

The allometry of cannibalism in piscivorous fishes

Francis Juanes

Abstract: Cannibalism is a widespread phenomenon that can have strong population and community effects. In this study, I compare the prey size – predator size relationships of diets with and without cannibalized prey for four piscivorous species and five populations that are commonly cannibalistic and where large databases exist. I then examine the resultant trophic niche breadths (range of relative prey size consumed) to quantify whether inclusion of cannibalized prey in the diet slows down the decline in trophic niche breadth that many large predators exhibit as they grow. When comparing diets including cannibalized prey with those without, consistent differences were found among all predator species. In all cases, the slope of the upper bound of the predator size – prey size scatters was larger for cannibal predators compared with noncannibals, suggesting selectivity for larger cannibal prey, which may be driven by higher rates of size-dependent capture success with familiar prey. The slopes of the upper bounds of the cannibal relative prey size vs. predator size scatter also tended to be larger than the upper-bound slopes for diets without conspecific prey. Finally, for all species, mean trophic breadth of diets including cannibalized prey were larger than those not including cannibal prey, suggesting that relatively large prey sizes may always be available for cannibals.

Résumé : Le cannibalisme est un phénomène répandu qui peut avoir d'importantes répercussions sur une population ou une communauté. On trouvera ici une comparaison des relations entre la taille des prédateurs et celle des proies dans des régimes alimentaires qui contiennent ou non des proies cannibalisées chez quatre espèces de poissons piscivores, ainsi que dans cinq populations qui sont généralement cannibales et pour lesquelles il existe de grands ensembles de données. L'examen de l'étendue résultante des niches trophiques (étendue de la taille relative des proies consommées) permet de vérifier quantitativement si l'inclusion de proies cannibalisées dans le régime ralentit le déclin dans l'étendue de la niche trophique que plusieurs grands prédateurs subissent au cours de leur croissance. La comparaison des régimes avec et sans proies cannibalisées montre des différences stables entre les espèces de prédateurs. Dans tous les cas, la pente de la limite supérieure des diagrammes de dispersion des tailles des prédateurs en fonction des tailles de proies était plus forte chez les prédateurs cannibales que chez les non cannibales; cela laisse croire à une sélection des proies cannibalisées plus grandes qui peut s'expliquer par un taux de succès plus élevé et relié à la taille, lorsque les proies sont plus familières. Les pentes des limites supérieures des diagrammes de dispersion des tailles des proies cannibalisées en fonction des tailles des prédateurs ont aussi tendance à être plus fortes que celles des régimes sans proies conspécifiques. Enfin, chez toutes les espèces, les niches trophiques qui incluent des proies cannibalisées sont en moyenne plus étendues que celles qui n'en contiennent pas, ce qui laisse croire que des proies de plus grande taille sont toujours disponibles aux cannibales.

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Introduction

Cannibalism is a widespread phenomenon that can have strong population and community effects (Polis 1981; Elgar and Crespi 1992). In most fish species, cannibalism represents only an occasional part of the diet but can increase under intense culture (Folkvord 1997) or when other fish prey are absent (Persson et al. 2000) or unavailable (Post et al. 1998). In a few species, however, cannibalized prey represent a major part of the diet. Among piscivorous marine fishes, cannibalism is prevalent in natural populations of various gadoid species (Smith and Reay 1991). For example, conspecifics can represent up to 40% of the diet in silver

hake (*Merluccius bilinearis*; Koeller et al. 1989), 49% in walleye pollock (*Theragra chalcogramma*; Yamamura et al. 2001), and >70% in Cape hake (*Merluccius capensis*, Macpherson and Gordo 1994).

The costs and benefits of cannibalism have been debated in the literature. Along with the direct cost resulting from mortality of cannibalized prey are potential costs of acquiring pathogens or parasites from conspecific prey (Hammar 2000) and the reduction in inclusive fitness from consuming kin (Polis 1981; Pfennig and Collins 1993). Potential benefits to cannibal predators include increased survival, developmental rate or fecundity (Polis 1981; Babbitt and Meshaka 2000), increased growth and (or) reduced competition (Claessen et al. 2000; Persson et al. 2000), or decreased predation risk (Chapman et al. 2000), all primarily resulting from density-dependent effects. A further, and as yet unexplored, benefit of cannibalism may be an increased availability and consequent encounter rate with relatively large prey sizes that otherwise may be fairly rare.

Although prey size generally increases as a function of predator size, smaller conspecifics are generally selected over

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F. Juanes. Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003-4210, U.S.A. (e-mail: juanes@forwild.umass.edu).

larger ones by cannibals (Macpherson and Gordoia 1994; Baras et al. 2000), as is observed with most piscivorous predator–prey interactions (Juanes 1994). Much less is known about ontogenetic patterns in relative prey size or selectivity among prey types in cannibalistic fishes, although it has been suggested that cannibalized prey may be preferred (Macpherson and Gordoia 1994). Trophic niche breadth (range of relative prey size consumed) in fishes may increase, decrease, or show no change with ontogeny depending on which developmental stage is examined and how niche breadths are measured (Pearre 1986; Pepin and Penney 1997). In large piscivorous fishes, trophic niche breadth has been shown to decline as predator size increases (Scharf et al. 2000), likely because of reduced abundance of large prey for large predators (i.e., the largest relative prey size ratios). Because relatively large prey sizes may regularly be available for cannibals, the decline in trophic niche breadth may not occur.

