea, Europe	Celtic-Biscay Shelf	50°50′ N	08°00′ W	102
17	Off the Bay of Biscay	NE Atlantic	45°00′ N	18°00′ W	4562
18	Catalan Sea	Mediterranean Sea	40°55′ N	02°40′ E	1783
19	Western North Pacific	Kuroshio Current	37°00′ N	143°00′ E	3322
20	Atlantic Ocean	NE US Continental Shelf	40°00′ N	71°00′ W	677
21	Eastern Mediterranean	Mediterranean Sea	38°00′ N	23°00′ E	75
	Total				

Note: Codes refer to the codes used for study locations in Tables 2 and 3 and Figs. 1 and 2.
† Data used with permission of Northwest Atlantic Fisheries Organization.

feasible for the range of predators and environments considered here.

Body size-related changes in realized PPMR would be expected to lead to size-related changes in trophic transfer efficiency (ε, the ratio of the production of a trophic level or mass category to that of its prey) if the slopes (β) of time-averaged size-spectra are relatively constant among ecosystems and across body size classes, as proposed by Boudreau and Dickie (1992). The *size spectrum* is the relationship, often linear, between the log numbers of individuals in log body mass categories and the category centers. If Boudreau and Dickie's (1992) examples are representative, then we can predict how changes in PPMR (μ) with body mass will affect ε. The slope of the numbers spectrum at equilibrium can be approximated as $\beta = (\log \varepsilon / \log \mu) - 0.75$ (Borgmann 1987, Andersen et al. 2008) where 0.75 is the assumed scaling of consumption (assumed to be driven by metabolic rate) with body mass. Thus, $\log \varepsilon = \log \mu \times (\beta + 0.75)$ or $\varepsilon = \mu^{\beta+0.75}$.

If trends in PPMR based on studies in many locations are indicative of trends in complete food webs in one location, then the rate of change of PPMR with body mass as determined by the linear mixed effects models of this study reflects the rate of change of PPMR with body mass in complete local food webs. The mean trophic level (λ) of animals of body mass W in a food web depends on PPMR (μ), as well as on the body mass W_r and the trophic level λ_r of animals in a reference body mass class for which trophic level is known or assigned (Jennings et al. 2008b). Following Jennings et al. (2008b,

their equation 2.10, expressed here using the current notation),

$$\lambda_x = \frac{\log W_x - \log W_r}{\mu} + \lambda_r$$

if the PPMR, μ, is constant. Replacing the fixed PPMR in the denominator with a mean value to account for the observed relationship between PPMR and body mass, and adopting subscript x to refer to the body mass class for which λ will be determined,

$$\lambda_x = \frac{\log W_x - \log W_r}{0.5(\log \mu_x + \log \mu_r)} + \lambda_r. \qquad (1)$$

Trophic levels were estimated assuming $\lambda_r = 4$ when $W = 10$ g. This assumption influences the absolute but not the relative values of λ.

RESULTS

A total of 29 582 records from 21 locations identified in 23 studies (Table 1) met the criteria for inclusion; 13 361 individual predators of 92 species and 183 types of prey were represented. Data were from a range of habitats, from a shallow estuary to an oceanic gyre. Mean sea surface temperature ranged from −1°C to nearly 30°C and average primary production from 90 to 1740 mg C·m^{-2}·d^{-1}.

Predators were larger than their prey in 99.8% of cases and prey mass increased with predator mass in all locations, with 20 of the 21 relationships significant at the 5% level (Fig. 1, Table 2). In 11 of the 21 locations, PPMR increased with predator mass, in two locations PPMR decreased and in the remaining eight PPMR

Table 1. Extended.

