Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei)

David A. Ebert · Joseph J. Bizzarro

Abstract Skates by virtue of their abundance and widespread occurrence appear to play an influential role in the food webs of demersal marine communities. However, few quantitative dietary studies have been conducted on this elasmobranch group. Therefore, to better understand the ecological role of skates, standardized diet compositions and trophic level (TL) values were calculated from quantitative studies, and compared within and among skate and shark taxa. Prey items were grouped into 11 general categories to facilitate standardized diet composition and TL calculations. Trophic level values were calculated for 60 skate species with TL estimates ranging from 3.48 to 4.22 (mean TL = 3.80 ± 0.02 SE). Standardized diet composition results revealed that decapods and fishes were the main prey taxa of most skate species followed by amphipods and polychaetes. Correspondingly, cluster analysis of diet composition data revealed four major trophic guilds, each dominated by one of these prey groups. Fish and decapod guilds were dominant comprising 39 of 48 species analyzed. Analysis of skate families revealed that the Arhynchobatidae and Rajidae had similar TL values of 3.86 and 3.79 (*t*-test, *P* = 0.27), respectively. The Anacanthobatidae were represented by a single species, *Cruriraja parcomaculata*, with a TL of 3.53. Statistical comparison of TL values calculated for five genera (*Bathyraja*, *Leucoraja*, *Raja*, *Rajella*, *Rhinoraja*) revealed a significant difference between *Bathyraja* and *Rajella* (*t*-test, *P* = 0.03). A positive correlation was observed between TL and total length (L_T) with larger skates (e.g. >100 cm L_T) tending to have a higher calculated TL value (>3.9). Skates were found to occupy TLs similar to those of several co-occurring demersal shark families including the Scyliorhinidae, Squatinidae, and Triakidae. Results from this study support recent assertions that skates utilize similar resources to those of other upper trophic-level marine predators, e.g. seabirds, marine mammals, and sharks. These preliminary findings will hopefully encourage future research into the trophic relationships and ecological impact of these interesting and important demersal predators.

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Introduction

Skates (Chondrichthyes: Rajiformes: Rajoidei) are the most diverse group of living cartilaginous

fishes, with approximately 245 species recognized worldwide (Ebert and Compagno 2007). This total represents nearly 25% of the described species of chondrichthyan fishes (Compagno 2005). In addition, skates appear to exhibit a fairly high degree of endemism, with many species having somewhat localized regional distributions (McEachran and Miyake 1990; Compagno et al. 1991; Menni and Stehmann 2000; Last and Yearsley 2002). A morphologically conservative group, skates are most commonly found along outer continental shelves and upper slopes. They are the only cartilaginous fish taxon to exhibit a great diversity of species at higher latitudes.

Skates, by virtue of their abundance and species diversity, may play influential roles in the food webs of demersal marine communities. It has been hypothesized that skates may negatively impact commercially valuable groundfishes via ecological interactions such as competition and predation (Murawski 1991; Mayo et al. 1992; Fogarty and Murawski 1998; Link et al. 2002; Orlov 2004). Quantifiable studies, however, on the diet composition and trophic relationships of skates are few (Garrison and Link 2000; Bulman et al. 2001; Davenport and Bax 2002). Additionally, although some skate species are considered top predators (Macpherson and Roel 1987; Ebert et al. 1991; Orlov 1998, 2003; Link et al. 2002) surprisingly few quantitative estimates of trophic level values exist to substantiate this perception (Morato et al. 2003; Braccini and Perez 2005). Furthermore, the impact that skates may have on associated demersal marine communities is still relatively unknown.

If skates are upper trophic level predators, as demonstrated for sharks (Cortés 1999; Estrada et al. 2003), marine mammals (Bowen 1997; Pauly et al. 1998), and seabirds (Sanger 1987; Hobson 1993), they may influence the relative abundance and diversity of co-occurring demersal species (Beddington 1984; Rogers et al. 1999). Therefore, to better understand the ecological role of skates, we present standardized diet compositions and trophic level values calculated from quantitative studies. We then compare results within skate taxa and among skate and shark taxa to investigate similarities and differences in these parameters between elasmobranch groups.

Materials and methods

Diet composition data were summarized from peer-reviewed journal articles, graduate theses, and gray literature (see Appendix I). Only sources that included quantitative information in the form of indices or provided sufficient information to facilitate index calculations were utilized. The following search engines were initially used to locate citations: Aquatic Sciences and Fisheries Abstracts, Biosis, Web of Science, and Zoological Record. After relevant articles were obtained, their literature cited sections were perused for additional references. Colleagues were also contacted to obtain supplemental literature and especially unpublished graduate theses that may have been overlooked during previous searches. All pertinent literature was accumulated and examined, regardless of publication language.

Prey items were grouped into 11 general categories to facilitate standardized diet composition and trophic level calculations (Table 1). Trophic levels for generalized prey categories were directly incorporated when available or estimated by calculating a mean value from information contained in the following sources: Fauchauld and Jumars (1979); Hobson and Welch (1992); Hobson (1993); Pauly and Christensen (1995); Pauly et al. (1998); Cortés (1999); and Nyssen et al. (2002). Because multiple diet studies existed for some skates, an index of standardized diet composition, weighted by relative sample size, was calculated after Cortés (1999) to determine the proportion of each prey category in the diet of a species (P_j):

$$P_j = \sum_{i=1}^{n} (P_{ij} * N_i) / \sum_{j=1}^{11} * \sum_{i=1}^{n} (P_{ij} * N_i),$$

where P_{ij} = the proportion of prey category j from source i, N_i = the number of stomach samples containing food that were used to calculate P_{ij} for source i, n = number of sources, j = total number of prey categories, and $\sum P_j = 1$.