In this study, I compare the prey size – predator size relationships of diets with and without cannibal prey for species that are commonly cannibalistic and where large databases exist. I then examine the resultant trophic niche breadths to quantify whether inclusion of cannibalized prey in the diet slows down the decline in trophic niche breadth that many large predators may experience as they grow.

Materials and methods

I searched the literature for predator size – prey size data for piscivorous fishes that commonly cannibalize prey. Much of the data that I analyzed were not directly presented in any of the papers examined but were requested from the authors. For a species to be included, there had to be a large database of predator and prey sizes for both cannibalized and non-cannibalized prey. Cannibalism had to be substantial enough to make the comparison to noncannibalistic predation meaningful. Because no diet is purely cannibalistic, I compared diets that included cannibalized prey (“cannibals”) with those that did not (“noncannibals”).

Three hypotheses are tested. (i) Cannibal predators and prey are larger than noncannibal predators and prey, respectively. I made these comparisons within species using a *t* test. (ii) Cannibal prey are larger than noncannibal prey over the size range of the predator. I tested this hypothesis by comparing the upper bounds of scatter plots of prey with predator length relationships. Upper bounds were usually represented by a 90th or 95th quantile (depending on sample size; see Scharf et al. 1998) and were estimated using quantile regression (Scharf et al. 1998, 2000). Comparisons among regression lines were done using an *F* test (Scharf et al. 2000). (iii) Relative prey sizes (i.e., prey size – predator size ratios) do not decline as quickly in predators that include cannibal prey in their diet compared with noncannibalistic predators. The difference between the predicted values of upper- and lower-bound regressions of relative prey size vs. predator size scatters is known as the trophic niche breadth. Here, I assess whether trophic niche breadths are larger in diets that include cannibalized prey compared with those with only noncannibal prey. First, for each predator, I compared the slopes of the upper bounds (90th quantile, as estimated using quantile regression) of the relative prey size vs. predator size scatter using an *F* test as above. To measure trophic niche

breadth, I calculated the difference between the predicted values of upper (90th quantile) and lower (10th quantile) bounds of the relative prey size vs. predator size regressions at all predator sizes (see Scharf et al. 2000). I then compared the average trophic niche breadths using a *t* test.

The data sets

I collected enough information on four species and five populations of primarily piscivorous fish: Atlantic cod (and Baltic cod; *Gadus morhua*), Cape hake, walleye pollock, and silver hake. Although stomach content data may exist for other cannibalistic species, these were either not published or not made available from the authors of the original studies. For each population, I obtained predator and fish prey lengths.

Prey body depths or widths (and predator mouth gapes) can be limiting factors in determining prey sizes consumed along with prey availability and behavioural differences of both predator and prey (Scharf et al. 2000). Only body lengths (and weights) were available from these data sets, precluding the possibility of testing for potential effects of prey body shape or differential digestion rates. However, recent work has shown that prey body depth – predator mouth width ratios correlate tightly with prey length – predator length ratios and either metric describes differences in predation components across various forage taxa (F.S. Scharf and F. Juanes, unpublished data).

Atlantic cod cannibalism is infrequent in populations where it occurs (see Bogstad et al. (1994) for a review). Atlantic cod cannibalism data were obtained from collections made on Spitsbergen Bank and off Newfoundland in 1985 (Sanchez-Lizaso 1996a, 1996b). Predator lengths ranged from 40 to 115 cm; cannibalized prey ranged from 16 to 49 cm. Non-cannibal prey included American plaice (*Hippoglossoides platessoides*; range 13–31 cm), pollock (*Pollachius virens*; range 10–37 cm), ocean perch (*Sebastes marinus*; range 10–31 cm), and haddock (*Melanogrammus aeglefinus*; range 16–34 cm).

Baltic cod (the common name used for Atlantic cod in the Baltic Sea) is the top piscivore in the Baltic Sea ecosystem (Sparholt 1994), and cannibalism by adults can be substantial in some years and have strong effects on recruitment success (Neuenfeldt and Koster 2000). Data on this stock were obtained from samples collected by the International Council for the Exploration of the Sea (ICES; The International Database on Baltic cod stomach contents; Jensen and Sparholt 1992; ICES 1997) from 1977 to 1994. Predator lengths ranged from 20 to 85 cm, cannibalized prey from 2 to 40 cm. The noncannibal prey included Atlantic herring (*Clupea harengus*; range 5–30 cm) and sprat (*Sprattus sprattus*; range 5–18 cm).

Cape hake occur off the east coast of South Africa where they can dominate demersal commercial catches. Cannibalized prey can represent up to 20% of the diet of larger individual size-classes (Pillar and Wilkinson 1995). Data on cannibal and noncannibal prey sizes were digitized from fig. 9 in Pillar and Wilkinson (1995). Predator lengths ranged from 10 to 100 cm; cannibal prey ranged from 10 to 60 cm. The noncannibal prey were anchovy (*Engraulis capensis*; range 5–14 cm), horse mackerel (*Trachurus trachurus capensis*;

Table 1. Mean predator and prey lengths (cm), standard errors, mean prey–predator length ratios, and sample sizes of cannibal and noncannibal predators.