| Temperature (°C)	Primary production (mg C·m^{-2}·d^{-1})	No. predator–prey pairs	No. individual predators	Reference
6.3	233	49	23	Bainbridge and McKay (1968)†
10.5	1739	606	405	Barraclough (1967)
24.1	866	115	78	Bethea et al. (2004)
7.6	782	43	14	Brodeur (1998)
15.6	469	827	77	Chancollon et al. (2006)
10.6	1414	1909	196	Chase (2002)
14.1	1031	113	113	Hunsicker and Essington (2006)
13.9	1142	297	101	Juanes and Conover (1995)
−1.3	230	2103	683	Kellermann (1987, 1990)
−1.1	245	105	90	Kellermann (1989)
12.2	1399	1315	35	Lancaster (1991)
28.4	316	4011	233	Menard et al. (2006)
10.4	946	21	21	Munk (1997)
2.1	357	163	163	Munk (2002)
29.0	91	34	34	Ostergaard et al. (2005)
12.9	607	2091	499	Pinnegar et al. (2003)
15.4	437	3585	39	Pusineri et al. (2005), Quéro et al. (2004)
18.9	524	420	244	Sabates and Saiz (2000)
17.9	601	414	110	Sassa and Kawaguchi (2004)
15.1	867	10 994	10 191	Scharf et al. (2000)
19.3	435	367	12	Stergiou and Fourtouni (1991)
		29 582	13 361	
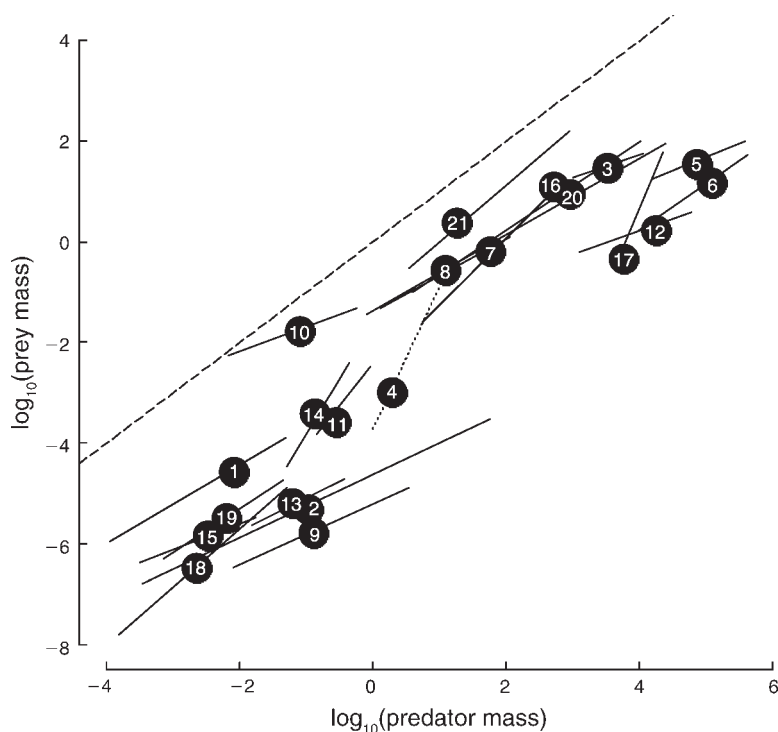
FIG. 1. Relationship between the body mass of predators and their prey by location. Locations are numbered following Table 1, and the numbers are centered on the means of $\log_{10}$(predator) and $\log_{10}$(prey mass). Solid lines show significant relationships, as estimated from a linear mixed effects model, between $\log_{10}$(prey mass) and $\log_{10}$(predator mass) in 20 of the 21 locations (PPMR = predator–prey mass ratio). Mass was measured in grams. The dotted line identifies a nonsignificant slope in one location. The dashed line is the 1:1 relationship. Separate slopes and intercepts are estimated for each location, with random effects for predator species and for predator individuals within species.

TABLE 2. Predator–prey body mass relationships in each study location and associated linear mixed effects statistics.