The proportion of each prey category (P_{ij}) was determined for each source using the following hierarchical criteria. Compound indices (e.g., index of relative importance, geometric index of importance, index of absolute importance) were

Table 1 Prey categories used to calculate standardized diet compositions and trophic levels of skates

Group code	Description	Trophic level
INVERT	Other invertebrates and unidentified invertebrates	2.5
POLY	Polychaetes and other marine worms	2.60
MOLL	Molluscs (excluding cephalopods) and unidentified mollusks	2.1
SQUID	Squids	3.2
CEPH	Octopi, cuttlefishes, and unidentified cephalopods	3.2
AMPH	Amphipods and isopods	3.18
EUPH	Euphausiids and mysids	2.25
DECA	Decapod crustaceans	2.52
OCRUST	Other crustaceans and unidentified crustaceans	2.4
CHOND	Chondrichthyan fishes	3.65
FISH	Teleost and agnathan fishes	3.24

used if available. If no compound index was available but more than one single index was used, a geometric index of importance was calculated on a percentage basis by averaging all available indices (e.g., (%N + %W)/2), as described by Assis (1996). Single indices were used when multiple indices were not available. Incidentally ingested materials (e.g., plant matter, sediment, detritus) and undeterminable items (e.g., offal, unidentified organic matter) were not incorporated in analyses. In addition, all non-additive indices, such as percent frequency of occurrence (%FO) or the original index of relative importance (Pinkas et al. 1971), were standardized so that the contribution of each index to diet composition calculations was equal. When only the total number of occurrences of each prey item was available, the occurrence index (O) was calculated after Mohan and Sankaran (1988). When only proportions (%FO) were provided, they were summed and standardized in the same manner.

Trophic levels were then calculated for each species using the following equation, after Cortés (1999):

$$TL_k = 1 + \left(\sum_{j=1}^{n} P_j * TL_j \right),$$

where TL_k = trophic level of species k, P_j = proportion of prey category j in the diet of species k, n = total number of prey categories, and TL_j = trophic level of prey category j. Mean trophic level (TL) values were also calculated for the order, families, and genera using TL estimates from individual species. When data were normally distributed and of equal variances, TL values were compared between and among groupings with t-tests and ANOVAs (SYSTAT, version 10, SPSS, Inc., Chicago, IL). If either of these assumptions were violated, data were log-transformed and re-evaluated prior to analysis. Because it was not possible to generate precision estimates from the available data (Ferry and Cailliet 1996), a minimum sample size of 20 individuals was arbitrarily chosen as the limit for inclusion of a species in all analyses.

Cluster analysis was utilized to compare standardized diet compositions among skate species. Calculations were preformed in SYSTAT (version 10, SPSS, Inc., Chicago, IL) using the unweighted pairwise group mean average method (UPGMA) with Euclidean distance as a measure of dissimilarity. Dissimilarity values among clusters that were ≥50% of the maximum overall dissimilarity distance were considered to indicate major divisions and used to distinguish trophic guilds of skates (Root 1967; Yoklavich et al. 2000).

Results

Standardized diet compositions and trophic levels were calculated for 60 skate species (Table 2). Overall, trophic level estimates ranged from 3.48 (*Rajella caudaspinosa*) to 4.22 (*Dipturus chilensis*). Eleven skate species were estimated to have TL values ≥4, with the genera *Bathyraja* and *Dipturus* each having four species represented. Two species, *Amblyraja radiata* and *Raja clavata*, had the most quantitative diet studies with nine each, followed by *Raja montagui* with six studies, and *Bathyraja aleutica* and *Leucoraja naevus* with five studies each. Three species had a total of four different diet studies, whereas six species and 14 species had three and two studies each, respectively. Thirty-two of

the species included in the present study had only a single diet study. The species with the most stomachs examined was *Leucoraja erinacea* (*n* = 19,738), whereas *Rajella dissimilis* (*n* = 2) had the fewest. Six species had >1,000 stomachs examined from various combined studies, 31 species had between 134 and 952 stomachs examined, and 23 species had <100 stomachs examined.

Standardized diet composition results revealed that decapod crustaceans and secondarily fishes were the main prey taxa of most skate species with sufficient sample sizes (Table 2). Overall, decapods comprised 36.35 ± 3.06 SE of mean percent diet composition, were present in the diets of all species examined, and ranged from 0.26% of dietary composition in *Rhinoraja maclovania* to 77.16% for *Rioraja agassizii*. Fishes contributed 28.61 ± 3.31 to the mean diet composition of the skate species studied and comprised >50% of the diet composition of nine species (Table 2). Fishes were of greatest dietary importance to *Dipturus batis* (70.76%) and *D. chilensis* (81.76%), but in contrast were not present in the diets of *Leucoraja melitensis* or *R. maclovania*. Polychaetes and amphipods were of supplemental importance in skate diets, only contributing >50% of the diet composition of *Bathyraja griseocauda* (52.54%), *Rhinoraja albomaculata* (51.53%), *R. maclovania* (89.24%), and *R. taranetzi* (52.71%). Squids (3.36 ± 0.87), euphausids and mysids (6.07 ± 1.55), and other crustaceans (3.68 ± 0.79) were minor prey items. Shelled molluscs, octopi and cuttlefishes, and chondrichthyans were not important prey items for skates, with maximum reported diet composition values of 10.92% (*Leucoraja erinacea*), 14.01% (*Rostroraja alba*), and 5.00% (*Leucoraja fullonica*), respectively. Other invertebrates and unidentified invertebrates were only reported from 35.4% of the species studied and contributed no more than 0.82% to diet composition (*A. radiata*).