Predator	Cannibals					Noncannibals						
	Mean predator length	Standard error	Mean prey length	Standard error	Mean ratio	<i>n</i>	Mean predator length	Standard error	Mean prey length	Standard error	Mean ratio	<i>n</i>
Baltic cod	56.411	1.023	13.158	0.432	0.233	248	55.128	0.411	12.759	0.113	0.231	1393
Atlantic cod	85.467	1.333	26.918	0.603	0.315	122	82.345	0.914	19.717	0.299	0.239	339
Cape hake	64.820	1.868	23.782	1.311	0.367	113	54.118	0.790	18.128	0.377	0.335	574
Walleye pollock	54.298	0.128	7.664	0.051	0.141	6713	57.041	0.164	6.204	0.061	0.109	3697
Silver hake	31.888	0.440	9.956	0.341	0.307	304	34.958	0.331	12.650	0.227	0.365	596

Table 2. Comparison of mean predator lengths and mean prey lengths between cannibal and noncannibal predators using *t* tests.

Predator	<i>t</i> predator	<i>p</i>	<i>t</i> prey	<i>p</i>
Baltic cod	-1.205	0.114	1.231	0.109
Atlantic cod	-1.815	0.035	11.692	<0.0001
Cape hake	5.448	<0.0001	4.144	<0.0001
Walleye pollock	-12.968	<0.0001	18.245	<0.0001
Silver hake	-5.578	<0.0001	-6.573	<0.0001

range 10–50 cm), and round herring (*Etrumeus whiteheadi*; range 10–25 cm).

Walleye pollock cannibalism is widespread, can dominate juvenile and adult diets, and as a consequence can regulate year-class strength (Bailey 1989; Wespestad et al. 2000). Cannibalism data were obtained for Bering Sea, Aleutian, and Gulf of Alaska regions from the National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center's Groundfish Food Habits Database (NMFS, AFSC, 7600 Sand Point Way NE, Seattle, WA 98115). Predator lengths ranged from 9 to 88 cm, cannibalized prey from 1 to 55 cm. The main noncannibal prey were Pacific sand lance (*Ammodytes hexapterus*; range 1–16 cm), northern rock sole (*Lepidopsetta polyxystra*; range 1–15 cm), capelin (*Mallotus villosus*; range 4–16 cm), lanternfish (Myctophidae; range 1–21 cm), and Greenland turbot (*Reinhardtius hippoglossoides*; range 1–6 cm).

Silver hake is one of the most abundant fishes in the northwest Atlantic (Helser et al. 1995). Cannibalized prey can represent up to 20% of the diet by volume (Garrison and Link 2000) but have been shown to exceed 40% of the diet of age-0 juveniles (Koeller et al. 1989). Silver hake data were obtained from the Food Web Dynamics Program of the NMFS Northeast Fisheries Science Center (166 Water St., Woods Hole, MA 02543). The data, collected during routine seasonal bottom trawl surveys, were available from 1973 to 1990. Predator lengths ranged from 6 to 76 cm, cannibalized prey from 1 to 30 cm. Noncannibal prey species included sand lance (*Ammodytes* sp.; range 1–25 cm), Atlantic herring (*Clupea harengus*), and other clupeids (range 1–27 cm).

Results

For Atlantic cod and Cape hake, predators with cannibalized prey were larger than those without, and cannibalized prey were larger than noncannibalized prey (Tables 1, 2). In contrast, silver hake noncannibal predators and prey were larger than cannibals. Baltic cod exhibited no differences between cannibal and noncannibal predators or prey sizes, whereas walleye pollock cannibal predators were smaller than noncannibal predators, but cannibalized prey were larger than noncannibalized prey (Tables 1, 2).

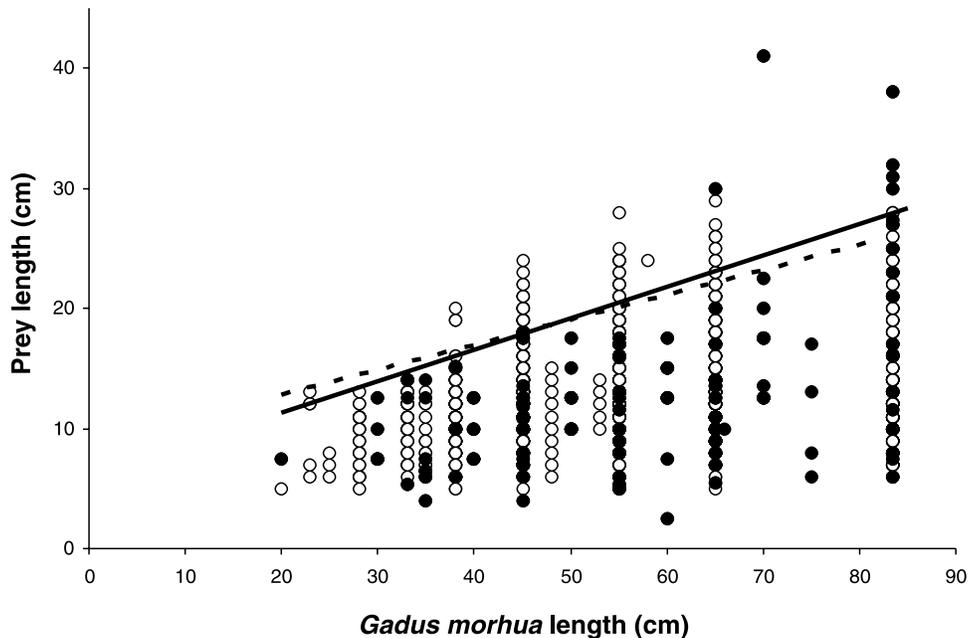
When comparing diets that included cannibalized prey with those that did not, consistent differences were found among all predator species. In all cases, the slope of the upper bound was larger for cannibal predators compared with noncannibals and ranged from 0.26 to 0.54 vs. 0.17 to 0.49 (Table 3, Figs. 1–5). In contrast, little difference was found between lower-bound slopes (0.05 or 0.1 quantiles, data not shown). Cannibal prey by themselves (i.e., not the whole

Table 3. Comparison of upper-bound slopes (estimated using quantile regression) of prey length vs. predator length relationships between diets including cannibalized prey and those without using an *F* test.