Code	Slope, b				Constant, a				Mean of $\log_{10}$(predator mass)	Mean of $\log_{10}$(prey mass)
	Mean	95% CL	df	P	Mean	95% CL	df	P		
1	0.78	0.41, 1.15	20	<0.001	−2.88	−3.90, −1.86	26	<0.001	−2.08	−4.58
2	0.62	0.53, 0.71	191	<0.001	−4.62	−4.78, −4.46	395	<0.001	−0.95	−5.32
3	0.44	0.20, 0.68	69	<0.001	−0.04	−0.87, 0.79	69	0.921	3.53	1.45
4	2.79	−1.21, 6.79	12	0.158	−3.71	−4.99, −2.43	29	<0.001	0.30	−3.00
5	0.55	0.33, 0.77	75	<0.001	−1.08	−2.18, 0.02	750	0.050	4.87	1.53
6	0.92	0.46, 1.38	1712	<0.001	−3.44	−5.84, −1.04	1712	0.004	5.10	1.15
7	1.32	0.84, 1.80	111	<0.001	−2.57	−3.43, −1.71	111	<0.001	1.78	−0.21
8	0.73	0.56, 0.90	195	<0.001	−1.40	−1.60, −1.20	195	<0.001	1.10	−0.58
9	0.59	0.53, 0.65	1419	<0.001	−5.21	−5.28, −5.14	1419	<0.001	−0.88	−5.79
10	0.48	0.42, 0.54	88	0.013	−1.21	−1.64, −0.78	88	<0.001	−1.08	−1.78
11	1.66	0.90, 2.42	33	<0.001	−2.43	−2.85, −2.01	1280	<0.001	−0.54	−3.59
12	0.47	0.23, 0.71	230	<0.001	−1.65	−2.80, −0.50	3778	0.005	4.25	0.21
13	0.65	0.45, 0.85	19	<0.001	−4.43	−4.68, −4.18	19	<0.001	−1.20	−5.21
14	2.23	1.71, 2.75	160	<0.001	−1.62	−2.13, −1.11	160	<0.001	−0.85	−3.43
15	0.50	0.28, 0.72	29	<0.001	−4.59	−5.17, −4.01	29	<0.001	−2.45	−5.84
16	0.88	0.81, 0.95	1591	<0.001	−1.54	−1.83, −1.25	1591	<0.001	2.74	1.07
17	3.08	1.44, 4.72	36	0.001	−11.63	−17.91, −5.35	3546	<0.001	3.78	−0.36
18	1.15	0.92, 1.38	175	<0.001	−3.42	−4.06, −2.78	238	<0.001	−2.63	−6.48
19	0.87	0.64, 1.10	107	<0.001	−3.57	−4.10, −3.04	304	<0.001	−2.19	−5.50
20	0.76	0.72, 0.80	802	<0.001	−1.37	−1.60, −1.14	10 173	<0.001	2.97	0.93
21	1.12	0.88, 1.36	10	<0.001	−1.13	−1.65, −0.61	355	<0.001	1.27	0.36

Notes: Codes refer to the codes used for study locations in Table 1. For each location, relationships were expressed as $\log_{10}$(prey mass) $= a + b \times \log_{10}$(predator mass), with predator species and individual predators within species as random factors.

increased in three and decreased in five, although the relationship was not significant at the 5% level (Table 3). These results are based on a model with fixed effects allowing a different slope and intercept for each of the 21 locations and random effects for predator species, and predator individuals within species, fitted to the whole data set. Conditional F tests of the model terms showed that (1) when location-specific slopes in the full model were constrained to be equal, model fit was very slightly but significantly reduced ($F = 4.3$, df $= 20$, 16 196, $P < 0.001$); (2) further constraining the common slope to be 0 caused a substantial and significant reduction in fit ($F = 269.3$, df $= 1$, 16 196, $P < 0.001$); and (3) still further constraining location-specific intercepts to be the same caused a substantial and significant reduction in fit ($F = 35.7$, df $= 20$, 13 253, $P < 0.001$).

TABLE 3. Predator–prey body mass relationships in each study location and associated linear mixed effects statistics.