Cluster analysis of calculated diet composition estimates for sufficiently sampled species revealed four major trophic guilds with Euclidean distances (ED) > 13.7, or 50% of maximum dissimilarity (Fig. 1). These guilds were dominated by the following prey taxa: polychaetes, amphipods,

fishes, and decapods. The polychaete guild (ED = 18.62) included only two species, both in the genus *Rhinoraja*; *R. albomaculata* and *R. macloviana*. The amphipod guild (ED = 16.86) was comprised of seven relatively small species; four of which are found within two genera, *Bathyraja* and *Rhinoraja*. Amphipods were the dominant prey taxon of this guild (41.90 ± 1.66), but decapods were also important (28.74 ± 2.68) and were the main taxon of *Bathyraja violacea* and *L. erinacea*. The fish guild (ED = 15.53), which contained many of the largest skate species within this study, had the greatest number of species at 20; half of which were represented by two genera, *Bathyraja* (*n* = 6) and *Raja* (*n* = 4). All representative species within the genera *Amblyraja* (*n* = 2) and *Dipturus* (*n* = 3) were found within this guild. Decapods were of substantial supplemental importance within the fish guild and were the primary prey taxon of one species (*Raja straeleni*). The decapod guild (ED = 13.9) contained 19 species, with the genus *Raja* represented by eight species. Decapods were dominant in the diets of all species within this guild, with fishes typically of secondary importance. Both the fish and decapod guilds had seven skate genera represented. Although no genera were represented among all four guilds, three genera, *Bathyraja*, *Leucoraja*, and *Rajella*, had representatives among three of the four trophic guilds.

The mean TL for all skate species combined was 3.80 ± 0.02 SE (*n* = 60). A breakdown of the three skate families revealed that the Arhynchobatidae and Rajidae had similar trophic levels of 3.86 and 3.79, respectively (Table 3). The Anacanthobatidae were represented by a single species, *Cruriraja parcomaculata*, with a TL of 3.53. Estimated TL values for the two families (Arhynchobatidae, *n* = 18 and Rajidae, *n* = 29) for which multiple samples were available showed normal distributions (Kolmogorov-Smirnov, *P* > 0.05) and equal variances (*F*-test, *P* > 0.05). Comparison of these two families using a two sample *t*-test revealed no significant difference (*t* = 1.11; *P* = 0.27).

The family Rajidae had eight genera represented, followed by the Arhynchobatidae with four and a single genus for the Anacanthobatidae.

Table 2 Standardized diet composition and trophic levels of skates

Family	Genus and species	TL	n	N	INVERT	POLY	MOLL	SQUID	CEPH	AMPH	EUPH	DECA	OCRUST	CHOND	FISH
Anacanthobatidae	*Cruriraja parcomaculata*	3.53	2	47	0.00	0.88	0.00	0.00	0.82	17.08	53.97	18.11	3.43	0.00	5.70
Arhynchobatidae	*Bathyraja aleutica*	3.96	5	416	0.34	3.44	0.00	11.46	3.04	8.76	1.47	31.39	0.00	0.16	39.94
	Bathyraja brachyurops	4.08	1	198	0.61	4.66	2.31	15.39	0.98	20.27	2.63	6.98	1.37	0.74	44.05
	Bathyraja griseocauda	4.09	1	154	0.37	4.33	2.43	5.23	0.74	52.54	5.18	1.85	1.01	3.00	23.32
	Bathyraja isotrachys	3.71	1	22	0.00	0.00	0.00	22.26	0.00	0.00	0.00	72.40	0.00	0.00	5.33
	Bathyraja kincaidii	3.54	2	134	0.00	18.22	0.15	2.27	0.30	4.83	31.46	37.35	0.10	0.00	5.48
	Bathyraja maculata	4.02	3	577	0.01	4.81	0.31	24.39	3.18	23.59	0.60	21.10	0.01	0.00	22.14
	Bathyraja matsubarai	3.87	2	257	0.00	2.41	0.00	19.69	2.73	0.63	0.12	46.71	0.00	0.00	27.41
	Bathyraja minispinosa	3.75	2	72	0.00	0.00	0.00	4.17	0.52	6.87	0.00	67.90	0.00	0.00	20.55
	Bathyraja parmifera	3.97	4	285	0.13	1.22	0.17	6.12	1.33	4.00	0.16	35.22	0.00	0.12	51.53
	Bathyraja smithii	3.91	1	32	0.00	0.00	0.00	0.00	5.66	0.00	5.60	37.93	0.00	0.00	50.81
	Bathyraja spinicauda	4.02	2	25	0.00	4.63	0.00	0.00	0.00	8.44	8.01	11.64	3.56	1.41	62.31
	Bathyraja trachura	3.78	1	4	0.00	37.02	0.00	6.57	1.61	16.07	10.82	11.82	2.19	0.00	13.90
	Bathyraja violacea	3.81	2	139	0.00	6.75	0.00	3.73	1.01	31.36	0.00	51.04	0.00	0.00	6.11
	Psammobatis extenta	3.84	2	693	0.00	4.24	0.00	0.00	0.00	48.42	0.00	46.61	0.68	0.00	0.06
	Rhinoraja albomaculata	3.85	1	201	0.82	51.53	0.00	5.70	0.00	36.17	1.25	2.38	0.61	0.00	1.54
	Rhinoraja interrupta	3.90	3	433	0.32	14.17	0.00	4.46	0.00	49.02	0.36	29.46	0.22	0.00	1.99
	Rhinoraja macloviana	3.66	2	186	0.01	89.24	0.00	0.00	0.00	10.47	0.00	0.26	0.01	0.00	0.00
	Rhinoraja taranetzi	3.91	1	63	0.20	17.36	0.00	3.67	0.17	52.71	10.06	9.05	2.59	0.00	4.19
	Rioraja agassizi	3.63	2	702	0.00	5.15	0.00	0.00	0.00	2.30	0.00	77.16	1.98	0.00	13.41
Rajidae	*Amblyraja hyperborea*	3.98	2	61	0.00	2.13	0.00	0.00	0.00	0.91	11.34	16.90	1.86	0.00	66.85
	Amblyraja radiata	3.82	9	8,381	0.82	18.78	0.20	0.63	3.21	9.65	4.29	22.55	9.87	0.11	29.89
	Dipturus batis	4.06	1	35	0.00	1.71	0.00	0.00	1.22	3.27	3.29	18.76	0.00	1.00	70.76
	Dipturus chilensis	4.22	1	353	0.02	0.04	0.02	11.55	0.26	5.08	0.00	0.87	0.33	0.07	81.76
	Dipturus laevis	3.52	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00
	Dipturus lineatus	3.85	1	4	6.33	0.00	0.00	0.00	0.00	12.86	0.00	46.34	0.00	0.00	34.47
	Dipturus nidarosiensis	4.01	1	5	0.00	0.00	0.00	0.00	0.00	0.00	18.33	0.00	18.33	26.67	36.67
	Dipturus pullopunctatus	3.84	2	172	0.00	0.00	0.00	0.00	0.85	0.00	1.96	41.29	9.86	0.00	46.04
	Dipturus springeri	4.07	1	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	80.00
	Leucoraja erinacea	3.70	4	19,738	0.00	13.35	10.92	0.00	0.00	24.16	0.01	39.29	3.40	0.00	8.86
	Leucoraja fullonica	4.06	1	636	0.00	1.20	0.00	0.00	4.37	3.70	0.00	22.15	3.12	5.00	60.46
	Leucoraja garmani	3.54	1	15	0.00	0.72	0.00	0.00	2.69	1.03	3.52	84.59	5.69	0.00	1.76
	Leucoraja melitensis	3.65	1	473	0.00	0.00	0.00	0.00	0.00	23.40	0.00	57.71	18.88	0.00	0.00
	Leucoraja naevus	3.91	5	926	0.13	12.19	0.59	0.00	2.05	8.08	0.67	20.31	10.42	0.12	45.45
	Leucoraja ocellata	4.04	1	595	0.00	8.64	8.94	6.40	0.71	2.24	0.00	4.88	0.41	0.51	67.28
	Leucoraja wallacei	3.68	1	40	0.00	0.00	0.62	0.00	0.62	0.00	1.24	75.75	0.00	0.62	21.16
	Malacoraja senta	3.57	2	307	0.00	2.05	0.00	0.00	0.00	2.15	30.27	35.53	11.56	0.00	18.43
	Malacoraja spinacidermis	3.70	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	75.01	0.00	0.00	24.99