Predator	Cannibals		Noncannibals		<i>F</i>	<i>p</i>
	Upper-bound slope	Standard error	Upper-bound slope	Standard error		
Baltic cod	0.264	0.017	0.208	0.021	4.228	<0.05
Atlantic cod	0.357	0.029	0.267	0.035	3.862	<0.05
Cape hake	0.543	0.012	0.486	0.016	8.105	<0.01
Walleye pollock	0.330	0.016	0.173	0.032	18.790	<0.01
Silver hake	0.522	0.031	0.428	0.036	3.843	<0.05

Note: *F*, *F* statistic; *p*, probability.

Fig. 1. Predator size – prey size relationship for Baltic cod (*Gadus morhua*). Data were obtained from Jensen and Sparholt (1992) and ICES (1997). The solid and broken lines represent the upper-bound regression for diets including and excluding cannibalized prey, respectively. Open symbols represent noncannibalized prey; solid symbols represent cannibalized prey.



diet) tended to produce much larger upper-bound slopes (0.36–0.68, data not shown) but were not further analyzed because fish diets are unlikely to be wholly cannibalistic.

The slopes of the upper bounds of the cannibal relative prey size vs. predator size scatter all tended to be larger than the noncannibal slopes. However, only two of the species (Cape hake and walleye pollock) showed significant differences, likely because of the extremely small values of these slopes (Table 4). The comparison of mean trophic breadths also resulted in consistent differences. For all species, mean trophic breadth of diets including cannibalized prey (range = 0.20–0.49) was larger than those not including cannibal prey (range = 0.16–0.48; Table 5).

Discussion

The five species used here are all gadoids, although it was not my original intention to restrict the analyses to any particular group of piscivorous fish. However, no other data sets were available. Other gadoids, in addition to the ones used here, are known to be highly cannibalistic, particularly hakes, in which cannibalism is reported for most species

(see Alheit and Pitcher 1995). The prevalence of cannibalism also varies across species; in the data sets used here, the proportion of cannibal prey in the diet ranged from 15% in Baltic cod to 65% in walleye pollock. What aspects of gadoid life histories make them particularly susceptible to cannibalism? Smith and Reay (1991) have suggested that the likelihood of cannibalism is enhanced by factors such as low food availability, high densities, size disparity, and lack of refuges. Most gadoids are demersal and live in large aggregations that, if composed of different ages and size-classes, could make smaller conspecifics readily accessible and (or) available. For example, Macpherson and Gordo (1994) have shown that, contrary to expectations, Cape hake cannibalism is density independent because of the tendency to aggregate. These aggregations often occur in the absence of alternative fish prey species (Koeller et al. 1989), and in Atlantic cod, the range of length ratios observed in shoals (Olsen and Soldal 1989) overlaps cannibal–prey length ratios obtained from stomach analyses (Blom and Folkvord 1997). As a consequence, recruitment success in some of these species can vary as a function of overlap of different size-classes (Wespestad et al. 2000). However, the dynamics of size and

Fig. 2. Predator size – prey size relationship for Atlantic cod (*Gadus morhua*). Data were obtained from Sanchez-Lizaso (1996a, 1996b). The solid and broken lines represent the upper-bound regression for diets including and excluding cannibalized prey, respectively. Open symbols represent noncannibalized prey; solid symbols represent cannibalized prey.