Code	Slope, b				Constant, a			
	Mean	95% CI	df	P	Mean	95% CI	df	P
1	0.22	−0.80, 1.24	20	0.227	2.88	2.51, 3.25	26	<0.001
2	0.38	0.22, 0.54	191	<0.001	4.62	4.53, 4.71	395	<0.001
3	0.56	−0.27, 1.39	69	<0.001	0.04	−0.20, 0.28	69	0.921
4	−1.79	−3.07, −0.51	12	0.353	3.71	−0.29, 7.71	29	<0.001
5	0.45	−0.65, 1.55	75	<0.001	1.08	0.86, 1.30	750	0.050
6	0.08	−2.32, 2.48	1712	0.722	3.44	2.98, 3.90	1712	0.004
7	−0.32	−1.18, 0.54	111	0.185	2.57	2.09, 3.05	111	<0.001
8	0.27	0.07, 0.47	195	0.002	1.40	1.23, 1.57	195	<0.001
9	0.41	0.34, 0.48	1419	<0.001	5.21	5.15, 5.27	1419	<0.001
10	0.52	0.09, 0.95	88	0.007	1.21	0.83, 1.59	88	<0.001
11	−0.66	−1.08, −0.24	33	0.087	2.43	1.67, 3.19	1280	<0.001
12	0.53	−0.62, 1.68	230	<0.001	1.65	1.41, 1.89	3778	0.005
13	0.35	0.10, 0.60	19	0.002	4.43	4.23, 4.63	19	<0.001
14	−1.23	−1.74, −0.72	160	<0.001	1.62	1.10, 2.14	160	<0.001
15	0.50	−0.08, 1.08	29	<0.001	4.59	4.37, 4.81	29	<0.001
16	0.12	−0.17, 0.41	1591	0.001	1.54	1.47, 1.61	1591	<0.001
17	−2.08	−8.36, 4.20	36	0.014	11.63	9.99, 13.27	3546	<0.001
18	−0.15	−0.79, 0.49	175	0.190	3.42	3.19, 3.65	238	<0.001
19	0.13	−0.40, 0.66	107	0.255	3.57	3.34, 3.80	304	<0.001
20	0.24	0.01, 0.47	802	<0.001	1.37	1.33, 1.41	10 173	<0.001
21	−0.12	−0.64, 0.40	10	0.291	1.13	0.89, 1.37	355	<0.001

Notes: Codes refer to the codes used for study locations in Table 1. For each location, relationships were expressed as $\log_{10}$(PPMR) $= a + b \times \log_{10}$(predator mass), with predator species and individual predators within species as random factors. PPMR is the predator–prey mass ratio.
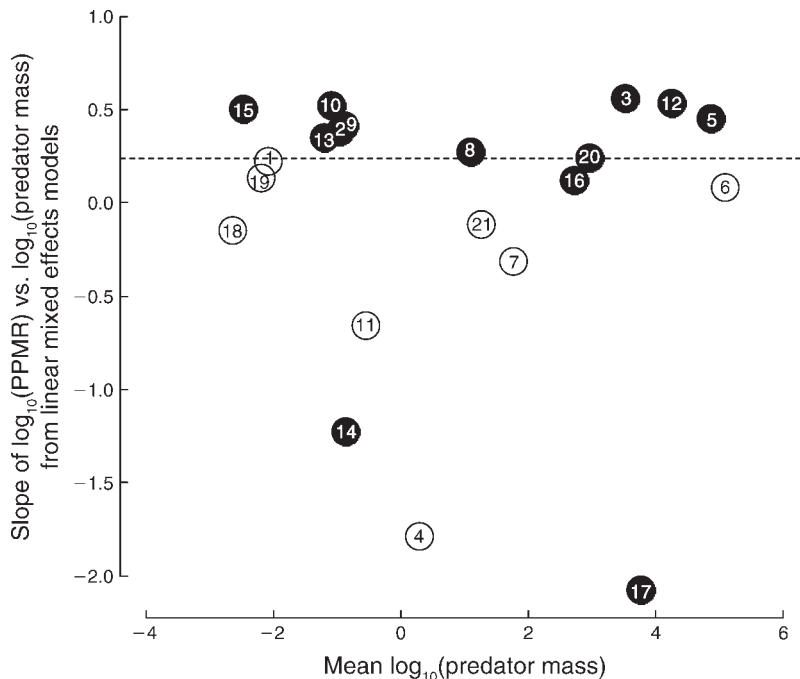
Fig. 2. Relationship between the mean of the $\log_{10}$(body mass) of the predators sampled in each location and the slope of the dependence of $\log_{10}$(PPMR) in the location on $\log_{10}$(predator body mass), as estimated from linear mixed effects models. Mass was measured in grams. Locations are numbered following Table 1. Significant slopes are identified by solid black circles. The models used here had the response variable $\log_{10}$(PPMR); separate slopes and intercepts were estimated for each location, with random effects for predator species and for predator individuals within species. The dotted line identifies the slope of the linear mixed effects model with a common slope in all 21 locations.