Table 2 continued

Family	Genus and species	TL	n	N	INVERT	POLY	MOLL	SQUID	CEPH	AMPH	EUPH	DECA	OCRUST	CHOND	FISH
	Neoraja stehmanni	3.52	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00
	Raja binoculata	3.84	1	214	0.00	0.00	0.00	0.08	1.12	0.40	0.04	55.83	0.03	0.01	42.49
	Raja brachyura	3.82	4	137	0.00	3.31	1.29	0.00	0.37	16.03	18.67	25.58	0.43	0.00	34.32
	Raja clavata	3.69	9	3,424	0.02	3.37	2.75	0.44	3.01	2.73	1.51	55.37	9.78	0.21	20.82
	Raja eglantaria	3.68	3	651	0.00	0.36	7.81	0.28	0.04	0.93	4.13	57.39	2.09	0.04	26.93
	Raja inornata	3.76	1	264	0.00	0.01	0.40	0.69	0.22	0.02	2.71	62.06	0.20	0.00	33.69
	Raja microocellata	3.88	2	952	0.00	1.73	0.21	0.76	0.00	0.21	1.23	46.39	0.25	0.21	49.00
	Raja miraletus	3.67	3	1,331	0.00	1.09	1.45	0.39	1.41	12.07	3.10	58.93	9.97	0.00	11.59
	Raja montagui	3.59	6	1,533	0.14	10.03	0.45	0.03	0.25	6.05	4.71	65.11	7.07	0.00	6.17
	Raja pulchra	3.77	1	564	0.06	0.00	0.12	4.57	0.76	0.00	0.00	65.07	0.06	0.00	29.36
	Raja radula	3.79	1	801	0.19	2.25	0.66	1.87	6.65	7.40	0.00	54.21	3.84	0.00	22.94
	Raja rhina	3.86	2	567	0.00	0.00	0.05	2.04	4.34	0.00	12.59	34.94	0.05	0.00	46.00
	Raja straeleni	3.74	1	421	0.00	0.55	0.55	0.18	0.37	0.00	1.11	43.29	20.40	0.00	33.53
	Rajella barnardi	3.55	1	80	0.00	3.74	0.00	0.00	1.71	8.09	18.33	56.63	8.09	0.00	3.41
	Rajella bathyphila	3.80	1	4	0.00	16.75	0.00	0.00	0.00	47.27	6.05	4.59	25.34	0.00	0.00
	Rajella bigelowi	3.79	1	11	0.00	32.37	0.00	0.00	0.00	42.11	4.70	6.94	13.88	0.00	0.00
	Rajella caudaspinosa	3.48	1	48	0.00	13.44	0.00	0.00	1.75	0.00	22.91	38.84	19.42	0.00	3.64
	Rajella dissimilis	3.69	1	2	0.00	0.00	0.00	0.00	20.00	0.00	40.00	20.00	0.00	0.00	20.00
	Rajella fyllae	3.78	3	210	0.20	29.67	0.00	0.00	1.49	35.09	5.68	23.87	1.75	0.00	2.24
	Rajella leopardus	3.77	1	137	0.00	1.54	0.00	0.26	0.51	2.03	20.61	31.08	4.05	0.77	39.15
	Rajella ravidula	3.55	1	8	0.08	33.20	0.00	0.00	0.25	0.00	0.00	66.39	0.00	0.00	0.08
	Rostroraja alba	4.15	3	1,168	0.00	0.00	0.00	2.57	14.01	0.00	0.00	9.57	3.82	4.85	65.18