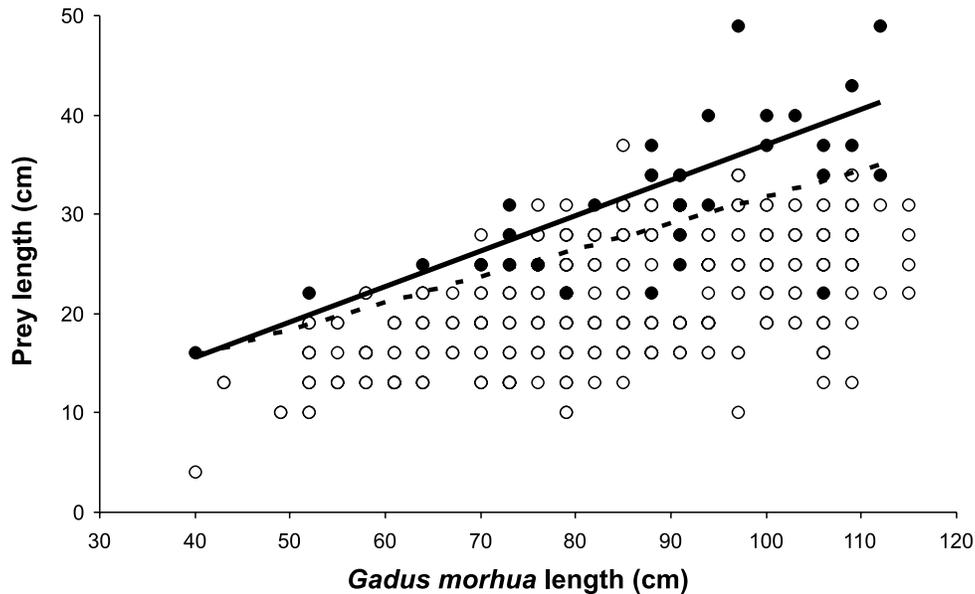
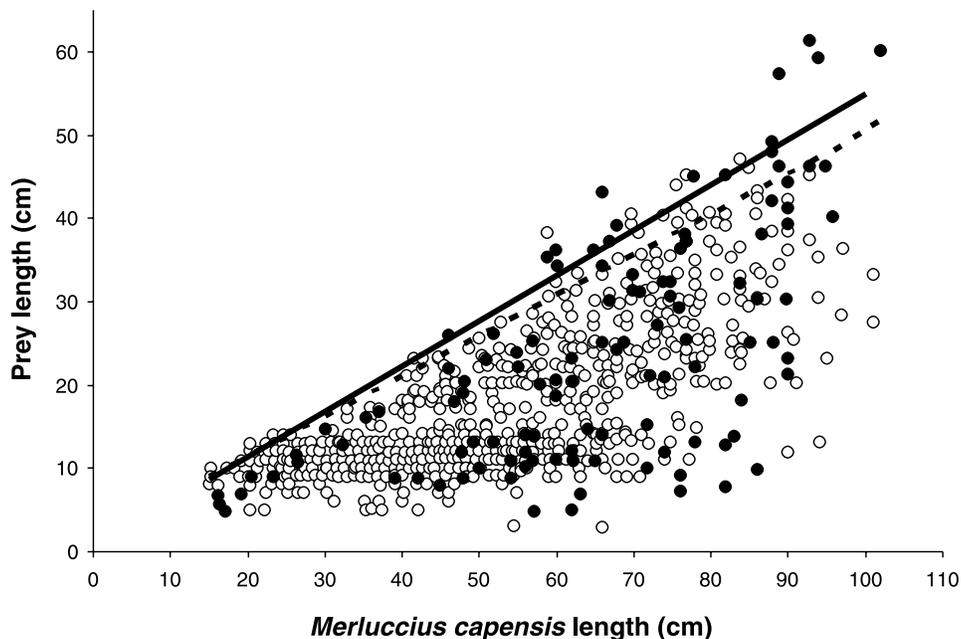


Fig. 3. Predator size – prey size relationship for Cape hake (*Merluccius capensis*). Data were obtained from Pillar and Wilkinson (1995). The solid and broken lines represent the upper-bound regression for diets including and excluding cannibalized prey, respectively. Open symbols represent noncannibalized prey; solid symbols represent cannibalized prey.



species selectivity between cannibalized and alternative prey and the ecological consequences of potential differences have remained unexplored.

The results of this study show a consistent pattern of greater upper-bound slopes for diets including cannibalized prey compared with those without, despite the fact that cannibal and noncannibal predator and prey sizes are not always larger than noncannibal predator and prey sizes. Larger upper-bound slopes indicate that at any predator size, cannibalized prey tend to be larger than alternative prey, suggest-

ing selection for larger cannibalized prey relative to alternative prey. There is, however, an indication that in some species (Baltic cod, walleye pollock, and silver hake) the cannibal and noncannibal upper-bound lines cross, so that at smaller predator sizes, larger noncannibalized prey may be selected. To conclusively demonstrate selectivity, information on prey availability is required but is generally not reported in studies of such temporal and geographical scale as those reviewed here. Results of laboratory experiments have shown selectivity for smaller conspecifics in dorada (*Brycon*

Fig. 4. Predator size – prey size relationship for walleye pollock (*Theragra chalcogramma*). Data were obtained by G. Lang from the Groundfish Food Habits Database (National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115). The solid and broken lines represent the upper-bound regression for diets including and excluding cannibalized prey, respectively. Open symbols represent noncannibalized prey; solid symbols represent cannibalized prey.