Differences among slopes in the unconstrained model were not related to predator mass (Fig. 2), temperature, depth, primary productivity, latitude, longitude or ecosystem (all $P > 0.05$, ordinary least squares regression). These results suggest it is reasonable to use a simpler model with a common slope for all locations henceforth (constraint 1 above): while the complex model was a slightly better fit, the small additional explanatory power was not worth the 20 additional parameters, which reduced interpretability and which appeared to vary randomly. The validity of this approach was confirmed by the nearly identical predicted values of the unconstrained model and the model with slopes equal but with no further constraints (Pearson correlation $r = 1.00$, $t = 13\,749$, df = 29\,580, $P < 0.001$).

A mixed effects model for $\log_{10}$(PPMR) vs. $\log_{10}$(predator mass) was fitted with a common slope for all locations, but intercepts differing by location according to a random effect. Random effects were also included for predator species within location, and predator individual within species. This model differed from the simpler model of the previous paragraph only insofar as the intercepts of the new model were random effects, whereas those of the previous model were fixed effects (implications of the nested random effects are shown in Fig. 3). The fitted model had a (common) slope for the generalized relationship between $\log_{10}$(predator mass)

and $\log_{10}$(PPMR) of 0.24 (0.21–0.27; mean and 95% CL), and random intercepts by location of 2.66 (2.08–3.24). When the analyses were repeated with invertebrate predators excluded, the generalized slope and mean intercept did not differ significantly from those calculated for all predators.

Since the predators in the data set were primarily fish and squid, and since these groups dominate the biomass of animals in size classes 10^1 to 10^6 g (e.g., Jennings et al. 2008b), we assumed that the trend in PPMR in this size range was representative for organisms greater than 10 g in all marine food webs. PPMR as predicted by the fixed effects of the final model ranged from 805:1 for predators of 10^1 to 13 239:1 for predators of 10^6 g. For $\beta = -1.05$, a typical slope of the numbers size spectrum (e.g., Borgmann 1987, Boudreau and Dickie 1989, Andersen et al. 2008), the corresponding transfer efficiencies would be 0.134 and 0.058, respectively (Fig. 4a), i.e., transfer efficiency fell with body mass. Since PPMR increased with predator size, the rate of increase in trophic level fell with body mass (Eq. 1; Fig. 4b), and transfer efficiency decreased at higher trophic levels (Fig. 4c).