See Table 1 for definitions of prey categories; n = number of studies incorporated for each species, N = total number of stomachs analyzed among studies. Species are listed in alphabetical order within families. A complete list of the original studies is given in Appendix I
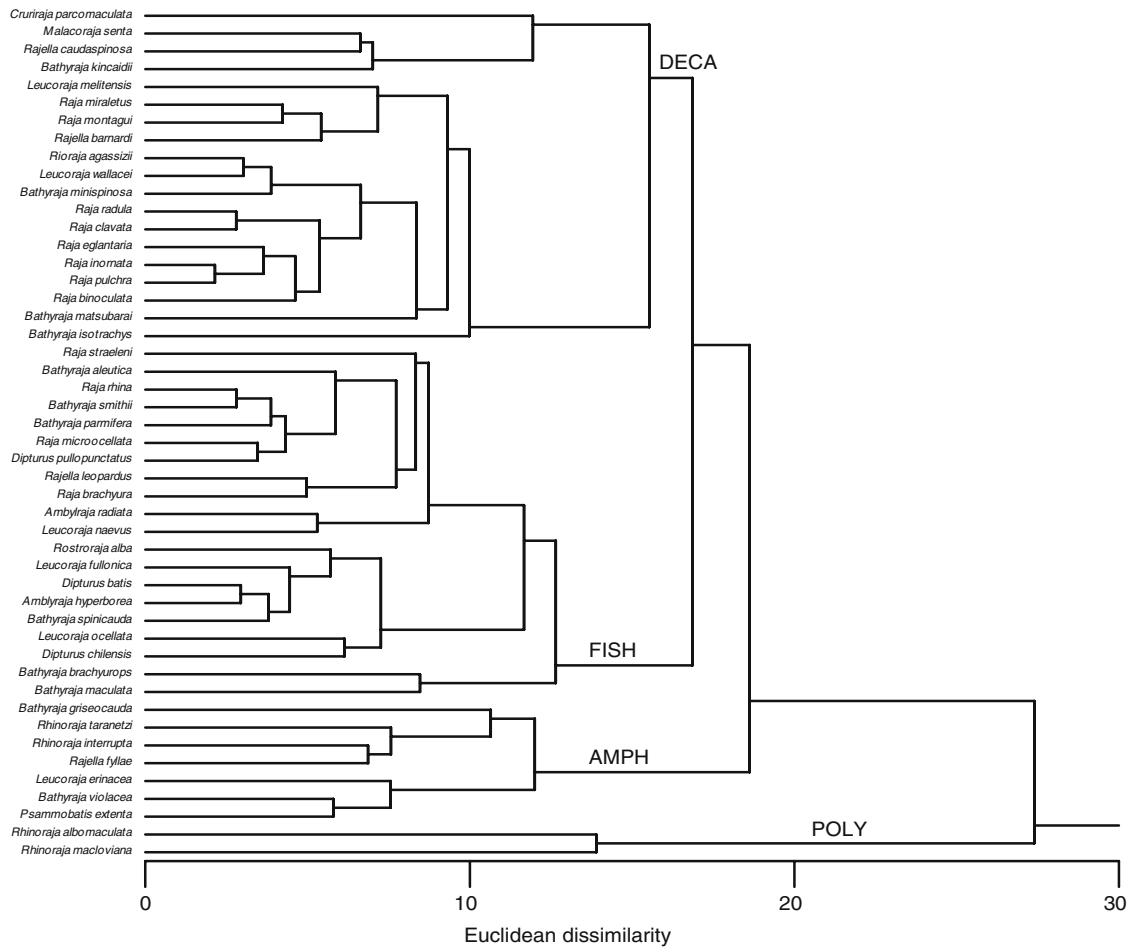
Fig. 1 Cluster analysis of standardized diet compositions of skate species ($n = 48$). Hierarchical clustering was performed using average linkage with Euclidean distance as a measure of dissimilarity. Major trophic guilds are indicated (see Table 2 for description of prey categories)

Of the 13 genera included in this study, five were represented by a single species. The remaining eight genera had at least two or more species studied within the genus. *Bathyraja* ($n = 13$) had the most species studied followed by the *Raja* ($n = 12$). All genera, except for the monotypic *Rostroraja* (TL = 4.15), had a mean TL between 3.5 and 3.9. The genera with the lowest TLs were *Cruriraja* and *Neoraja* at 3.53 and 3.52, respectively.

Statistical comparison of log-transformed TL values calculated for five genera (*Bathyraja, Leucoraja, Raja, Rajella, Rhinoraja*) for which sample size was reasonably high (Table 3) revealed a significant difference among samples

(ANOVA, $F = 2.85$; $P = 0.04$). *Bathyraja* ($n = 12$) was found to feed at a higher TL than *Rajella* ($n = 4$) (Tukey's, $P = 0.04$). There were no significant differences found in comparisons between any of the other genera.

A positive relationship was observed between TL and total length (L_T) of skates (Fig. 2). Skates with TL values >3.9 ($n = 15$) were usually the larger species, e.g. those exceeding 100 cm L_T, however, *Bathyraja brachyurops* (73 cm L_{Tmax}) was an exception (TL = 4.08). Of those skates with TLs between 3.8 and 3.9 ($n = 17$) most were <100 cm L_T; three species (*Dipturus pullopunctata, Raja brachyura, R. rhina*) grow to between 120 and 137 cm L_T and one (*Raja binoculata*)

Table 3 Trophic levels of skates by family (in **bold**) and genera

Taxonomic group	n	Mean	UCL	LCL	Max	Min
Anacanthobatidae	**1**	**3.53**				
Cruriraja	1	3.53				
Arhynchobatidae	**19**	**3.86**	**3.93**	**3.78**	**4.09**	**3.54**
Bathyraja	13	3.89	3.98	3.79	4.09	3.54
Psammobatis	1	3.84				
Rhinoraja	4	3.83	4.02	3.65	3.91	3.66
Rioraja	1	3.63				
Rajidae	**40**	**3.79**	**3.84**	**3.73**	**4.22**	**3.48**
Amblyraja	2	3.90	4.92	2.88	3.98	3.82
Dipturus	7	3.94	4.15	3.73	4.22	3.52
Leucoraja	7	3.80	3.99	3.61	4.06	3.54
Malacoraja	2	3.64	4.46	2.81	3.70	3.57
Neoraja	1	3.52				
Raja	12	3.76	3.81	3.70	3.88	3.59
Rajella	8	3.68	3.79	3.57	3.80	3.48
Rostroraja	1	4.15				