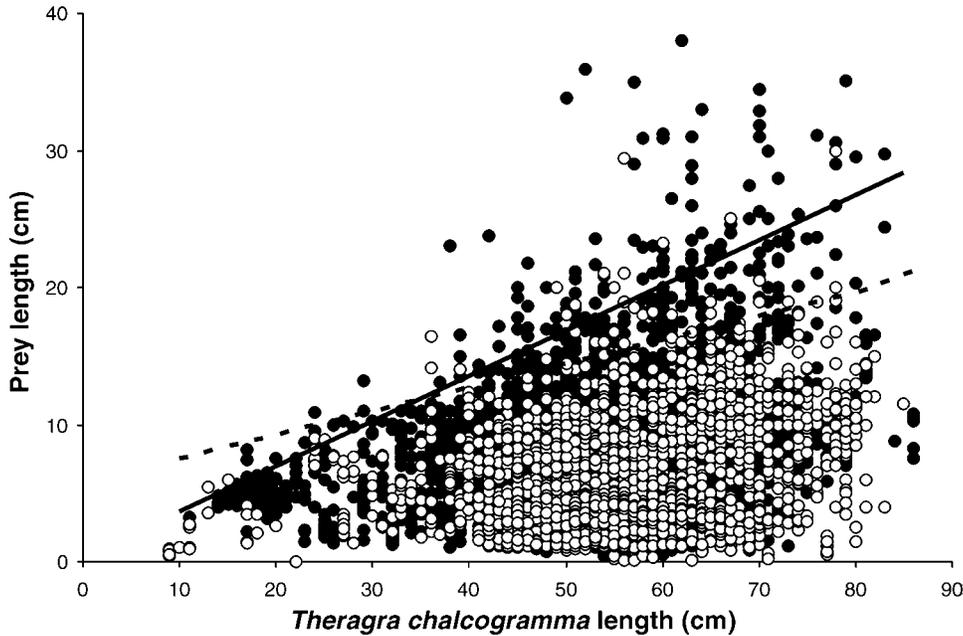


Fig. 5. Predator size – prey size relationship for silver hake (*Merluccius bilinearis*). Data were obtained from the Food Web Dynamics Program (National Marine Fisheries Service, Northeast Fisheries Science Center, 74 Magruder Road, Sandy Hook, Highlands, NJ 07732). The solid and broken lines represent the upper-bound regression for diets including and excluding cannibalized prey, respectively. Open symbols represent noncannibalized prey; solid symbols represent cannibalized prey.



moorei; Baras et al. 2000) and walleye pollock (Sogard and Olla 1994). In contrast, field collections of walleye pollock have shown no apparent size selectivity for conspecific prey, likely because of size-dependent vertical migration (Bailey

1989; Yamamura et al. 2001). However, no studies have compared size selectivity between cannibalized and non-cannibalized prey. There is evidence that some cannibalistic fish ingest cannibalized prey at sizes near the maximum possible

Table 4. Comparison of upper-bound slopes (estimated using quantile regression) of prey size – predator size ratio vs. predator size relationships between diets including cannibalized prey and those without using an *F* test.

Predator	Cannibals		Noncannibals		<i>F</i>	<i>p</i>
	Upper-bound slope	Standard error	Upper-bound slope	Standard error		
Baltic cod	-0.001 991	0.000 259	-0.002 674	0.000 472	1.611	ns
Atlantic cod	-0.000 222	0.000 614	-0.000 819	0.000 402	0.661	ns
Cape hake	-0.000 099	0.000 380	-0.001 088	0.000 311	4.054	<0.05
Walleye pollock	-0.000 933	0.000 329	-0.002 974	0.000 441	13.794	<0.01
Silver hake	-0.000 266	0.000 079	-0.000 404	0.000 146	0.689	ns

Note: *F*, *F* statistic; *p*, probability; ns, nonsignificant.

Table 5. Comparison of mean trophic niche breadths (difference between the predicted values of upper and lower bounds of the relative prey size vs. predator size regressions at all predators sizes) between diets including cannibalized prey and those without using an *F* test.

Predator	Cannibals		Noncannibals		<i>t</i>	<i>p</i>
	Mean trophic breadth	Standard error	Mean trophic breadth	Standard error		
Baltic cod	0.247 519	0.000 108	0.238 566	0.000 333	27.240	<0.0001
Atlantic cod	0.202 536	0.000 347	0.161 188	0.000 003	102.239	<0.0001
Cape hake	0.382 532	0.000 750	0.359 386	0.000 035	30.831	<0.0001
Walleye pollock	0.336 883	0.000 040	0.266 755	0.000 396	176.000	<0.0001
Silver hake	0.494 607	0.001 018	0.485 844	0.000 938	6.330	<0.0001

Note: *t*, *t* statistic; *p*, probability.

(as measured by mouth gape; Johnson and Post 1996), a pattern rarely seen among noncannibalistic species (Scharf et al. 2000; Juanes et al. 2002).

A combination of size- or species-specific differences in capture success and encounter rates can lead to differences in prey size selectivity, even without any active selection (see Juanes 1994). Because size and species selectivity in piscivorous fishes is thought to be driven primarily by size-dependent capture success rates (Juanes 1994; Scharf et al. 1998), it is likely that the observed trend of consuming larger conspecifics is due to higher rates of capture on cannibalized prey. Recent comparative work has suggested that species-specific capture success rates can predict the resultant mortality patterns when prey are offered simultaneously (Scharf et al. 2003). Similarly, capture success increases as predators learn (Croy and Hughes 1991), and thus repeated experience with familiar prey may make conspecific prey easier to capture than more unfamiliar prey types, resulting in selectivity for larger relative prey sizes. For example, experienced cannibalistic Arctic charr (*Salvelinus alpinus*) consumed a higher range of prey–predator ratios than naïve predators, even though both groups consistently selected the smallest prey fish offered (Amundsen et al. 1995). These results were likely due to differences in capture success, as prey densities (and thus encounter rates) were kept constant. In contrast, Bell et al. (1999) found that bluefish (*Pomatomus saltatrix*), which are rarely cannibalistic in field situations, attacked conspecifics more often than alternative prey in the laboratory but still consumed more of the alternative prey because of much higher capture success rates.

In addition to capture success, differences in encounter rate can also determine the outcome of predator–prey interactions (Juanes et al. 2002). Thus differential abundance (or availability) of prey types or sizes can lead to higher encounter rates and increased selectivity (Juanes 1994). The

patterns of selectivity observed in cannibalistic fish suggest that encounter rates with larger conspecifics are greater than encounters with other prey. This conclusion is supported by the observed aggregation of mixed sizes of most gadoid species and is further evidenced by the observed increases in trophic breadth of cannibal predators.