DISCUSSION

Predator–prey mass ratios generally increased with predator mass. The specific nature and magnitude of the change of PPMR with predator body mass varied
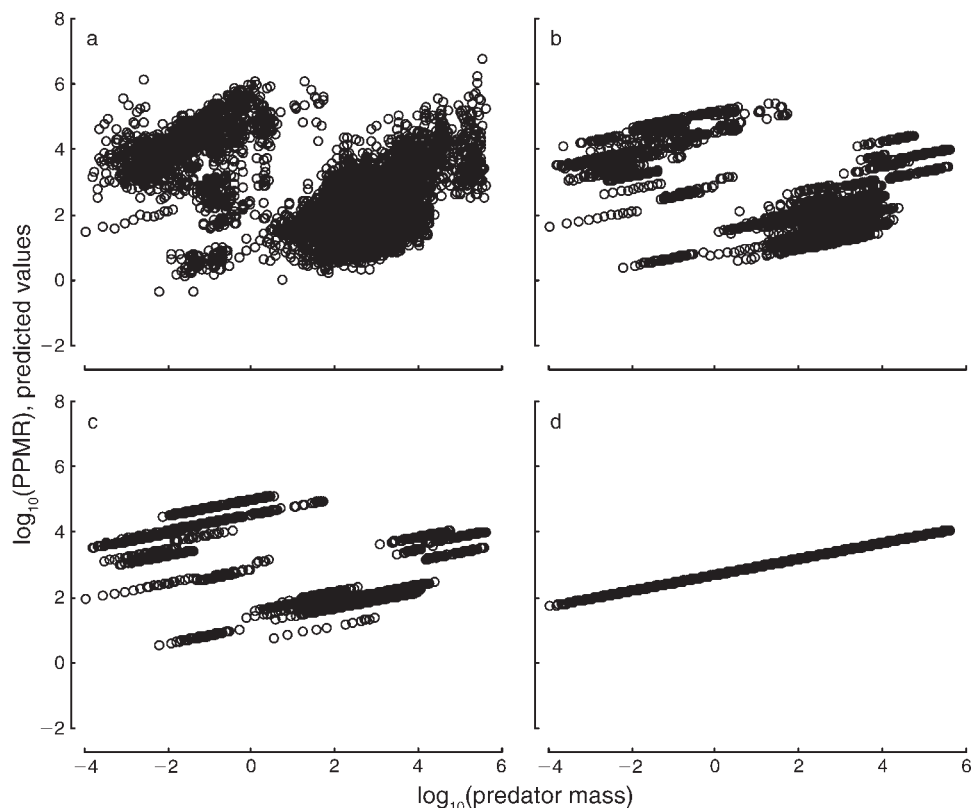
FIG. 3. Predictions of a linear mixed effects model with a common slope for all locations and nested random intercept effects for location, predator species within location, and predator individual within predator species. Predictions are based on (a) including all the random effects, (b) excluding the random effects of predator individual, (c) additionally excluding the random effects of predator species, and (d) additionally excluding the random effects of location. Mass was measured in grams.

among locations, but this change was not significantly influenced by temperature, latitude, depth or primary production. Unmeasured environmental factors or methodological factors such as the species selected for analysis in each location may explain some of the deviations of individual studies from the general increase in PPMR with predator body mass, as a power law with exponent 0.24.

The increases in PPMR with predator mass led to nonlinear relationships between log(body mass) and trophic level and suggest that there are reductions in transfer efficiency with increasing body size. The analyses of the effects of changing PPMR on transfer efficiency are predicated on the assumption that size spectra slopes are constant across the body mass range of a system. This is a reasonable assumption that is supported by data for time-averaged size spectra that include all animals in marine food webs (Boudreau and Dickie 1992). If size spectrum slopes are broadly constant among ecosystems and a function of transfer efficiency and PPMR, as suggested by theory (Borgmann 1987, Boudreau and Dickie 1989, Brown and Gillooly 2003, Brown et al. 2004, Andersen et al. 2008) and supported by some empirical evidence (Jennings and Mackinson 2003, Blanchard et al. 2008) then transfer

efficiency must decrease when PPMR increases and must not vary systematically with temperature or primary production, since PPMR was found here not to vary with those factors. This is consistent with the observation that primary production determines the intercept rather than the slope of size spectra and that temperature acts predominantly to alter the rate at which energy is passed through the spectrum rather than its slope (Boudreau and Dickie 1992). These broad characteristics of size spectra, although not the focus of the present research, can belie complex dynamics that result from spatial and temporal variations in primary production, PPMR and transfer efficiency and which may not be apparent or detectable when observations are averaged over time, space and a range of body mass classes (Pope et al. 1994, Blanchard et al. 2008).