n = number of species. Mean, 95% upper (UCL) and lower (LCL) limits, maximum, and minimum values are given
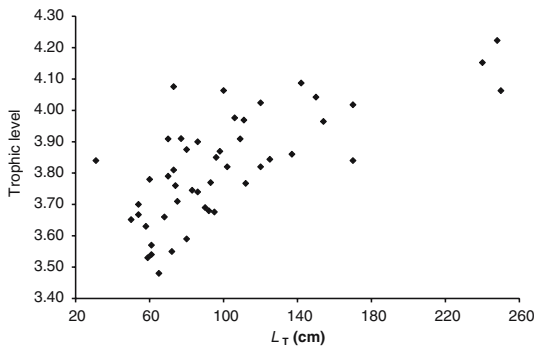
Fig. 2 Relationship between total length (L_T) and trophic level of skates for 48 species representing three families and 12 genera

exceeds 200 cm L_T. At the other extreme, *Psammobatis extenta*, at 31 cm L_{Tmax}, appears to have a much higher TL (3.84) than would be expected for a skate of this size. All skates with TLs <3.8, except for two species (*Amblyraja radiata* and *Raja pulchra*), have a maximum L_T of <100 cm.

Comparison of TL values at the ordinal level (Table 4) between skates and sharks showed that skates (Rajiformes) had lower trophic levels than all but two shark orders; the Heterodontiformes and Orectolobiformes. Log-transformed trophic level values for skate families (Table 4) relative to values for sympatric demersal shark families (Scyliorhinidae, Squalidae, Squatinidae, and Triakidae) revealed significant differences (ANOVA, $F = 10.04$; $P < 0.001$). The combined data for Arhynchobatidae and Rajidae were not significantly different from those of Scyliorhinidae, Squatinidae, and Triakidae (Tukey's, $P < 0.05$), but were significantly lower than the TL value calculated for Squalidae (Tukey's, $P < 0.001$). The Pristiophoridae, a small group of demersal sharks, were represented by a single species (*Pliotrema warreni*), that appeared to feed at a higher TL (4.2) than skates.

Discussion

Of the 245 described skate species (Ebert and Compagno 2007) <24% have had any quantitative dietary information reported, with a single study conducted for most of these species (53.3%). Furthermore, only 37 (14.6%) of 253 skate species have had >100 stomachs examined. In contrast to the relatively small percentage of individual skate species that have been studied, coverage at the generic level has been relatively broad, with quantitative diet information reported for 13 of 27 recognized skate genera (Ebert and Compagno 2007). Although significant differences were found between some skate genera, it appears that phylogeny is a less important predictor of TL than the prey categories used to calculate TL values, size, and possibly regional differences.

Table 4 Trophic levels of skates and sharks by order (in **bold**) and family

Order	Family	*n*	Mean	UCL	LCL	Max	Min
Rajiformes		**60**	**3.8**	**3.8**	**3.7**	**4.2**	**3.5**
	Anacanthobatidae	1	3.5				
	Arhynchobatidae	19	3.9	3.9	3.8	4.1	3.5
	Rajidae	40	3.8	3.9	3.7	4.2	3.5
Carcharhiniformes		**90**	**4.0**	**4.1**	**3.9**	**4.3**	**3.2**
	Carcharhinidae	39	4.1	4.2	4.1	4.3	3.8
	Hemigaleidae	2	4.2	4.3	4.1	4.3	4.3
	Proscyllidae	2	4.1	4.1	4.0	4.1	4.0
	Pseudotriakidae	1	4.3				
	Scyliorhinidae	21	3.9	4.0	3.8	4.2	3.5
	Sphyrnidae	6	3.9	4.2	3.6	4.3	3.2
	Triakidae	19	3.8	3.9	3.7	4.2	3.5
Lamniformes		**8**	**4.0**	**4.4**	**3.7**	**4.5**	**3.2**
	Alopiidae	2	4.2	4.2	4.2	4.2	4.2
	Cetorhinidae	1	3.2				
	Lamnidae	3	4.3	4.5	4.2	4.5	4.2
	Megachasmidae	1	3.4				
	Odontaspididae	1	4.4				
Orectolobiformes		**6**	**3.6**	**3.9**	**3.4**	**4.1**	**3.1**
	Ginglymostomidae	2	4.0	4.2	3.8	4.1	3.8
	Hemiscyllidae	2	3.6	3.8	3.5	3.7	3.5
	Rhincodontidae	1	3.6				
	Stegostomatidae	1	3.1				
Hexanchiformes		**5**	**4.3**	**4.5**	**4.5**	**4.7**	**4.2**
	Chlamydoselachidae	1	4.2				
	Hexanchidae	4	4.3	4.5	4.5	4.7	4.2
Pristiophoriformes		**1**	**4.2**				
	Pristiophoridae	1	4.2				
Squatiniformes		**6**	**4.1**	**4.2**	**4.0**	**4.2**	**4.0**
	Squatinidae	6	4.1	4.2	4.0	4.2	4.0
Squaliformes		**32**	**4.1**	**4.2**	**4.0**	**4.4**	**3.5**
	Echinorhinidae	1	4.4				
	Squalidae	31	4.1	4.2	4.0	4.3	3.5
Heterodontiformes		**1**	**3.2**				
	Heterodontidae	1	3.2				

Values for sharks taken from Cortés (1999). Mean, 95% upper (UCL) and lower (LCL) limits, maximum, and minimum values are given

Determination of prey categories used to calculate standardize diet compositions may influence the TL of individual species. *Psammobatis extenta*, for example, was found to have a lower TL (3.53) (Braccini and Perez 2005) based on the more general categories established for sharks by Cortés (1999) as compared to our higher estimated TL (3.84) using slightly different prey categories than we determined from a review of published skate diet studies. We attributed this difference mainly to our use of amphipods, a primary prey taxon of this and other skate species, as a distinct prey category. Based on published stable isotope studies (Hobson and Welch 1992; Nyssen et al. 2002), amphipods had a much higher calculated TL value (Table 1) than was estimated using the broad category of marine invertebrates (TL = 2.5; Cortés 1999). Therefore, the actual TL of this species was likely underestimated by Braccini and Perez (2005). Similarly, Morato et al. (2003) collapsed their data for *Raja clavata* into the same categories used by Cortés (1999) and then compared trophic levels among size classes and regions; probably affecting the accuracy of their results. These examples highlight the importance of calculating and perhaps refining prey categories that are more realistic to the predator in question.