All species that I examined showed a consistent pattern of increased trophic breadth when cannibalized prey were included in the diet. The increase in trophic breadth is due primarily to larger prey sizes consumed by larger predators and could in some cases be due to intracohort cannibalism (when ratios exceed 0.6–0.7). The pattern observed here is in contrast to the ontogenetic reductions in trophic niche breadth exhibited by other large piscivorous fishes and marine mammals, a reduction likely due to decreased prey availability of relatively large prey sizes (Scharf et al. 2000; F. Juanes, unpublished data). Cannibals may therefore accrue an advantage in selectively consuming large conspecific prey, thereby ensuring a broad prey size niche as they grow.

Cannibalism is most often associated with low alternative food availability or crowded conditions (Babbitt and Meshaka 2000). In these situations, cannibal populations may benefit directly from consuming conspecifics. For example, cannibalism has been suggested to act as a “lifeboat mechanism” leading to reduced extinction probability of cannibalistic populations when under food shortage (van den Bosch et al. 1988). Most models including cannibalism do not consider the increase in population persistence gained by cannibals and the differential effects on growth of feeding on different sizes of prey. The cannibal species studied here may exhibit increases in growth directly as a consequence of selection of large prey and indirectly by the reduction in large competitors. In Eurasian perch (*Perca fluviatilis*), high recruitment leads to dramatic increases in growth of cannibals, and growth is further increased when prey sizes are larger (Persson et al.

2000). Further, the interplay between the extent of size-dependent cannibalism and competition determines the dynamics of inter- and intra-cohort perch size distributions (Claessen et al. 2000).

Predation has been shown to be a large source of natural mortality for many fish populations (Bax 1998; Juanes et al. 2002). Cannibalism, as a type of predatory mortality, has also been estimated to contribute to mortality rates in natural populations (Post et al. 1998) and can potentially regulate recruitment and therefore population size (Neuenfeldt and Koster 2000; Weststad et al. (2000), but see Macpherson and Gordo (1994)). The results of this study suggest that the impact of cannibalism may be even higher than suspected if cannibals select for large conspecifics because of their larger reproductive potential. Recent work on Atlantic cod has shown that the older (larger) individuals, in addition to contributing the largest amount of eggs, also produce the largest number of recruits likely to produce offspring with higher rates of survival (Cardinale and Arrhenius 2000). Models including cannibalism have assumed that cannibal prey are a random subset of the diet with respect to prey size (Livingston and Methot 1998), although it has been suggested that cannibal prey can be preferred over alternative prey (Macpherson and Gordo 1994; Bell et al. 1999). Future modeling of these populations should explicitly consider the implications of size selectivity differences among conspecific and alternative prey.

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References

- Alheit, J., and Pitcher, T.J. (Editors). 1995. Hake: biology, fisheries and markets. Chapman & Hall, London.
- Amundsen, P.-A., Damsgard, B., Arnesen, A.M., Jobling, M., and Jorgensen, E.H. 1995. Experimental evidence of cannibalism and prey specialization in Arctic charr, *Salvelinus alpinus*. *Environ. Biol. Fishes*, **43**: 285–293.
- Babbitt, K.J., and Meshaka, W.E. 2000. Benefits of eating conspecifics: effects of background diet on survival and metamorphosis in the Cuban treefrog (*Osteopilus septentrionalis*). *Copeia*, 2000: 469–474.
- Bailey, K.M. 1989. Interaction between the vertical distribution of juvenile walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea and cannibalism. *Mar. Ecol. Prog. Ser.* **53**: 205–213.
- Baras, E., Ndao, M., Maxi, M.Y.J., Jeandrain, D., Thome, J.P., Vandewalle, P., and Melard, C. 2000. Sibling cannibalism in dorada under experimental conditions. I. Ontogeny, dynamics, bioenergetics of cannibalism and prey size selectivity. *J. Fish Biol.* **57**: 1001–1020.
- Bax, N. 1998. The significance and prediction of predation in marine fisheries. *ICES J. Mar. Sci.* **55**: 997–1030.
- Bell, G.W., Buckel, J.A., and Stoner, A.W. 1999. Effects of alternative prey on cannibalism in age-1 bluefish. *J. Fish Biol.* **55**: 990–1000.
- Blom, G., and Folkvord, A. 1997. A snapshot of cannibalism in 0-group Atlantic cod (*Gadus morhua*) in a marine pond. *J. Appl. Ichthyol.* **13**: 177–181.
- Bogstad, B., Lilly, G.R., Mehl, S., Palsson, O.K., and Stefansson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua*) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). *ICES Mar. Sci. Symp.* **198**: 576–599.
- Cardinale, M., and Arrhenius, F. 2000. The relationship between stock and recruitment: are the assumptions valid? *Mar. Ecol. Prog. Ser.* **196**: 305–309.
- Chapman, J.W., Williams, T., Martinez, A.M., Cisneros, J., Caballero, P., Cave, R.D., and Goulson, D. 2000. Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? *Behav. Ecol. Sociobiol.* **48**: 321–327.
- Claessen, D., de Roos, A.M., and Persson, L. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. *Am. Nat.* **155**: 219–237.
- Croy, M.I., and Hughes, R.N. 1991. The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback (*Spinachia spinachia* L.). *Anim. Behav.* **41**: 161–170.
- Elgar, M.A., and Crespi, B.J. (Editors). 1992. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford.
- Folkvord, A. 1997. Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In *Early life history and recruitment in fish populations*. Edited by R.C. Chambers and E.A. Trippel. Chapman & Hall, London. pp. 251–278.
- Garrison, L.P., and Link, J.S. 2000. Diets of five hake species in the northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* **204**: 243–255.
- Hammar, J. 2000. Cannibals and parasites: conflicting regulators of bimodality in high latitude Arctic charr, *Salvelinus alpinus*. *Oikos*, **88**: 33–47.
- Helser, T.E., Almeida, F.P., and Waldron, D.E. 1995. Biology and fisheries of North-west Atlantic hake (silver hake: *M. bilinearis*). In *Hake: biology, fisheries and markets*. Edited by J. Alheit and T.J. Pitcher. Chapman & Hall, London. pp. 203–237.
- International Council for the Exploration of the Sea. 1997. Report of the study group on multispecies model implementation in the Baltic. *ICES CM* 1997/J:2.
- Jensen, H., and Sparholt, H. 1992. Estimation of predation mortality in the Central Baltic using the MSVPA. *ICES CM* 1992/J:23.
- Johnson, J.M., and Post, D.M. 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. *Trans. Am. Fish. Soc.* **125**: 809–812.
- Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? In *Theory and application in fish feeding ecology*. Edited by D.J. Stouder, K.L. Fresh, and R.J. Feller. Belle W. Baruch Li-