Since PPMR varied systematically with body size but not with temperature or primary production, the rate of increase of trophic level with body size is not predicted to vary systematically among ecosystems. This implies that the rate of decrease in energy availability for a given increase in body size is broadly comparable among ecosystems. The nonlinearity of the relationship between trophic level and logged body size was inconsistent with commonly held theoretical assumptions and with the

results of the few empirical studies of community-wide PPMR. If this effect is real, as implied by the predator and prey mass data assembled, then it is perhaps not surprising that it has not been assumed or detected when the deviations from linearity are relatively subtle over narrow size windows (three to four orders of magnitude in body mass) and thus the potential to detect these deviations statistically would be low when applying methods such as size-based stable isotope analysis (Jennings et al. 2008*a*).

One consequence of increasing PPMR with size is that it allows predators to feed down the food chain on relatively smaller prey that have greater total production. However, theoretical analyses suggest that predators feeding on prey much smaller than themselves can destabilize size spectra (Law et al. 2009). Higher PPMR for some larger predators may only be possible in real food webs because they have greater capacity to store energy over longer periods and to forage over larger scales, thus reducing their vulnerability to local changes in prey dynamics. Extreme examples include the large sharks such as *Rhincodon typus* (whale shark), which feeds on zooplankton nine orders of magnitude smaller, and *Cetorhinus maximus* (basking shark), which forages on oceanic scales (e.g., Sims et al. 2003).

As each record in the data set represents an individual predator and all available records were included, the number of observations is proportional to the abundance of each species in the data set. To avoid treating each observation as independent we used a mixed effects model, which reflects the average effects on PPMR across location and species, rather than reflecting the number of individuals per species. This is similar to taking an average from sampling designed to give equal representation of species although we recognize that the different motivations of the original investigators mean their sampling designs do not necessarily allow us to achieve this.

Most predators in the data set of this study were fish (91 fish species and only one species of squid). These groups typically dominate the biomass and production of marine animals with body sizes of 10 g to 10^6 g, but are minor contributors to the biomass of animals with body sizes less than 1 g. As such, the estimated dependence of PPMR on body mass described in this study is probably indicative of PPMR for marine food webs only in the size range 10–10^6 g. PPMR of fish and squid is likely a consequence of their morphologies and feeding modes, which have developed through evolutionary time. These species often rely on visual identification and pursuit of prey (e.g., Hunter 1981). Other animals of the same size and smaller, such as zooplankton, have evolved a wider range of feeding strategies such as filter feeding that allow them to consume very small prey.

Sheldon et al. (1977) expressed realized predator–prey size ratios for a range of zooplankton in terms of equivalent spherical diameter (ESD), and concluded that
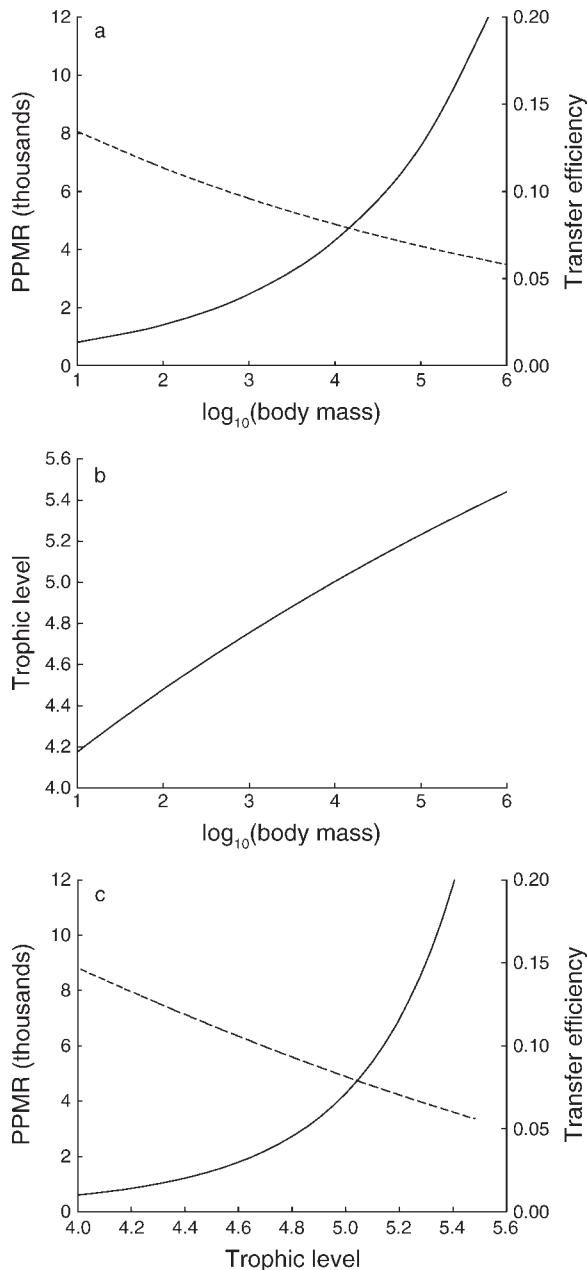