Of the four guilds that characterized the diet of skates, fish and decapod guilds were dominant comprising 39 of 48 species. This finding is consistent with other studies that reveal skates to be primarily benthopelagic piscivores or epibenthic predators specializing on invertebrates and small crustaceans (Garrison and Link 2000; Bulman et al. 2001; Davenport and Bax 2002). It is noteworthy that 13 of 20 species in the fish guild had TL values >3.90, and with no species having a TL < 3.77. Fifteen of 20 species in this guild exceed 100 cm L_{Tmax}, with three species >2 m L_{Tmax}. This is not unexpected as larger fish species, including skates, generally have a higher proportion of fish in their diet (Garrison and Link 2000; Davenport and Bax 2002). By comparison, the decapod guild had a TL range of 3.48–3.87 and was composed of smaller species, with 17 of 19 species <100 cm L_{Tmax}.

Total length and TL were positively correlated, with larger skates tending to have a higher calculated TL value. This positive trend between body length and TL was similar to Cortés' (1999) findings for sharks, but differed from Pauly et al.'s (1998) who found that body length and TL were inversely related for marine mammals. Many marine mammals, e.g. baleen whales, are plankton feeders and like the two largest shark species, i.e. *Cetorhinus maximus* and *Rhincodon typus*, tend to feed at a lower TL; usually within a TL range of 3.2–3.4 (Cortés 1999; Pauly et al. 1998). Cortés (1999) suggested that body mass may be a better predictor of TL, but this variable was not available for many species.

Trophic level comparisons among species are best made at identifiable and comparable life history stages or at a similar maximum body size (Jennings 2005). Although ontogenetic shifts in diet are well documented among individual skate species (e.g., Ajayi 1982; Ellis et al. 1996; Muto et al. 2001; Brickle et al. 2003; Robinson et al. 2007; Treloar et al. 2007), only one study has attempted to calculate TL values at different size classes (Morato et al. 2003). Several studies have shown a shift from a diet primarily consisting of amphipods and crustaceans in smaller individuals to a diet primarily consisting of teleosts in larger skates (Smale and Cowley 1992; Yeon et al. 1999; Robinson et al. 2007). Using a fixed TL for an individual species that does not take into account an increase in body size, coupled with a likely shift in diet, will not appropriately describe the structure of aquatic food webs (Jennings 2005). Different size classes within a species may be considered functionally different species in terms of trophic dynamics (Ross 1986; Garrison and Link 2000). Therefore, calculations and comparisons of diet composition for different size classes or life history stages are more appropriate than those using all available data and result in more accurate estimates of TL and determinations of trophic roles within food webs.

The importance of skates to regional ecosystems in terms of abundance and biomass, and their subsequent impact via predation on commercially important groundfish has been the subject of much debate. On Georges Bank off the northeast coast of the U.S., for example, it has been suggested that predation by skates and other elasmobranchs may negatively influence recruitment of potentially important groundfish species (Murawski 1991; Mayo et al. 1992; Fogarty and Murawski 1998). However, there is little evidence to support this hypothesis, and in fact the predatory impact by skates on commercially valuable groundfish on the Georges Bank is considered by some to be insignificant (Link et al. 2002). Conversely, in the Aleutian Islands and Bering Sea skates are considered to be major predators of commercially important groundfish species (Orlov 2003; Gaichas et al. 2005).

Trophic level analysis of allopatric skate species provides little insight into the true role of these fish as predators or competitors within an ecosystem. Conversely, examination of co-occurring skate species will provide a more accurate understanding of these high TL predators. Although skates are secondary or tertiary consumers, their TL appears to vary between, and within, different ecosystems. *Raja clavata*, perhaps one of the best studied skate species (Ajayi 1982; Ellis et al. 1996; Holden and Tucker 1974; Quiniou and Andriamirado 1979), had a significantly higher TL in the Azores than in other regions of the northeastern Atlantic. This difference was attributable to a higher proportion of teleosts in the diet of individuals from the Azores (Morato et al. 2003).

Individual skate species within an ecosystem often occupy different TLs. However, when treated as a species complex, skates may occupy different TLs among different ecosystems. For example, in the eastern Bering Sea, skates appear to occupy somewhat higher mean TLs (3.88, $n = 9$ species) than those in the Benguela Current (3.73, $n = 9$) and California Current (3.75, $n = 4$) ecosystems. Reasons for these differences are unclear, but there are very few other demersal elasmobranch competitors, e.g. sharks, in the eastern Bering Sea (Mecklenberg et al. 2002). Since diets of demersal sharks typically include a greater proportion of fishes than skate diets (Cortés 1999) the higher TL observed for skates in the eastern Bering Sea may be reflective of a lack of other demersal sharks and the associated niche expansion of skates in this region. By comparison, the Benguela Current Ecosystem has one of the most diverse elasmobranch faunas with >60 different species (Compagno et al. 1991). Many of the shark families found within the Benguela Current Ecosystem, e.g. the Squalidae and Scyliorhinidae, have higher TL values, as calculated by Cortés (1999), relative to sympatric skates. Likewise, the California Current Ecosystem has several demersal scyliorhinid and squalid species (Ebert 2003) that, at least at the family level, have higher TL values (Cortés 1999) than the four skate species reported here. Conversely, the eastern Bering Sea has no scyliorhinids and only a single squalid species that is considered rare within that ecosystem (Mecklenberg et al. 2002).