- brary in Marine Sciences No. 18, South Carolina University Press, Columbia. pp. 79–100.
- Juanes, F., Buckel, J.A., and Scharf, F.S. 2002. Feeding ecology of piscivorous fishes. In *The handbook of fish biology and fisheries*. Vol. 1. Fish biology. Edited by P.J.B. Hart and J.D. Reynolds. Blackwell Scientific Publications, London. pp. 267–283.
- Koeller, P.A., Coates-Markle, L., and Neilson, J.D. 1989. Feeding ecology of juvenile (age-0) silver hake (*Merluccius bilinearis*) on the Scotian shelf. *Can. J. Fish. Aquat. Sci.* **46**: 1762–1768.
- Livingston, P.A., and Methot, R.D. 1998. Incorporation of predation into a population assessment model of Eastern Bering Sea walleye pollock. In *Fishery stock assessment models*. Edited by F. Funk, T.J. Quinn, J. Heifetz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and C.I. Zhang. University of Alaska Sea Grant College Program, Anchorage. pp. 663–678.
- Macpherson, E., and Gordo, A. 1994. Effect of prey densities on cannibalism in Cape hake (*Merluccius capensis*) off Namibia. *Mar. Biol.* **119**: 145–149.
- Neuenfeldt, S., and Koster, F.W. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES J. Mar. Sci.* **57**: 300–309.
- Olsen, S., and Soldal, A.V. 1989. Observations on inshore distribution and behavior of 0-group northeast Arctic cod. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **191**: 296–302.
- Pearre, S. 1986. Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Mar. Ecol. Prog. Ser.* **27**: 299–314.
- Pepin, P., and Penney, R.W. 1997. Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? *J. Fish Biol.* **51**(Suppl. A): 84–100.
- Persson, L., Bystrom, P., and Wahlstrom, E. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology*, **81**: 1058–1071.
- Pfennig, D.W., and Collins, J.P. 1993. Kinship affects morphogenesis in cannibalistic salamanders. *Nature (Lond.)*, **362**: 836–838.
- Pillar, S.C., and Wilkinson, I.S. 1995. The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. *S. Afr. J. Mar. Sci.* **15**: 225–239.
- Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* **12**: 225–231.
- Post, D.M., Kitchell, J.F., and Hodgson, J.R. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Can. J. Fish. Aquat. Sci.* **55**: 2588–2600.
- Sanchez-Lizaso, J.L. 1996a. Alimentacion del bacalao, *Gadus morhua* L., en los bancos de Terranova en la primavera de 1985. XII Bienal Real Sociedad Española de Hist. Nat. pp. 229–232.
- Sanchez-Lizaso, J.L. 1996b. La alimentacion del bacalao (*Gadus morhua* L.) en el banco de Spitsbergen (Artico Oriental) con particular referencia al canibalismo. XII Bienal Real Sociedad Española de Hist. Nat. pp. 233–236.
- Scharf, F.S., Juanes, F., and Sutherland, M. 1998. Inferring ecological relationships from the edges of scatter diagrams: a comparison of least squares and quantile regression techniques. *Ecology*, **79**: 448–460.
- Scharf, F.S., Juanes, F., and Rountree, R.A. 2000. Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* **208**: 229–248.
- Scharf, F.S., Buckel, J.A., McGinn, P.A., and Juanes, F. 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. *J. Exp. Mar. Biol. Ecol.* In press.
- Smith, C., and Reay, P. 1991. Cannibalism in teleost fish. *Rev. Fish Biol. Fish.* **1**: 41–64.
- Sogard, S.M., and Olla, B.L. 1994. The potential for intracohort cannibalism in age-0 walleye pollock, *Theragra chalcogramma*, as determined under laboratory conditions. *Environ. Biol. Fishes*, **39**: 183–190.
- Sparholt, H. 1994. Fish species interactions in the Baltic Sea. *Dana*, **10**: 131–162.
- van den Bosch, F., de Roos, A.M., and Gabriel, W. 1988. Cannibalism as a life boat mechanism. *J. Math. Biol.* **26**: 619–633.
- Wespestad, V.G., Fritz, L.W., Ingraham, W.J., and Megrey, B.A. 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES J. Mar. Sci.* **57**: 272–278.
- Yamamura, O., Yabuki, K., Shida, O., Watanabe, K., and Honda, S. 2001. Spring cannibalism on 1 year walleye pollock in the Doto area, northern Japan: is it density dependent? *J. Fish Biol.* **59**: 645–656.