FIG. 4. (a) Relationship between PPMR (continuous line), transfer efficiency (dashed line), and predator mass; (b) relationship between trophic level and predator mass (measured in grams) from Eq. 1; and (c) relationship between PPMR (continuous line), transfer efficiency (dashed line), and trophic level. These plots are based on the central tendency of the linear mixed effects model ($\log_{10}[\text{PPMR}] = 0.24 \times \log_{10}[\text{predator mass}] + 2.66$), and on the dependency $\varepsilon = \mu^{\beta+0.75}$ where ε is the trophic transfer efficiency, μ the predator–prey mass ratio, and β the slope of the time-averaged size spectrum.

the modal ratio was around 14:1. If weight is proportional to ESD^3 this is equivalent to a PPMR of 2744:1. Hansen et al. (1994) reported a median ratio based on ESD of approximately 10:1 (PPMR = 1000:1). Given

that invertebrate zooplankton dominate biomass and production in small size classes, these results, when combined with those from the present study, imply that mean PPMR in the community probably decreases gradually with decreasing predator size, but not so rapidly in the smaller size classes as implied by the relationship for fish and squid. Invertebrate zooplankton were not included in our analysis owing to limited information on individual prey size.

Transfer efficiency is widely assumed to be unrelated to trophic level and yet our results suggest that it may decrease with increasing trophic level, as previously suggested by some modelers (e.g., Christensen and Pauly 1993). High rates of transfer efficiency have been measured in plankton communities (Hairston et al. 1993, Cebrian 1999, Elser and Hessen 2005) but there are few systematic assessments of transfer efficiency through food chains that are independent of model structures and assumptions (e.g., Ware 2000). Our results suggest that the assumption that transfer efficiency is unrelated to trophic level could usefully be revisited and that modelers might like to look at the consequences of changing PPMR with size (either for the whole community or a subset thereof).

Estimates of mean PPMR in food webs would be improved by more systematic analyses of the realized prey size selection by all individuals in all size classes, either through stomach contents analysis or nitrogen stable isotope analysis. Given the very variable dynamics of smaller individuals and the difficulty of reliably recording and measuring prey that are digested very rapidly, it is unrealistic to expect that these methods could be applied to many food webs. Our approach is a compromise, synthesizing the results from many studies and locations to make inferences about trends in mean PPMR with predator size, and among ecosystems. Not surprisingly, the analyses reveal variation in realized PPMR among locations, a result consistent with the diversity of species and feeding strategies studied. Such variation is expected in food webs (Sheldon et al. 1977, Cohen et al. 1993, Hansen et al. 1994, Brose et al. 2006), but of greater relevance in the present context are the generalities occurring across locations and that these generalities provide insight into size-related, rather than species-related, structure and energy flux which are not systematically related to the environment.

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