Comparison of the skates to the eight major shark taxonomic groups at the ordinal level is somewhat misleading given the variety of external body morphologies, habitats, life-styles, foraging strategies, and prey items consumed by sharks (Compagno 1990). As an example, skates were found to occupy a higher TL than two of the shark orders (Cortés 1999; Table 4). Both of these orders have representatives that differ morphologically and generally occupy distinctly different habitats than most skate species. The Heterodontiformes are small, stout-bodied sharks with one living family and genus. Unlike skates, heterodontids are primarily durophagous, feeding on such hard-bodied prey items as sea urchins and gastropods (Compagno et al. 2005). The Orecto-

lobiformes contain seven families and 14 genera of mostly small benthic, warm temperate to tropical sharks. This order includes the whale shark *Rhincodon typus*, the largest living fish and a plankton feeder (Compagno et al. 2005). Although the heterodontids somewhat overlap the skates in portions of their distribution, the orectolobids generally do not spatially overlap with skates in terms of habitat (Compagno 1990). It would have been of interest to compare the skates to other batoid groups, but unfortunately no comparable study, to the best of our knowledge, exists.

At the family level, skates were found to occupy TLs similar to those of several co-occurring shark families including the Scyliorhinidae, Squatinidae, and Triakidae (Cortés 1999; Table 4). Of the 23 shark families that Cortés (1999) examined, 14 had TL values ≥4 whereas the remaining 9 had TLs ≤3.9. Six of these nine families occupy distinctly different habitats from that of skates. Three of them (Cetorhinidae, Megachasmidae, Rhincodontidae) are plankton feeders and three (Hemiscyllidae, Sphyrnidae, Stegostomidae) are considered shallow warm temperate to tropical groups (Compagno et al. 2005). Five of these families (Cetorhinidae, Hemiscyllidae, Megachasmidae, Rhincodontidae, Stegostomidae) have TLs <3.6. The similarity of TL between the squatinids and skates is not unexpected as both occupy a similar habitat, co-occur in many areas, and are of similar size. Dietary studies on squatinids have shown them to be consumers of benthic and epibenthic teleosts, cephalopods, and crustaceans (Capape 1975; Ellis et al. 1996; Ebert 2003; Volger et al. 2003). Squatinids, with a mean TL of 4.1, are similar to many of the larger skates (e.g. *Dipturus batis*, *D. chilensis*, *Rostroraja alba*), mainly those with a $L_T > 100$ cm, whose TL is ≥4. Although some larger skate species may occupy similar TLs to that of squatinids, it appears based on limited evidence that these co-occurring species do not overlap in their dietary preferences. In a comparative study of the feeding ecology of six sharks (including members of the families Scyliorhinidae, Squatinidae, and Triakidae) and four skate species, Ellis et al. (1996) found a wide variety of food preferences with little overlap. In fact, only two of the skate species (*Raja clavata* and

R. montagui) in this study exhibited slight dietary overlap with a single shark species, the triakid shark *Mustelus asterias* (Ellis et al. 1996). In diet studies conducted along the west coast of southern Africa it was determined that most skates preferred crustaceans and small benthic teleosts whereas scyliorhinids preferred myctophids (Ebert et al. 1991, 1996). Therefore, though skates may occupy similar habitats, and have similar TLs, to scyliorhinids, squatinids, and triakids, they appear to exhibit very little dietary overlap with these shark families. It is interesting to note that the Squalidae and Pristiophoridae both had significantly higher TLs at 4.1 and 4.2, respectively, than skates of the families Arhynchobatidae and Rajidae; Anacanthobatidae was represented by one species and not statistically tested. Members of both these aforementioned shark families occupy similar habitats to those of many skate species. Numerous diet studies on squalids have shown that members of this family tend to feed mainly on teleosts and cephalopods (Ebert et al. 1992; Ellis et al. 1996; Cortés 1999; Link et al. 2002). On a species level the most frequently studied squalid, *Squalus acanthias*, had a calculated TL value of 3.9 (Cortés 1999), similar to many of the studied skates.

Skates are versatile colonizers of bottom habitats, with an abundant and diverse fauna on continental shelves and insular slopes in cool temperate to boreal and deepsea environs (Compagno 1990). They are among the top predators in demersal marine habitats and appear to play important trophic roles (Ebert et al. 1991; Orlov 2003). Results from this study support recent assertions that skates utilize similar resources to those of other upper trophic-level predators, e.g. seabirds, marine mammals, large teleosts, and some sharks (Sanger 1987; Bowen 1997; Cortés 1999; Garrison 2000; Davenport and Bax 2002). However, skates, unlike these other high TL marine vertebrates, have historically often been overlooked as top predators. This is most evident by the lack of quantitative diet studies on skates. All quantitative diet studies used in our analysis, with one exception, have been published since 1972 (see Appendix I). Reasons for the lack of quantitative studies are several and include a lack of adequate systematic knowledge of the group, a lack of resources to study non-target species or those of little economic value, and because skates often live in habitats (e.g. deepsea benthic habitats) that are difficult to study.

Skates as top predators and potential competitors with groundfishes may play an influential role in structuring demersal marine communities in which they occur. It has been well documented that some batoid groups, e.g. myliobatids and rhinobatids, do in fact play an influential role in shaping infaunal communities on soft-bottom substrates (Lasiak 1982; VanBlaircom 1982; Rossuow 1983; Smith and Merriner 1985; Gray et al. 1997; Ebert and Cowley 2003). However, similar studies on skates are still wanting. It is hoped that these preliminary findings will encourage future research, perhaps incorporating the use of stable isotopes, into the trophic relationships and ecological impact of these interesting and important demersal predators.

Appendix I

List of all skate diet references used for this study.

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